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POSITIVE AND NEGATIVE EFFECTS OF INTERTIDAL ALGAL CANOPIES ON FUCOID RECRUITMENT

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Master of Science

by
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ABSTRACT

POSITIVE AND NEGATIVE EFFECTS OF INTERTIDAL ALGAL CANOPIES ON FUCOID RECRUITMENT

by Amber I. Szoboszlai

Positive and negative factors associated with intertidal algal cover can modify juvenile survival of the fucoid alga *Pelvetiopsis limitata. Pelvetiopsis* recruits <1cm high were counted monthly in different treatments of dominant algal species for one year in Central California. Density of *Pelvetiopsis* juveniles varied as a function of algal cover: survival was enhanced at intermediate levels of algal cover, and reduced at very low and high levels. High densities of *Pelvetiopsis* juveniles and grazers co-occurred, suggesting grazers do not control post-settlement survival. The strong association between the ephemeral alga *Porphyra perforata* and survival of *Pelvetiopsis* juveniles emphasized the potential for individual species to structure the system. These relationships suggest that in stressful systems, habitat modification by algae can facilitate algal recruitment by modifying the microhabitat. However, as algal cover increases and physiological stress levels are reduced, the positive effects of algal cover are replaced by negative, competitive interactions among species.

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INTRODUCTION

Much of the research on species interactions in rocky intertidal systems has focused on understanding competitive interactions when bare space is a limiting resource (sensu Foster 1992). As a result, conceptual models of intertidal community structure have for the most part been dominated by competitive interactions (e.g., Bruno and Bertness 2001). In the 1960s to 1990s, marine ecologists established the role of competitive mechanisms in determining the zonation patterns evident across the steep gradient of environmental variables characteristic of intertidal habitats. By using manipulative, experimental approaches, these researchers began to disentangle competitive hierarchies among species, and developed a model wherein biological, or competitive, factors determined the lower distributional limit of individual species, and physical factors (i.e. tolerance to increasing stress) determined the upper limits (Connell 1961, 1970, Paine 1966, Dayton 1971, Menge 1976, Lubchenco 1978). Researchers also described species interactions in the lower intertidal as density dependent, where space is limiting, and density-independent in the high intertidal, where space is more readily available (e.g., Connell 1972). This model has since been updated to include the effect of variable upwelling conditions on larval supply rates, and subsequent settlement (Roughgarden et al. 1988, Connolly and Roughgarden 1998). Thus, oceanographically driven variation in larval supply can further modify competitive interactions at large spatial scales by influencing the densities of different organisms. This work has led to an improved understanding of the importance of competitive interactions relative to density dependent and density independent processes.

Marine ecologists have also employed models of succession, developed largely by terrestrial plant ecologists, to describe the sequence by which species occupy space (Connell and Slatyer 1977, Sousa 1979, 1984). Because these models often imply a predictable, steady progression to a stable state typical of terrestrial plant communities, they do not adequately characterize the role of disturbance in determining species distributions in intertidal habitats. Disturbance (e.g., winter storms, high temperatures in summer) frequently interrupts the sequence of succession in intertidal habitats (e.g., Dayton 1971, Levin and Paine 1974, Paine and Levin 1981, Sousa 1979, Dayton et al. 1984, Gaylord et al. 1994). As a result, disturbance has been recognized as a mechanism that drives the patchy distributions of intertidal organisms, with each "patch" at a different stage in successional development (Sousa 1984). Marine ecologists rely upon the succession-derived concept of facilitation to describe the sequence by which intertidal organisms re-colonize bare space following disturbance. By definition, facilitation is a process by which early successional species increase the survival of later successional species. Many studies have found that facilitative mechanisms can influence community structure, particularly when physical stress is high (Bertness and Callaway 1994, Callaway and Walker 1997, Crain and Bertness 2006, Gutiérrez et al. 2007).

As a result, ecologists have recently directed more attention toward understanding the relative roles of positive and negative factors in determining species' distributions (Holmgren et al. 1997, Bertness et al. 1999, Bruno et al. 2003). When environmental stress is high, positive interactions (i.e. facilitation) can be a primary determinant of community structure relative to negative interactions (i.e. competition, Crain and

Bertness 2006). In addition, the control of positive and negative factors on community structure can change relative to life history stages (Callaway and Walker 1997). For example, the distribution of stress-sensitive early algal life history stages may start off as a function of positive factors, with negative interactions becoming more important as they grow to adult size and compete for resources. Furthermore, individual species can act as ecosystem engineers, exerting disproportionate positive effects on community structure relative to other species (Jones et al. 1997, Wright and Jones 2006). Because the role of competitive interactions in structuring marine communities has been a paradigm of marine ecology, the inclusion of facilitation into marine ecological theory has often been in opposition to competitive interactions (Bertness et al. 1999). However, the relative roles of competitive and facilitative interactions can shift over different scales of space and time, and are not necessarily mutually exclusive (Jonnson et al. 2006, Altieri et al. 2007).

Intertidal macroalgae (hereafter algae) have a strong potential to influence community structure, given that they can be the dominant space occupiers in temperate intertidal systems. These organisms, along with subtidal algae, form the basis of nearshore marine food webs, and provide food and habitat for numerous species (e.g., Dayton 1975, Lubchenco 1978, Bustamante and Branch 1995, Thompson et al. 1996, Schiel 2004, Wieters 2005). Current research on how marine algae impact nearshore ecosystems addresses how these primary producers influence ecosystem function. By studying primary productivity (i.e. carbon assimilation), algal diversity, and key species and food web dynamics, researchers are working to define the critical role of sessile, photosynthetic organisms in sustaining nearshore ecosystems (Schiel 2004, Bruno et al. 2005, Menge et al. 2005, Bracken and Stachowicz 2006, Lilley and Schiel 2006). In addition to providing food and habitat for other organisms, algae can influence ecological processes like succession, recruitment, and competition, as introduced above. In the intertidal, algal cover can influence species distributions by modifying both physical factors such as temperature and desiccation (Brawley and Johnson, 1991, Johnson and Brawley 1998, Schoenwaelder et al. 2003, Helmuth et al. 2006), light (Dring 1987), and water flow (Vogel 1981, Nowell 1984, Carpenter and Williams 1993, Denny 1995, Williams and Carpenter 1998, Cheroske et al. 2000, Taylor and Schiel, 2003) and biological factors including grazing and competition (Underwood and Jernakoff 1981, Bruno and O'Connor 2005) at relatively small spatial scales (i.e. 5-10 cm). Although intertidal algae are abundant and known to influence nearshore processes, the mechanisms by which they do this remain poorly understood. Furthermore, the ways in which individual species (relative to a set of diverse species) contribute to ecosystem function is largely unknown.

Algae in the order Fucales (Phaeophyceae), such as *Pelvetiopsis limitata*, are good study organisms because they are ubiquitous in temperate marine ecosystems and create the dominant biomass in intertidal areas of many cold and temperate regions (Chapman 1995, Southward et al. 1995, Serrao et al. 1999). As a result, there is a large body of research and literature that focuses on many aspects of their biology, physiology, and ecology (for a review, see Chapman 1995). Furthermore, fucoids possess a simple life history relative to other types of macroalgae: embryos develop directly from fused gametes, as opposed to the alternating generations of gametophytes and sporophytes common to many other dominant macroalgae (van den Hoek et al. 1995). This simplified life history is amenable to developing population models, and makes fucoid algae useful as model study organisms (Schiel 2004). Researchers have already documented that fucoid algae are sensitive to a suite of environmental factors that can cause reduced growth rates, cell death, and increased juvenile mortality. These factors include physical variables (light, ultraviolet radiation, temperature, desiccation and water flow; Vadas et al. 1990, Brawley and Johnson 1991, Davison et al. 1993, Wiencke et al. 2000, Coelho et al. 2001, Haring et al. 2002, Ladah et al. 2003, Taylor and Schiel 2003, Schoenwaelder et al. 2003, Li and Brawley 2004, Coleman and Brawley 2005, Dethier et al. 2005, Holzinger and Lütz 2006), biological variables (competition and grazing; Lubchenco 1983, Johnson et al. 1998, Worm and Chapman 1998), and anthropogenic variables (human trampling and increased pollutants; De Vogelaere and Foster 1994, Schiel and Taylor 1999, Thibaut et al. 2005). Because fucoids are abundant, well-studied, have a simplified algal life history, and are sensitive to environmental variables, they provide a model study organism for understanding how key species and positive interactions affect the ecology of nearshore marine ecosystems. By concentrating research on key Fucalean species, we can clarify the mechanisms by which intertidal algae contribute to intertidal ecosystem structure and function.

Many types of fucoid algae (e.g., the genera *Fucus, Pelvetiopsis*, *Silvetia*, *Pelvetia*, *Ascophyllum*, and *Hesperophycus* in the Northern hemisphere, and *Hormosira* and *Durvillea* in the Southern hemisphere) occur in areas where stress levels can be high, such as the mid to upper intertidal. Additionally, they generally occur in zones where bare space may not be a limiting resource, a premise of the competitive theory. As a result, these genera are particularly useful model organisms for understanding how positive interactions may impact species distributions. Previous researchers have found that survival of small life history stages (i.e. post-settlement recruitment) is the most critical time during population development of intertidal fucoid algae (Brawley and Johnson 1991, Johnson and Brawley 1998, Schiel 2004). Not only is this stage particularly sensitive to environmental variables and grazing (Brawley et al 1999, Wiencke et al. 2000, Ladah et al. 2003), but intertidal fucoid algae are also understood to have high fertilization rates and limited dispersal (Bellgrove et al. 1997, Brawley et al. 1999, Berndt et al. 2002, Kinlan and Gaines 2003, Schiel 2004). Therefore post-settlement recruitment has been identified as an important topic for further research (Brawley et al. 1999, Schiel 2004). *Pelvetiopsis limitata* (Setchell) Gardner is a common, dominant species of fucoid algae found in the high intertidal habitats of exposed rocky shores from British Columbia, Canada to central California (Abbott and Hollenberg 1976). Improving our understanding of this key species and what affects its distribution and survival will enhance our ability to predict (1) the role of algae in structuring nearshore ecosystems, (2) by which mechanisms individual algal species contribute to the increased ecosystem function associated with higher levels of diversity, and (3) the relative roles of positive and negative factors in determining species distributions in stressful habitats.

Conceptual models can help us to better understand the population dynamics of key species living in stressful environments. By examining how the presence of algal cover and species identity affects the survival of recruits of a key species (i.e. *Pelvetiopsis*), we can better predict the context of when algae will influence the outcome of ecological interactions in nearshore ecosystems. To understand the potential positive and negative effects of algal cover on post-settlement recruitment of *Pelvetiopsis,* it is necessary to clarify the positive and negative factors associated with different levels of algal cover and different species of dominant algae. Positive and negative effects will vary with increases in algal cover (Fig. 1). If algal cover has a positive effect on *Pelvetiopsis* recruitment, recruitment will increase as algal cover increases (facilitative); if the effect is negative, recruitment will decrease as algal cover increases (inhibitive).

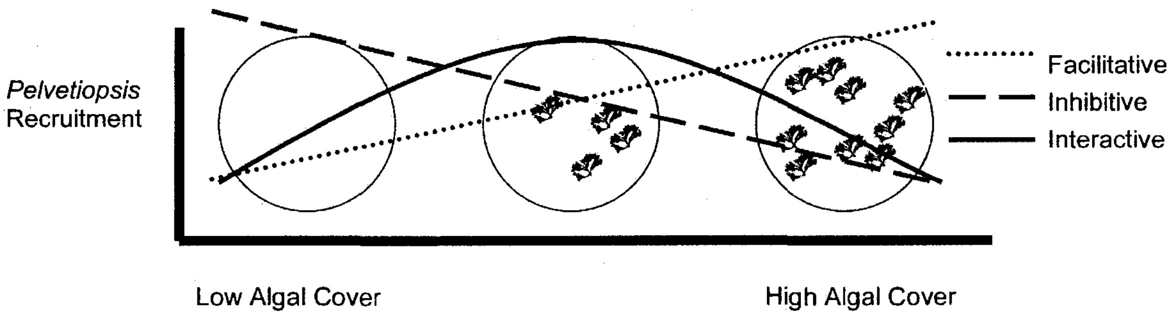

Fig. 1. Conceptual model of the relationship between algal cover and *Pelvetiopsis* recruitment. Algal cover can have positive (i.e. facilitative) effects, negative (i.e. inhibitive) effects, or interactive (positive and negative) effects on *Pelvetiopsis* recruitment.

The relationship between algal cover and recruitment could also vary as a function of algal cover, resulting in an interactive effect such that low levels of cover are positive (i.e. facilitative), and high levels of cover are negative (i.e. competitive). The positive and negative effects of algae on *Pelvetiopsis* recruitment based on species identity are outlined in Table 1. This table highlights how the biogenic structure of the two dominant algae in this system, *Pelvetiopsis* and *Endocladia muricata* (Endlichter) J. Agardh, modify light, temperature, humidity, and abrasion as individuals or in combination. The comparison between single species and two species in combination provides for the consideration of the what happens to *Pelvetiopsis* recruitment when more than one species is present. Together, these two models of how variability in algal cover and species composition may impact *Pelvetiopsis* recruitment provide a framework for understanding how positive and negative factors influence species distributions.

Table 1. Positive and Negative Effects of Key Algal Species on *Pelvetiopsis* recruitment.

	Treatment Type			
Effect	*Pelvetiopsis*	*Endocladia*	*Pelvetiopsis + Endocladia*	Bare Rock
Positive				
	Propagule supply	Low abrasion	Generally interactive	Abundant bare space
	High humidity	High humidity		Abundant light
	Low temperature			
Negative				
	Reduced light	Reduced light	Less available substrate for settling organisms	Low humidity
	Abrasion	No propagule supply	Reduced light	High temperature

The primary objective of this study was to explore how algal cover influences the patterns and distribution of the alga *Pelvetiopsis* in the high intertidal zone. Natural algal cover composition was manipulated in plots to include either a single species or a combination of species and monthly *Pelvetiopsis* recruitment was measured for one year. I tested the hypothesis that *Pelvetiopsis* recruitment would vary based on (1) algal species identity (i.e., in areas with only *Pelvetiopsis* cover vs. areas with only *Endocladia* cover) and (2) the number of species present (i.e., in areas with one species vs. areas with *Pelvetiopsis* and *Endocladia*). The study addresses how the biogenic structure of algae influences patterns of macroalgal distribution by modifying the biotic and abiotic factors that affect small algal life history stages. It is vital to understand how small-scale variability in these factors influences algal survival because these processes likely affect patterns of algal distribution and diversity. Because algal diversity is intimately linked to invertebrate diversity and abundance, this information will help describe how small-scale processes that affect algae can impact and potentially structure higher trophic levels, thereby impacting ecosystem-level processes. This type of information is useful for incorporating experimental marine ecology into coastal management and conservation (Castilla 2000).

METHODS

Study site

This study was conducted at Soberanes Point, an exposed rocky shore habitat located on the central California coast, approximately ten miles south of Monterey, CA in Garrapata State Park and the Monterey Bay National Marine Sanctuary (Latitude 36°26.871', Longitude -121°55.723'). The rocky substratum at this site is primarily the metamorphic rock horneblende-biotite-quartz diorite (granodiorite) and is highly resistant to erosion (Rosenberg 2001).

Study organisms

This project focused on two species of algae ubiquitous to the upper intertidal of the temperate Pacific coast: *Pelvetiopsis* and *Endocladia.* These species comprise the majority (50-70%) of algal cover in this zone at the study site. *Pelvetiopsis limitata* is a brown alga in the order Fucales, and is similar to other fucoid algae that locally include *Fucus gardneri* and *Silvetia compressa.* The thallus of *Pelvetiopsis* is upright, 4-10 cm tall, and with slightly thick (5mm) branches. This alga is monoecious, with male and female gametangia found on the same thallus; liberation of sperm and eggs is followed by fertilization, and the resulting zygotes develop directly into new diploid thalli. It ranges in distribution from Vancouver Island, British Columbia to San Luis Obispo, California, and is common to exposed surf zones (Abbott and Hollenberg 1976). Development of reproductive tissue (conceptacles found at the tips of branches) is thought to occur during the late spring to summer months (D. Steller, pers. comm.). *Endocladia muricata* is a red alga with a short, 4-8 cm tall, profusely branched thallus and exhibits an alternation of isomorphic generations. *Endocladia muricata* is common in the mid-upper intertidal from Alaska to Baja California, Mexico (Abbott and Hollenberg 1976).

The upper intertidal zone at this exposed study site is characterized by a patchy distribution of organisms and bare space. Other common species include the study organisms, the algae *Porphyra perforata* J. Agardh and *Mastocarpus papillatus* (C. Agardh) Kützing, and several invertebrates: the mussel *Mytilus californianus* Conrad, 1837, barnacles (*Pollicipes polymerus* Sowerby, 1833, *Balanus glandula* Darwin, 1854, *Chthamalus fissus* Darwin, 1854, *Chthamalus dalli* Pilsbry 1916 (combined due to morphological similarity), *Tetraclita rubescens* Darwin, 1854, *Anthopleura elegantissima* (Brandt, 1835), *Littorina scutulata* Gould, 1849/ *Littorina plena* Gould, 1849 (combined due to morphological similarity), *Littorina keenae* Rosewater, 1978, a suite of limpets from the genus *Lottia* (*Lottia digitalis* Rathke 1833, *Lottia paradigitalis* Fritchman 1960, *Lottia austrodigitalis*, *Lottia pelta* Rathke 1833, and *Lottia scabra* Gould 1846), chitons and other gastropods and crustaceans.

Experimental design

In this experiment I manipulated algal cover to test its effect on *Pelvetiopsis* recruitment in the absence of sessile, habitat-forming invertebrates. I tested the hypothesis that *Pelvetiopsis* recruitment was higher within areas of *Endocladia* canopies than within areas of *Pelvetiopsis* canopies. This hypothesis was based on (1) the field observation that *Pelvetiopsis* recruits appeared to be associated with the presence of *Endocladia* and (2) previous research on the association of *S. compressa* recruits with *Endocladia* (Brawley and Johnson 1991, Johnson and Brawley 1998). To understand the effect of multi-species algal cover on *Pelvetiopsis* recruitment, I tested the hypothesis that *Pelvetiopsis* recruitment would vary between areas with only a single species present and areas with *Endocladia* and *Pelvetiopsis* growing in combination. This hypothesis was non-directional, and was based on the understanding that the presence of multiple species in combination can have both positive effects (i.e. increased propagule supply (*Pelvetiopsis* presence) and increased suitable habitat (*Endocladia* canopy)) and negative effects (i.e. less substrate available for recruitment because algal species occupy more space when grown in combination).

During the experiment I established and monitored 50 0.5m-diameter circular plots (area=0.2 m^2) in the high intertidal in the zone exposed when the tidal height dropped below +2.0 feet above mean sea level. Plots were positioned in areas where both *Pelvetiopsis* and *Endocladia* were present, and had >50% combined total algal cover at the beginning of the study. The 50 plots consisted of 10 replicates of 5 plot types: an unmanipulated control and four treatments: a *Pelvetiopsis*-only plot, an *Endocladia*-only plot, a *Pelvetiopsis* + *Endocladia* plot, and a complete removal plot (Fig. 2). These plots were arranged in a randomized blocked experimental design to account for variability due to block location (10 blocks x 5 types of plot = 50 plots); treatments were randomly assigned within each block and distances among blocks ranged from 0.5 – 15.0 m. The use of a blocked experimental design can help detect patterns by accounting for unexplained heterogeneity in the environment. In this experiment, potential sources of

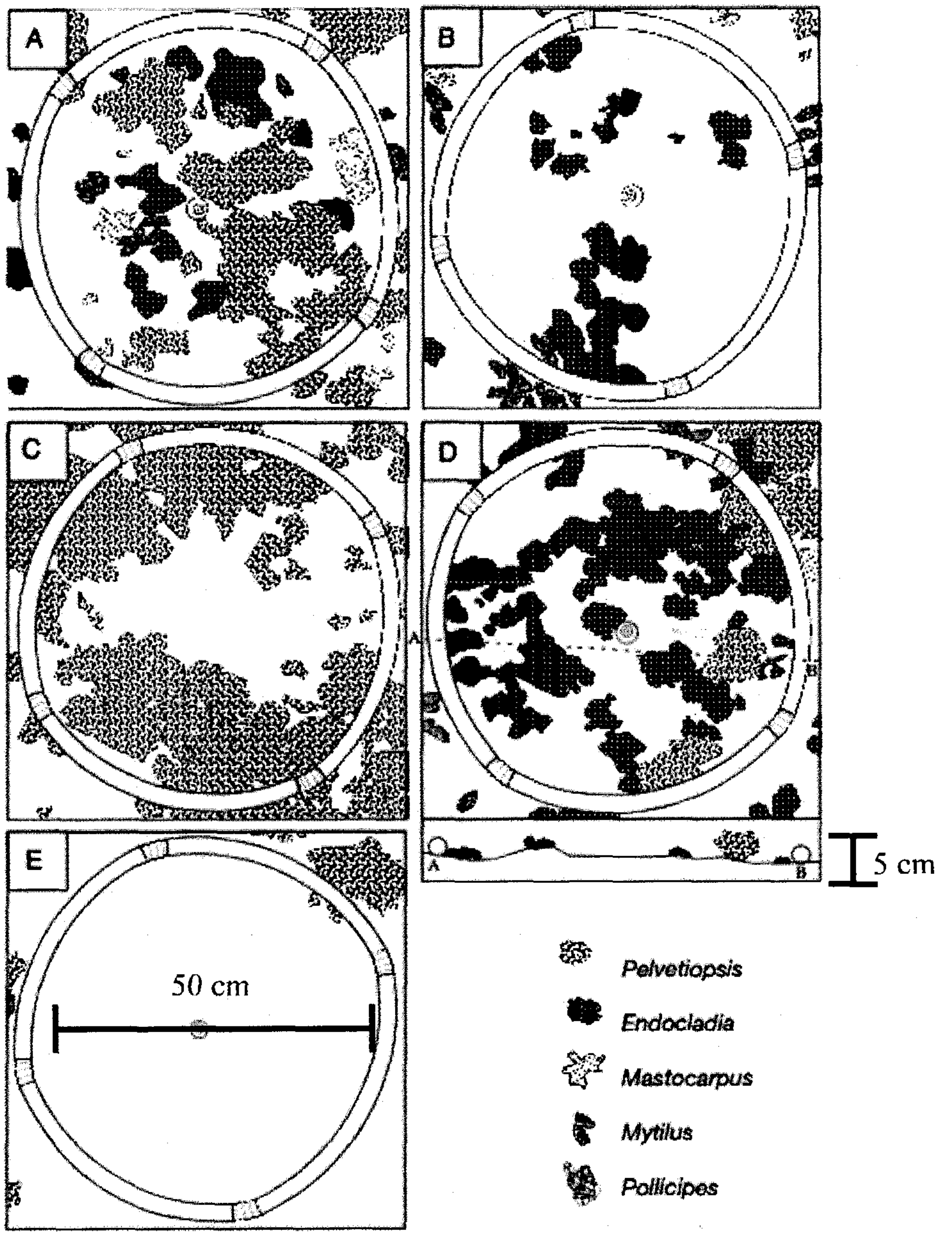

Fig. 2. Illustration of organisms in the different treatments. A. Control plots. B. *Endocladia* plots. C. *Pelvetiopsis* plots. D. *Pelvetiopsis+Endocladia* plots, dashed line indicates cross-sectional view from point A to B, illustrating the three-dimensionality of the algal canopies. E. Total removal plots. Plot diameter = 0.5m (area = $0.2m^2$).

small-scale heterogeneity included exposure to waves (both wave forces and wave direction) and gradients in herbivore abundances associated with wave exposure, as well as unknown factors.

To establish the different treatments, all sessile invertebrates (including *Mytilus californianus*, *Pollicipes polymerus*, *Balanus glandula* > 3mm diameter, *Tetraclita rubescens*, *Chthamalus* spp. and *Anthopleura elegantissima*) were removed by scraping, along with all algal species except those designated by the treatment. Encrusting species of algae were left untouched because there was no effective method to remove them entirely. In addition, the complete removal plots were scraped then burned with a blow torch to ensure removal of microscopic fucoid stages. Control plots were unmanipulated, and to avoid disturbance to the natural system, sessile invertebrates were not removed from control plots. Plots were established in July-September 2005, with the exception of the complete removal plots, which were established in October/November 2005. The four types of treatment plots were "weeded" monthly to maintain the assigned treatments, except for a 2-month period in the complete removal from January 2006-March 2006 (see results). In addition to these removals, all new juvenile *Pelvetiopsis* <1 cm tall were removed from the four treatments after being counted, so that new recruitment/survival could be quantified at monthly intervals.

Monthly sampling

The 50 plots were monitored and maintained for 13 months, from October 2005-October 2006; this allowed for seasonal changes in recruitment to be measured. Each month, measurements of total biotic percentage cover, motile invertebrate grazer composition, and *Pelvetiopsis* recruitment were taken.

Total biotic cover

Percentage cover (or total biotic cover) of sessile organisms was measured monthly with a 50-point Random Point Contact (RPC) quadrat that was the same size as the circular plots (Foster et al. 1991). Total biotic cover values included only algae in the four types of treatment plots, whereas in the control plots this value also included sessile invertebrates. Any future reference to "total biotic cover" implies that this includes only algae in the treatment plots, and algae plus sessile invertebrates in the control plots. The random points on the quadrat were arranged with 5 points on each of 10 spokes. The 10 spokes were positioned from the center to the edge of the quadrat at random points between 0 and 360°, stratified within 36° intervals. Along a spoke, points were randomly stratified to achieve a spatially balanced configuration. To avoid temporal pseudoreplication, the circular quadrat was rotated each sampling period to reposition the spokes relative to a permanent side marker. Photoquadrats were taken monthly to verify RPC measurements of percentage cover.

Pelvetiopsis *recruitment*

To assess monthly *Pelvetiopsis* recruitment, the number of individuals <1 cm tall within a plot were counted, after which these new recruits were removed except in the control plots. Therefore, recruitment in the control plots tracks the monthly presence of recruit-sized *Pelvetiopsis*, rather than the appearance of new individuals from month to month.

Additional sampling

The following biotic factors were measured because of their potential to confound *Pelvetiopsis* recruitment among plots, and/or treatments: invertebrate grazers, proximity of adult *Pelvetiopsis* thalli, and reproductive condition of *Pelvetiopsis.* Additionally, abiotic factors including daily climate, temperature and humidity, ambient light, geologic characterization, and water flow were measured to determine if the plots were placed in an unbiased fashion, to understand environmental variability among treatment types, and to characterize the local environment.

Invertebrate grazer composition

Grazing pressure was estimated monthly to account for differences among plots due to invertebrate grazer composition. Visible motile invertebrates were counted to species level within a 0.25 m diameter circle (area = 0.05 m^2) placed in the center of the plot, allowing for a buffer zone from the plot edge. Small crustaceans (i.e. amphipods, isopods) were not quantified. Cryptic species of limpets and Littorinid snails were grouped due to difficulty distinguishing among species based on field observations; these included the limpets *Lottia digitalis, L. paradigitalis*, and *L. austrodigitalis*, and the snails *Littorina scutulata* and *L. plena.*

Proximity of adult Pelvetiopsis *thalli*

Because dispersal distances of intertidal fucoids are believed to be short (i.e. fewer than 10m; Williams and Di Fiori 1996, Kinlan and Gaines 2003, Coleman and Brawley 2005), the density of adult individuals immediately adjacent to the treatments could influence *Pelvetiopsis* recruitment. Therefore, *Pelvetiopsis* cover adjacent to the study plots was quantified during peak recruitment in March 2006 to assess the potential availability of *Pelvetiopsis* propagules from individuals in close proximity to the study plots. These data provided spatial information on the extent of *Pelvetiopsis* cover adjacent to the plots, as well as additional reproductive state characteristics at that time of the individuals sampled (see below). Adjacent *Pelvetiopsis* cover was measured by extending the spokes on the RPC hoop 15 cm beyond the outside edge of the hoop, and sampling points at 5,10 and 15 cm along the extended spoke. This survey measured *Pelvetiopsis* cover in a 15cm-wide ring surrounding the study plots. To assess availability of propagule supply relative to adult % cover, the cover of these adjacent adults was combined with mean *Pelvetiopsis* cover from within the plots for the analysis.

Reproductive condition of Pelvetiopsis

To assess the potential for spatial variability in *Pelvetiopsis* propagule supply, the reproductive condition of *Pelvetiopsis* thalli was qualitatively characterized during peak recruitment in March and April 2006 within and adjacent to the plots that included *Pelvetiopsis* (control, *Pelvetiopsis* only, and *Pelvetiopsis* + *Endocladia* plots). Two parameters were measured to assess reproductive state: conceptacle development and level of mucilage. Up to ten individual thalli per plot were examined and assigned a discrete rating from 0-3 (low to high) for each parameter (Table 2). Each plot was then assigned a reproductive condition value that was the mean of the values for the individual thalli in that plot. The reproductive state was also measured for the adult thalli encountered adjacent to the study plots in the adult proximity survey above.

Table 2. *Pelvetiopsis* reproductive state rating scheme.

	Criteria
Conceptacle Developmental Stage	
0	None, no bumps whatsoever
1	Slight appearance of raised bumps, likely not mature
2	Bumps clearly present, thallus tissue in good condition
3	Bumps clearly present, thallus tissue deteriorating
Mucilage Level	
0	Thallus may be wet, but no mucilage present
1	Mucilage present, but not ubiquitous, and not exuding from entire thallus
2	Mucilage present on entire thallus, but not abundant
3	Mucilage so thick that it drips off thallus, and extends between branches

Daily climate and wave height

Local sea surface and air temperature data were from the Granite Canyon Marine Pollution Studies Laboratory daily record that is part of SCOOS (Southern California Ocean Observing System), located 1 km south of the study site on the coast. Maximum daily wave height data were downloaded from the National Oceanic and Atmospheric Administration's National Data Buoy Center for the Monterey, California buoy #46402 located 27 nautical miles west of Monterey Bay (36°45'11" N 122°25'21" W).

Temperature and humidity

Temperature and humidity in intertidal systems are typically correlated, such that high temperatures occur with reduced humidity, and low temperatures are indicative of high humidity. Temperature and humidity levels within and adjacent to algal cover were measured with iButton temperature/ humidity dataloggers (Dallis/Maxim DS1923 - Humidity and Temperature Logger: 0 to 100% RH and -20°C to 85°C, temperature accuracy ±0.5°C) during both sunny and cloudy conditions in March and October 2006.

These thermister/hygrochrons are 2cm in diameter and were easily concealed within algal cover. Fifty iButtons were placed in various configurations to compare temperature and humidity levels among the different plots, and among different substrates that included bare rock, and *Pelvetiopsis* and *Endocladia* cover. The iButtons were placed directly beneath algal cover or on bare rock and collected data every fifteen seconds for a minimum of 60 minutes.

Ambient light

Light (scalar spectral irradiance, denoted as $E_{\circ}\lambda$ was measured using a quantum scalar irradiance sensor with a small head (1.9 cm diameter sensor, Biospherical Instruments QSL-2100). This instrument measures Photosynthetically Active Radiation (PAR) in microEinsteins ($\mu Em^{-2}s^{-1}$), (sensitivity to 0.55 $\mu Ecm^{-2}s^{-1}$). Data were collected from bare rock, and beneath the cover of *Endocladia* and *Pelvetiopsis* on a sunny day without clouds in March, April and October 2006, during midday and afternoon.

Geological characterization

The dominant directional aspect (strike) and dominant inclination (dip) of each plot was measured using a Brunton geological compass. An unequal distribution of aspects or inclinations among plots and treatments could bias the recruitment results because aspect can cause variation in temperature and desiccation exposure, as well as species distributions (e.g., Kendall et al. 2004). Strike and dip measurements define the geometric orientation of a planar geologic feature (Compton 1962). The strike line runs horizontal to the plane, and is measured in degrees, representing the compass direction the plane faces. The dip is the line on the plane with the steepest inclination, it represents the number of degrees the surface is below horizontal (0°-90°), where low values indicate an almost flat surface, and high values a steep surface. One measurement was taken for each plot, the variability in the non-flat planar features was averaged out by placing a flat board on the dominant plane. The compass was placed on this surface to take measurements for strike and dip, and magnetic declination was set to 15°.

Water velocity

The study site is located on an exposed shore and the topographic heterogeneity of the rocks cause fluctuations in water flow that may influence *Pelvetiopsis* recruitment. To account for variability in water velocity among blocks, water flow was quantified using clod cards placed into bare rock areas within the total removal plots during a single high tide cycle in November 2007. These values give an indication of variability in water flow due to factors like rock topography, direction of wave forcing and "exposure" (i.e. sheltered vs. exposed). Water flow was measured only in the total removal plots to avoid clod card dissolution by abrasion from algal cover in the other treatment plots. Clod cards were created using Plaster of Paris (Customs Building Products) and an ice cube tray as a mold, following established methods (Doty 1971, Thompson and Glenn 1994). The Plaster of Paris was mixed with water, poured into the ice cube tray, allowed to form, and once solid, removed and dried in a low temperature oven for 24 hours prior to placing in the field. Clod cards were mounted to small PVC rectangles using aquarium glue, weighed, and placed in the field during low tide. Three clod cards were bolted down in a haphazard arrangement in each of the ten total removal plots. After a single high tide, twelve hours later, the clod cards were removed, dried for 24 hours in the oven, and re-weighed. To quantify the rate of dissolution of the clod cards at a known velocity, two clod cards from the same batch of cards used in the field were weighed and mounted to a PVC board. The board was then placed in a uni-directional flume filled with salt water that ran at 1 m/s until the clod cards had lost approximately 50% of their mass. The clod cards were removed, dried for 24 hours and re-weighed. The average change in mass at the known velocity was calculated, and used as a reference point for the field-based dissolution rates. This allowed for a very rough estimate of average water velocities in the field relative to the controlled velocity of 1 m/s in the lab.

Data analysis

Response variables including *Pelvetiopsis* recruitment, total biotic cover and motile invertebrates were compared using a 3-way Model III blocked analysis of variance (ANOVA) on two dates: March 2006 because it was six months into the experiment and during peak recruitment, and August 2006 because it was near the end of the experiment and the peak recruitment period was over. Random factors included date and block, and treatment was a fixed factor. The experimental design took into consideration assumptions of independence among plots, treatments and blocks; additionally, all sample sizes were equal. Assumptions of normality were evaluated by examining the residuals, and the assumption of homogeneity of variances was tested using a Cochran's C test of equal variance ($C=\text{largest } s_i^2/\sum s_i^2$). When needed, data were transformed to meet these assumptions, however in general when replication is equal, the ANOVA is considered robust to differences in variances (Underwood 1997).

An analysis of covariance (ANCOVA) was used to evaluate if covariate values for additional variables measured (adult proximity, rock inclination, rock temperature, water flow) could help to explain the variability in *Pelvetiopsis* recruitment among treatments, and to verify that the placement of plots was not biased with respect to these variables. In addition to meeting the standard assumptions of ANOVA stated above, the regression assumptions of the presence of a linear relationship, independent samples, normal distributions, and equal variances at each value of the covariate were tested by examining the residuals and using a Cochran's C test. Assumptions considered specific to the ANCOVA included homogeneity of regressions (i.e. equal slopes), and independence of treatment and covariate (McCullough and Nelder 1989, Underwood 1997).

Comparisons of ranked reproductive state among plots were made using a log-likelihood test (Zar 1999). Assumptions for correlation analyses included a normal distribution of Y at each value of X, and that random values of X came from a normal population (Zar 1999). Variability in water flow was compared among and within blocks using variance components (Vaughn and Corballis 1969, Winer et al. 1991, Graham and Edwards 2001).

RESULTS

The natural system at Soberanes Point was dominated by intertidal macroalgae. Macroalgal cover in the unmanipulated control plots occupied from 50%-70% of primary space during the one-year study period, and was dominated by *Endocladia* and *Pelvetiopsis* (Fig. 3). Bare space ranged from 10-30%, and sessile invertebrates occupied about 20% of primary space. There was a seasonal trend in the relationship between *Endocladia* cover and bare space: in winter months (November 2005-March 2006) *Endocladia* cover was reduced and bare space increased; during the summer months (April-August 2006), *Endocladia* cover increased and available bare space was lower. Sessile invertebrate cover, *Pelvetiopsis* cover, and cover of other algal species in the control plots did not change greatly during the course of the study.

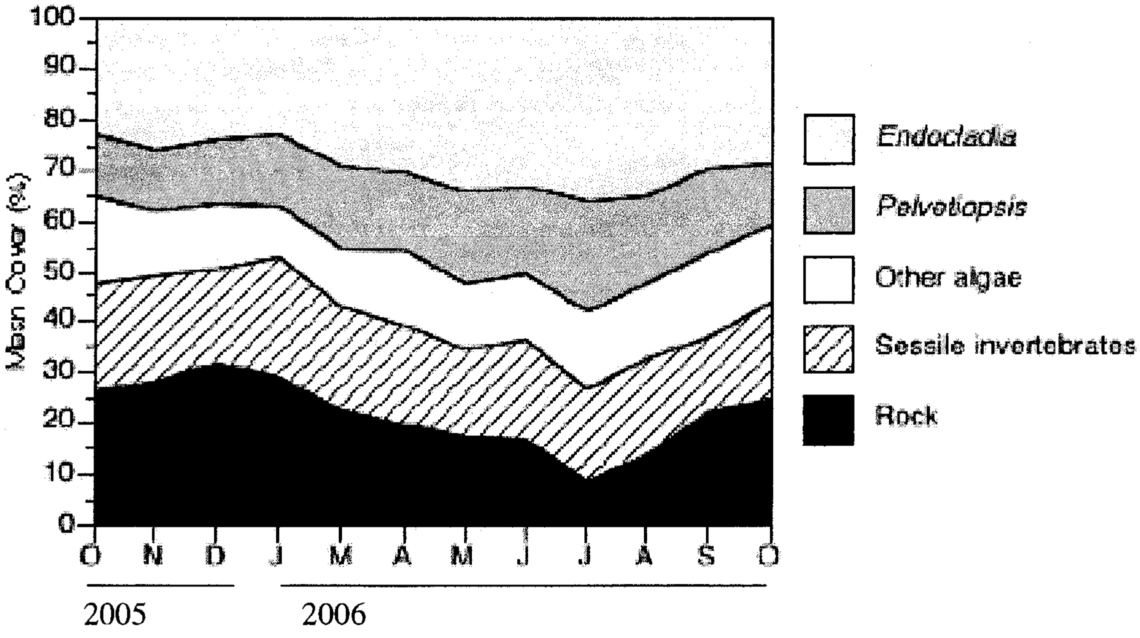

Fig. 3. The natural system: monthly biotic cover in the Control plots, October 2005-October 2006. Algal cover was dominant: total algal cover (*Endocladia, Pelvetiopsis*, and other algae) occupied from 50 to 70% of primary space. Values are monthly means. Sessile invertebrate cover was dominated by the barnacles *Tetraclita rubescens* and *Pollicipes polymerus*, and the mussel *Mytilus californianus*, and occupied from 15-25% of bare space.

Sea surface and air temperature varied seasonally. Daily climate records from Granite Canyon indicated the coolest air temperatures were during the mid to late spring when the seven-day average air temperature did not exceed 15°C between March and May 2006; the warmest average air temperatures occurred during late fall/winter 2005 and summer 2006 (Fig. 4). The coolest sea surface temperatures (10-12 °C) occurred during early summer, and the warmest water temperatures (12-16 °C) were during late summer to fall 2006. Maximum daily wave height was greatest during the winter season (November 2005-February 2006), intermediate from March-June 2006, and reduced from July-September 2006 (Fig. 4).

The temporal variability of *Pelvetiopsis* recruitment and total biotic cover varied among the different treatments (Fig. 5). *Pelvetiopsis* recruitment did not vary among treatments on the dates tested, however it was highest in the treatments with the lowest cover (i.e. there was more available substrate in the *Pelvetiopsis* plots, *Endocladia* plots, and Total Removal plots). Recruitment was highest in May 2006, this was also the period of coolest air temperatures (see Fig. 4). To examine temporal differences among treatments during the course of the experiment, mean data were compared on two dates: March 2006, because it was well into the course of the study and occurred during peak *Pelvetiopsis* recruitment, and late summer in August 2006, to evaluate if any differences persisted after five months. In general, there was no significant effect of treatment on *Pelvetiopsis* recruitment on the March and August 2006 dates (Table 3, Appendix B, $F_{4,10}$=1.14, P=0.45), but total biotic cover did vary among treatments. Dominant invertebrates also varied among treatments and blocks, and differences among dates

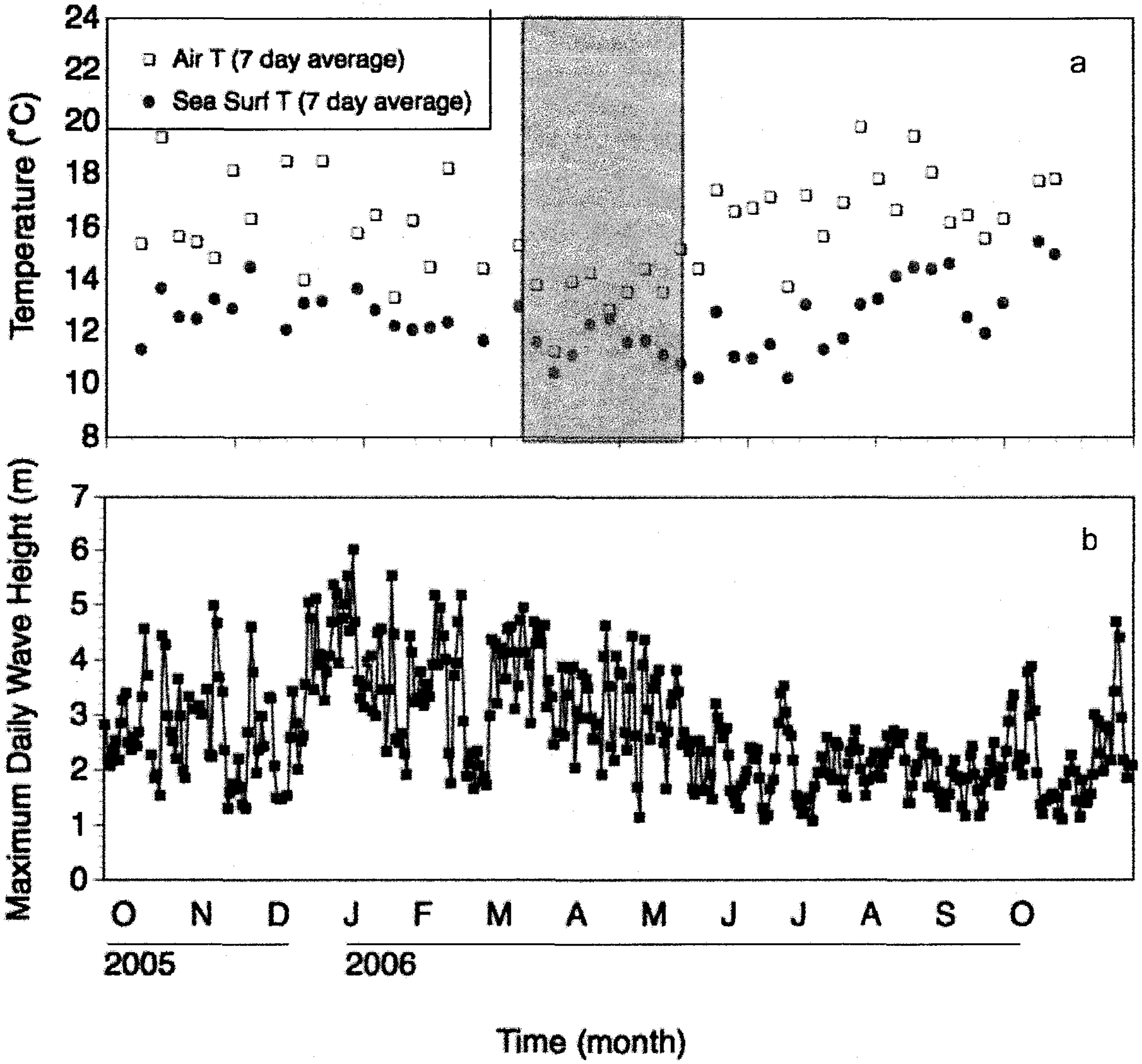

Fig. 4. Local climate and wave height. A. Weekly air and sea surface temperatures measured at shoreline. Reduced springtime temperatures from March to May, 2006 indicated by the shaded bar. B. Maximum daily offshore wave height from NOAA buoy # 46042 (Monterey Bay).

existed for some invertebrates (summarized in Table 3, for complete ANOVA tables see Appendix B, also discussed in more detail below in invertebrate discussion and in Figs. 10-11).

Pelvetiopsis limitata recruitment peaked (values were > 10/0.2 m^2) during March to May 2006, and July 2006 (Fig. 5a). This springtime peak in *Pelvetiopsis* recruitment was not evident in the plots with the highest biotic cover (in general, >50%): the *Pelvetiopsis* + *Endocladia* and control plots had low recruitment throughout the study. Cumulative recruitment from January to October 2006 was highest in the *Pelvetiopsis* plots, the *Endocladia* plots, and the total removal plots (Table 4). Cumulative recruitment data from October-December 2005 were not included to allow time for propagule dispersal to total removal plots following the November 2005 clearings.

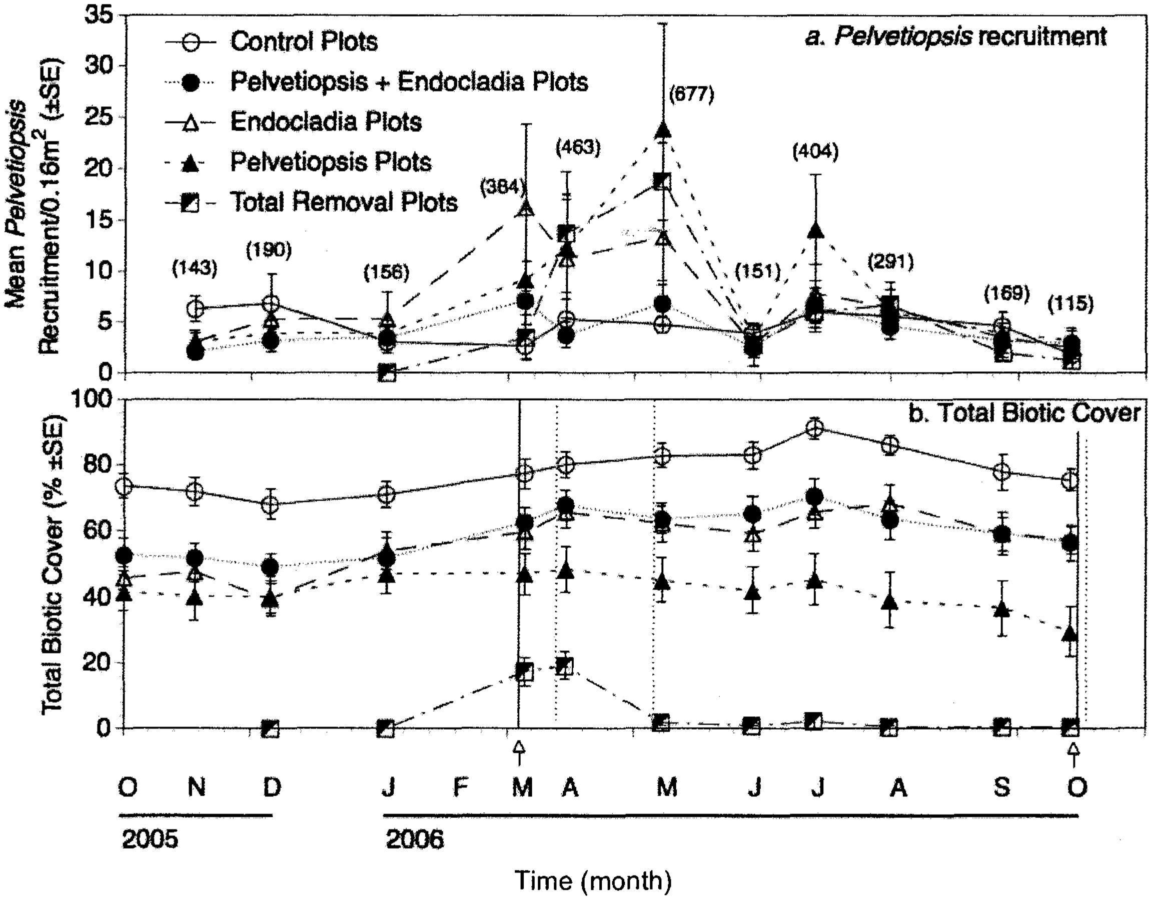

Fig. 5. Monthly *Pelvetiopsis* recruitment and total biotic cover by treatment. Mean differences among treatments were compared on two dates: March and August 2006, indicated by the open arrows on the x axis. 5a. *Pelvetiopsis* recruitment (<1cm tall). Values above the symbols indicate total recruitment for each sampling date in all treatments. 5b. Total biotic cover of all living organisms except encrusting algae. Dashed lines indicate the dates temperatures were compared between algal cover and rock (April, May, and October, 2006); solid lines indicate the dates light levels were compared (March and October, 2006) (see Table 5).

Table 3. Analysis of variance results for monthly recruitment and total biotic cover data. P values for two way, model III ANOVA results, trt=treatment (fixed), block (random), date (random). P values correspond to panels in Figure 5; complete ANOVA tables can be found in Appendix A, post-hoc comparisons are given in the text.

	Response Variable	
Factor	Recruitment (Fig. 5a)	Total Biotic Cover (Fig. 5b)
TRT	0.45	0.01
BLOCK	0.09	<0.01
DATE	0.48	0.99
TRT*DATE	0.18	0.02

Peak *Pelvetiopsis* recruitment from March to May 2006 coincided with the coolest daytime air temperatures during the study period (see Fig. 4).

Total biotic cover (all living sessile organisms except encrusting algae) was consistently different among treatments (Fig. 5b and Table 3). In general, control plots had the highest biotic cover (because sessile invertebrates were not removed), followed by *Pelvetiopsis* + *Endocladia* plots, *Endocladia* plots, *Pelvetiopsis* plots, and total removal plots. All treatments had significantly different mean biotic cover except *Endocladia* and *Pelvetiopsis* + *Endocladia* plots (Table 3, Appendix B, $F_{4,10}$=16.29, P=0.01; Ryan's Q multiple comparison test). Note the increase and subsequent decrease in biotic cover in the total removal plots during March-April 2006 that resulted from recruitment of the ephemeral alga, *Porphyra perforata*. Due to the striking co-occurrence of *Porphyra* and *Pelvetiopsis* recruitment during this period, *Porphyra* cover was left undisturbed until April 2006 sampling was completed. The relationship between *Porphyra* cover and *Pelvetiopsis* recruitment is discussed in further detail below. The significant interaction between date and treatment in the analysis was caused by the increased *Porphyra* cover in the total removal plots in spring 2006, and disappeared when the *Porphyra* was excluded from the analysis.

Table 4. Cumulative and mean *Pelvetiopsis* recruitment (January-October 2006) in the different treatments.

Treatment	Cumulative *Pelvetiopsis* recruitment (n=10 plots, sampled for monthly from Jan.-Oct. 2006)
Pelvetiopsis	796
Endocladia	689
Total Removal	545
Pelvetiopsis+Endocladia	408
Control	372

Due to the obvious differences in total biotic cover among treatments, and the conspicuous recruitment of *Pelvetiopsis* to low cover treatments, the relationship between mean total biotic cover and maximum *Pelvetiopsis* recruitment was compared in each plot (Fig. 6a). Maximum values of *Pelvetiopsis* recruitment were used because they represent the ultimate capacity of the organism to respond to cover; mean total biotic cover was used because it gives a good representation of biotic cover in the plots during the course of the study. The highest maximum recruitment (>50 recruits per plot) occurred in plots with <50% total biotic cover. At mean biotic cover levels >70%, maximum *Pelvetiopsis* recruitment did not exceed 20 recruits per plot. The pattern of highest *Pelvetiopsis* recruitment at intermediate cover levels was the same for cumulative and mean recruitment. Additionally, high *Pelvetiopsis* recruitment (20-55 recruits per plot) did occur at relatively low total biotic cover (<10%) in the total removal plots. These occurrences of maximum recruitment were during the March-April 2006 *Porphyra* recruitment event noted above.

Increased *Pelvetiopsis* recruitment was found with greater cover of adult *Pelvetiopsis* within and adjacent to the study plots (Fig. 6b). At low levels of adult cover

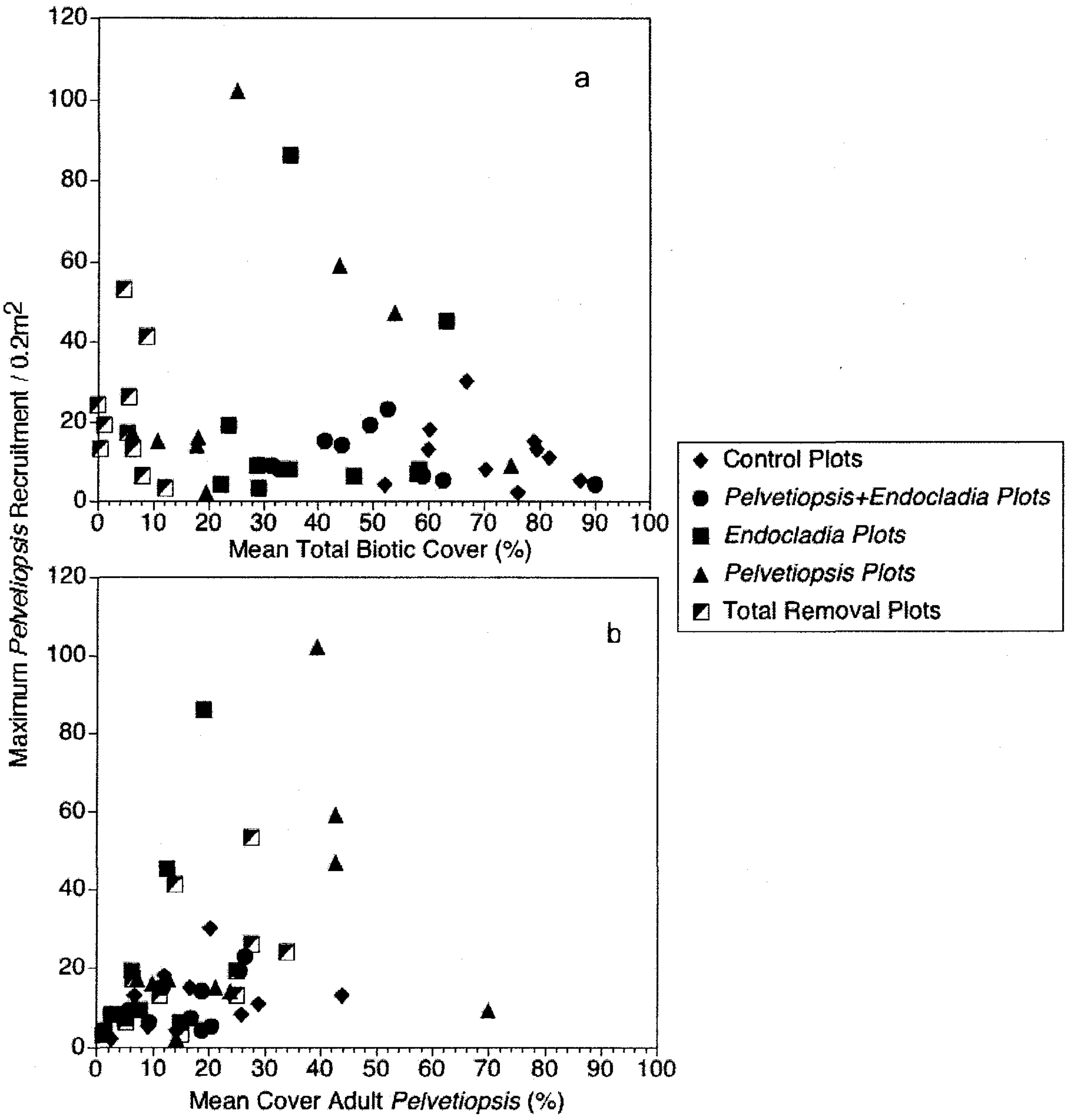

Fig. 6. Relationship between biotic cover and *Pelvetiopsis* recruitment (all months combined). 6a. Relationship between total biotic cover and maximum *Pelvetiopsis* recruitment (maximum=highest monthly value during the experiment), Pearson's grand correlation: r_{48}=-0.16, *P*=0.27. 6b. Relationship between proximity of adult *Pelvetiopsis* (sum of *Pelvetiopsis* cover within plots and 15cm adjacent to plots) and maximum *Pelvetiopsis* recruitment, Pearson's grand correlation: r_{48}=0.39, *P*=0.005.

(i.e. less than 10%), maximum *Pelvetiopsis* recruitment did not exceed 20 per plot; above this level, *Pelvetiopsis* recruitment was highly variable but could exceed as many as 50 recruits per plot. Because the naturally occurring mean amount of *Pelvetiopsis* cover is about 30% (see Fig. 2), it is difficult to predict the effects of *Pelvetiopsis* cover at levels greater than 50%.

The presence of algal cover reduced mean air temperature relative to bare rock by up to 8°C and mean humidity by up to 40% when measured in April, May and October 2006 (Table 5, indicated by dashed line in Fig. 5b). Mean temperature was lowest beneath *Pelvetiopsis* canopies, slightly higher beneath *Endocladia* canopies, and highest on bare rock. Mean humidity levels were highest beneath algal canopies and lowest on bare rock (Table 5). Light levels were reduced under algal cover relative to bare rock,

Table 5. Mean (±SE) temperature, humidity and light levels (in PAR, photosynthetically active radiation) under different types of algal cover and on bare rock at different times of year and day.

	Temperature (°C)		
	April 4/18/06 8:30-9:30	May 5/16/06 9:00-10:00	October 10/8/06 15:00-16:00
Sensor location			
Pelvetiopsis canopy	11.4 (0.5)	15.7 (0.8)	18.0 (0.5)
Endocladia canopy	13.1 (1.1)	18.5 (1.0)	20.5 (0.5)
Bare rock	16.8 (1.7)	23.9 (0.9)	24.8 (0.6)

	Humidity (%)		
	April 4/18/06 8:30-9:30	May 5/16/06 9:00-10:00	October 10/8/06 15:00-16:00
Sensor location			
Pelvetiopsis canopy	95.5 (2.5)	99.2 (1.2)	89.9 (1.7)
Endocladia canopy	99.1 (1.9)	103.9 (1.91)	92.2 (1.3)
Bare rock	60.6 (2.4)	57.7 (3.7)	65.0 (1.9)

	PAR (μEm-^{2}s-^{1})	
Sensor location	3/24/06 15:00	10/22/06 12:00
Pelvetiopsis canopy	11.4 (1.8)	44.3 (13.4)
Endocladia canopy	13.6 (1.7)	47.2 (7.7)
Bare rock	646.4 (16.2)	1135.1 (70.3)

but the light meter was unable to distinguish differences in light among algal species because the spherical head was too large to be completely covered by the *Endocladia* canopy (Table 5). Light levels were sampled at midday on March 24, 2006 and in the afternoon on October 22, 2006 (indicated by a solid line in Fig. 5b).

The relationship between biotic cover and *Pelvetiopsis* recruitment was further explored during the peak recruitment period (March to May 2006, Fig. 5a) because 49% of *Pelvetiopsis* recruitment (1,524 individuals) occurred during these three months (Table 4). The total removal plots (n=10) were broken down into categories of "bare" (n=3, total biotic cover <5%) and "*Porphyra*" (n=7, total biotic cover >5%) during this period to evaluate differences in *Pelvetiopsis* recruitment among plots with virtually no cover, and plots with low cover (i.e. the total removal plots that had *Porphyra* recruit to them). Mean *Pelvetiopsis* recruitment varied with total biotic cover of the treatments (Fig. 7). In

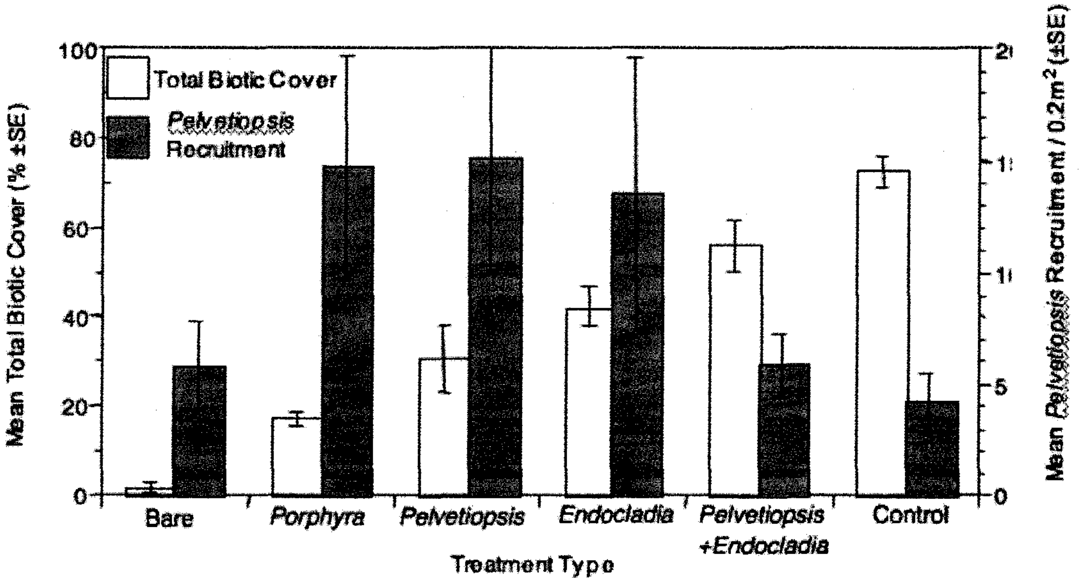

Fig. 7. Peak *Pelvetiopsis* recruitment: effect of treatments and their associated biotic cover on *Pelvetiopsis* recruitment. Data presented are mean values from March, April and May, 2006. Data from Total Removal plots were separated into "bare" and "*Porphyra*" categories to account for plots in which *Porphyra* cover was present during early spring 2006.

treatments with very low total biotic cover (i.e. <5%, bare plots) and high biotic cover (>50%, *Pelvetiopsis* + *Endocladia* plots, control plots), *Pelvetiopsis* recruitment was reduced (~5 recruits/plot). At intermediate levels of total biotic cover (10-40%, *Porphyra* plots, *Pelvetiopsis* plots, *Endocladia* plots), *Pelvetiopsis* recruitment was three times higher (~15 recruits/plot). Due to unequal sample sizes, these results were not analyzed.

The springtime recruitment (March-May 2006) of *Porphyra* to the total removal plots provided an opportunity to understand the relationship between total biotic cover and *Pelvetiopsis* recruitment at cover levels below 50%. There was a positive relationship between biotic cover and *Pelvetiopsis* recruitment in March 2006 (r_8=0.65, P=0.04) (Fig. 8). In April and May 2006 this relationship was also positive, but not

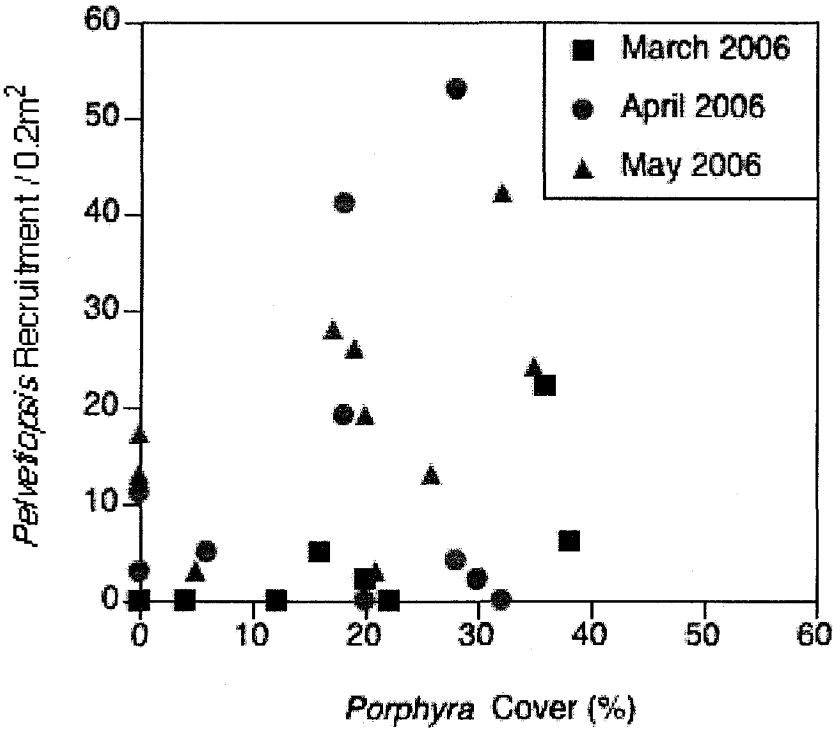

Fig. 8. *Porphyra* cover relative to *Pelvetiopsis* recruitment in total removal plots during peak recruitment (March, April, May 2006, n=10 plots/month).

significant (April: r_8=0.014, P=0.70; May: r_8=0.50, P=0.14). Recruitment in the total removal plots with <10% cover did not exceed 20 recruits/plot, whereas when *Porphyra* cover was >10%, recruitment reached up to 55 recruits/plot. The association between *Porphyra* cover and *Pelvetiopsis* recruitment was very striking: high densities of *Pelvetiopsis* recruits were concentrated immediately below and adjacent to *Porphyra* cover (Fig. 9).

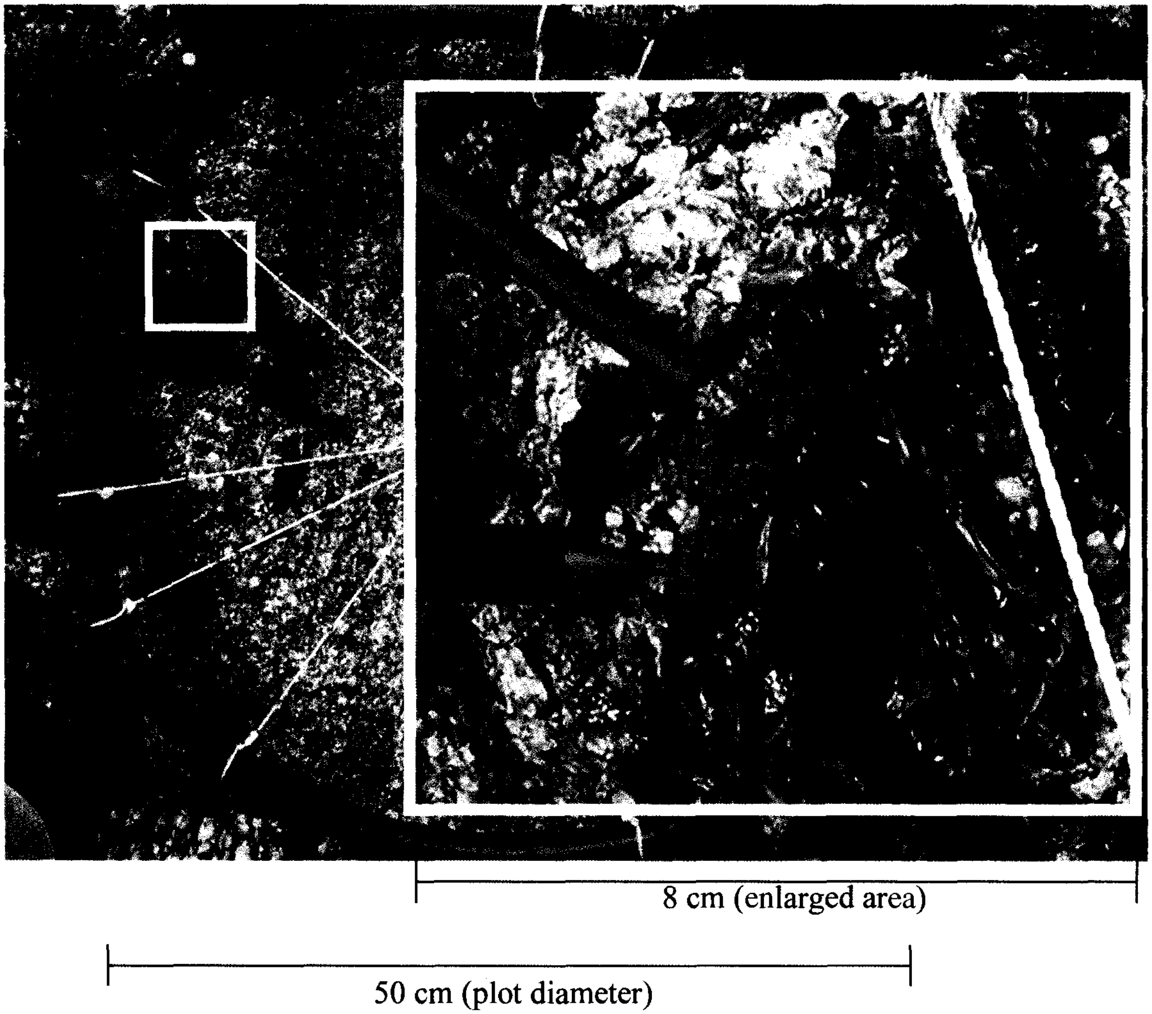

Fig. 9. *Pelvetiopsis* recruitment co-occurred with *Porphyra* cover (March 2006).

The dominant invertebrate grazer groups and temporal variability in invertebrate grazers among the different treatments are highlighted in Table 6 and Fig. 10. Mean invertebrate densities were compared among treatments on two dates (March and August

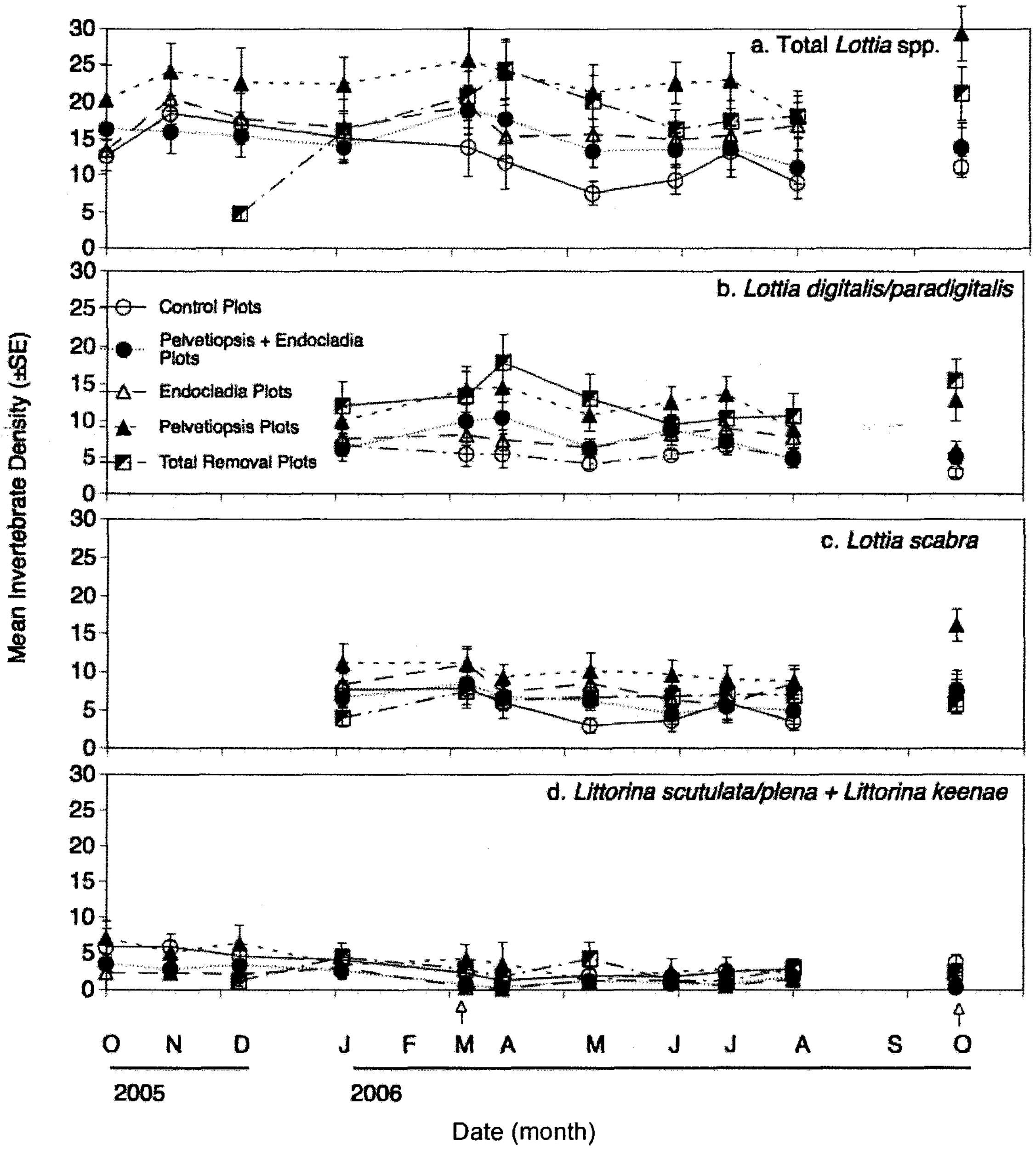

Fig. 10. Motile invertebrate density by treatment (monthly). 10a. All limpets combined, which included all *Lottia* spp. (see Table 6 for breakdown). 10b. *Lottia digitalis/Lottia paradigitalis*. 10c. *Lottia scabra*. 10d. *Littorina keenae + Littorina scutulata/Littorina plena.*

2006) similar to the recruitment and biotic cover data (indicated by arrows on the x axis in Fig. 10). Limpets and littorinid snails comprised 95% of the motile invertebrate assemblage (limpets=78%, littorinid snails=17%, Table 6). *Lottia digitalis, Lottia austrodigitalis* and *Lottia paradigitalis* dominated the limpet composition (43%), (these three species were combined for analyses because of the difficulty of distinguishing them in the field), followed by *Lottia scabra* (35%). Mean density of combined limpets (*Lottia digitalis, Lottia paradigitalis, Lottia austrodigitalis* and *Lottia scabra*) varied among treatments when compared in March and August 2006 (Table 7, Fig. 10a, Appendix B, $F_{4,10}$=11.04, P=0.02); limpets were more abundant in plots with low biotic cover (i.e. high available space: total removal plots and *Pelvetiopsis* plots) than in plots with high biotic cover (i.e. limited available space: control plots). This pattern was the same for differences in mean *Lottia digitalis/ Lottia paradigitalis* and *Lottia scabra* among treatments (Fig. 10b, 10c, Appendix B, *Lottia digitalis / Lottia paradigitalis* $F_{4,10}$=6.00, P=0.06; *Lottia scabra* $F_{4,10}$=6.54, P=0.05). *Littorina scutulata/ Littorina plena* + *Littorina keenae* did not vary among treatments when compared in March and August 2006 (Fig. 10d, Appendix B, $F_{4,10}$=2.962, P=0.16).

To better understand the relationship between total biotic cover and the highest limpet abundances, the maximum abundance of the dominant grazer group (*Lottia digitalis/paradigitalis/austrodigitalis*) was plotted against total biotic cover. Total biotic cover had a negative effect on the maximum abundance of the dominant grazer group, *Lottia digitalis / Lottia paradigitalis* (Fig. 11a). The same pattern existed when total biotic cover was compared with maximum density of total motile invertebrates. If

Table 6. Percentage composition and abundance of motile invertebrates, January-October 2006.

Mobile Invertebrate Species	% Composition	Number
Lottia digitalis /L. paradigitalis	42.7	3,608
Lottia scabra	35.22	2,976
Littorina scutulata/L. plena	16.88	1,426
Littorina keenae	1.99	168
Lottia pelta	1.96	166
Nuttalina californica	0.27	23
Lottia limatula	0.22	19
Nucella emarginata	0.21	18
Tegula funebralis	0.17	14
Lepidochitona sp.	0.13	11
Mopalia sp.	0.12	10
Hemigrapsus sp.	0.07	6
Nucella canaliculata	0.04	3
unknown limpet	0.01	1
Total	100	8,449

Table 7. Analysis of covariance results for differences in maximum recruitment. The final model compared the regression slopes for proximity of adult *Pelvetiosis* and rock inclination with maximum *Pelvetiopsis* recruitment results.

Source	Degrees of freedom	Type III Sum of Squares	Mean square	*F*-value	*P*-value*
Model	2	21693.5	10846.7	32.11	0.000
Adult proximity	1	6129.8	6129.8	18.15	0.000
Rock inclination	1	2184.1	2184.1	6.47	0.014
Error	48	16215.5	337.8		

* All covariate*trt interactions were nonsignificant (P>0.25). Nonsignificant factors (P>0.25) were left out of the model; they included treatment, block, temperature, and water flow.

grazers were to confound *Pelvetiopsis* recruitment, this would likely occur at the lower cover levels because this is when grazer density was highest. Due to the co-occurrence of 1) the highest grazer abundances at low cover levels, and 2) substantial *Pelvetiopsis* recruitment at low cover levels, the relationship between mean *Lottia digitalis/ Lottia paradigitalis* and maximum *Pelvetiopsis* recruitment was further explored (Fig. 11b). There was no striking pattern of maximum *Pelvetiopsis* recruitment relative to *Lottia digitalis/ Lottia paradigitalis* density, however, maximum *Pelvetiopsis* recruitment was high (> 20 recruits per plot) at high grazer densities (up to 20 per plot). *Pelvetiopsis limitata* recruitment did not exceed 20 recruits/plot at grazer levels above 20 per plot.

There was a significant block effect for all response variables including cover, total limpets, *Lottia digitalis/ Lottia paradigitalis*, *Lottia scabra*, and *Littorina* spp. ($P<0.05$ for all variables, except *Pelvetiopsis* recruitment, $P=0.09$, Table 3, Appendix B).

Of the factors that were measured to evaluate potential differences among treatments that could have confounded the recruitment results, adult proximity was the only one that varied significantly among treatments; temperature and humidity, inclination, aspect, reproductive condition, and light did not vary (Table 8). The only difference in adult proximity was between the *Endocladia* (lowest) and the *Pelvetiopsis* (highest) plots. This difference was predictable because the *Endocladia* plots were intentionally devoid of *Pelvetiopsis*, while the *Pelvetiopsis* plots had no *Pelvetiopsis* removed from them. Furthermore, note that although *Endocladia* plots had low values for adult proximity, they still had higher *Pelvetiopsis* recruitment than other treatments

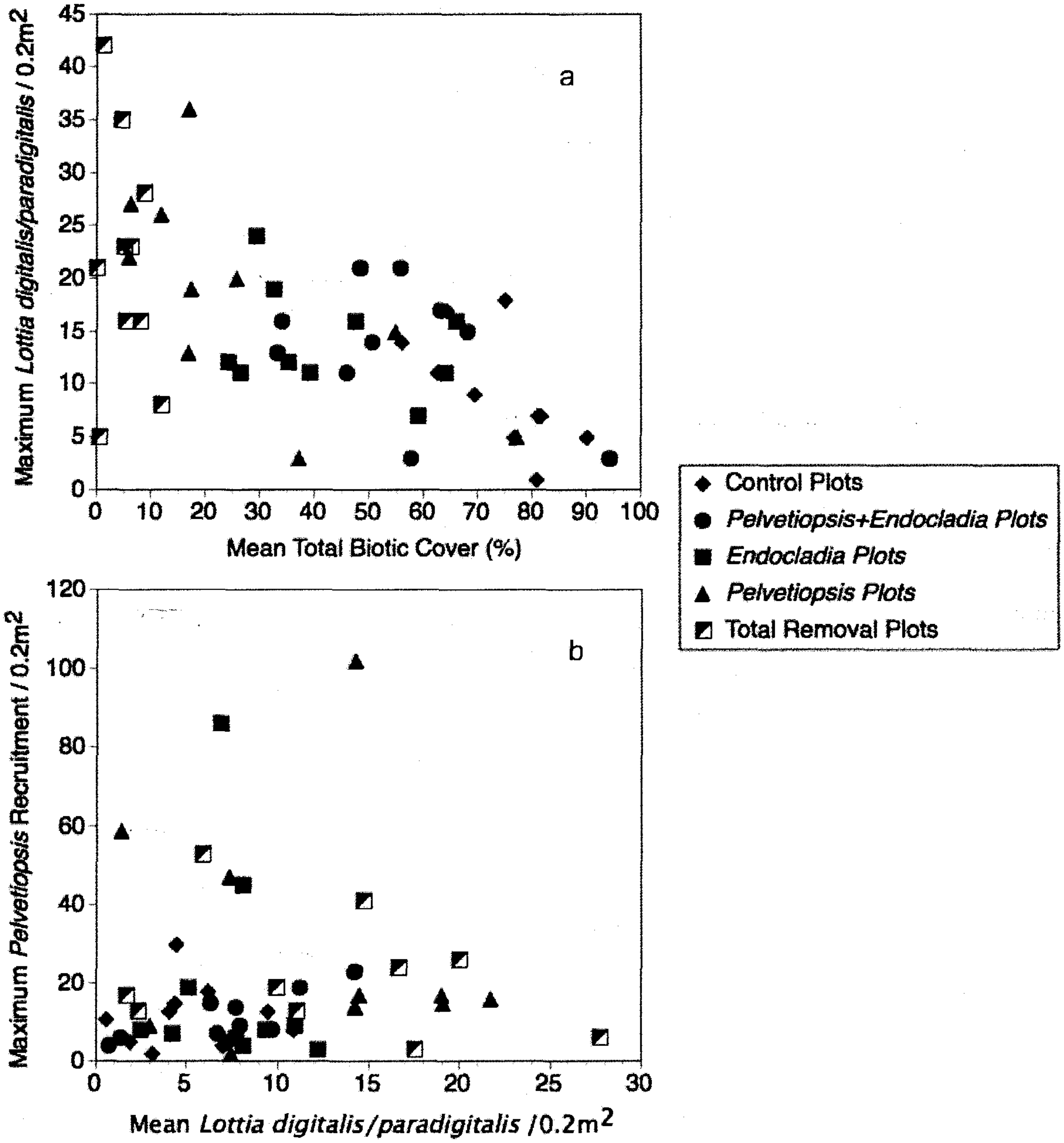

Fig. 11. Patterns of *Lottia digitalis/paradigitalis* density relative to biotic cover and *Pelvetiopsis* recruitment. 11a. Relationship between total biotic cover and *Lottia digitalis/paradigitalis* density, Pearson's grand correlation: $r_{48}=-0.61$, $P<0.001$. 11b. Relationship between *Lottia digitalis/paradigitalis* density and *Pelvetiopsis* recruitment, Pearson's grand correlation: $r_{48}=0.05$, $P=0.76$.

with higher values for adult proximity (i.e. *Pelvetiopsis* + *Endocladia* plots, control plots, see Fig. 5a and Fig. 7).

An ANCOVA was used to evaluate if covariate values for adult proximity, rock inclination, rock temperature, and water flow could help to explain variability in *Pelvetiopsis* recruitment among treatments. Maximum recruitment during the course of the study was used as a response variable, and was compared among treatments in a full ANCOVA model. Non-significant factors and interactions (P>0.25) were removed from the model; the final ANCOVA model included adult proximity, and inclination (Table 9). Both adult proximity and inclination had a significant, positive effect on *Pelvetiopsis* recruitment (adult proximity $F_{1,50}$=32.11, P<0.000, inclination $F_{1,50}$=18.15, P=0.104). However, ultimately, accounting for the effect of adult proximity on *Pelvetiopsis* recruitment in the ANCOVA did not resolve any recruitment differences among treatments (i.e. treatment remained a non-significant factor even once covariances in adult proximity and inclination were accounted for).

The following factors did not vary among treatments, and will not be considered further: mean reproductive condition, mean temperature and humidity when measured on bare rock, directional aspect of rock faces, and mean rock inclination. There was no difference in reproductive condition among treatments, both within plots (log-likelihood ratio, April: G=4.23, P>0.995, df=16 May: G=5.27, P>0.975, df=14) and adjacent to plots (log-likelihood ratio, G=9.94, P>0.999, df=36), suggesting that there was no bias in the distribution of the plots and treatments relative to reproductive *Pelvetiopsis* thalli (see Table 8). Mean temperature and humidity of bare rock among treatments ranged from

Table 8. Analysis of variance results for motile invertebrate data. *P* values for two way, model III ANOVA results, trt=treatment (fixed), block (random), date (random). *P* values correspond to panels in Figure 10; complete ANOVA tables can be found in Appendix A.

	Motile Invertebrate Group			
Factor	Total *Lottia* spp. (Fig. 10a)	*Lottia digitalis*/ *Lottia paradigitalis*/ *Lottia austrodigitalis* (Fig. 10b)	*Lottia scabra* (Fig. 10c)	*Littorina scutulata*/ *Littorina plena*+*Littorina keenae* (Fig. 10d)
TRT	0.02	0.06	0.05	0.16
BLOCK	0.00	0.00	0.01	0.01
DATE	0.01	0.06	0.02	0.82
TRT*DATE	0.79	0.52	0.83	0.60

Table 9. Differences in physical factors among treatment types: mean (±SE) temperature, humidity, inclination, aspect, proximity of adult *Pelvetiopsis*, and reproductive condition.

Treatment Type	Temperature °C	Humidity %	Inclination (0-90°)	Aspect (0-360°)	Adult *Pelvetiopsis* Proximity (% cover)	*Pelvetiopsis* Reproductive Condition (within plots) (rated 0-3)	*Pelvetiopsis* Reproductive Condition (adjacent to plots) (rated 0-3)
Total Removal	18.7 (0.2)	74.3 (0.8)	21.2 (1.3)	171.0 (31.7)	19.0 (3.2)	*	1.9 (0.1)
Pelvetiopsis	18.0 (0.2)	77.7 (1.0)	30.0 (5.5)	232.6 (21.6)	28.3 (6.3)	2.6 (0.1)	2.1 (0.2)
Endocladia	17.9 (0.2)	78.3 (1.1)	29.9 (4.9)	176.3 (23.2)	7.6 (1.9)	*	1.7 (0.3)
Pelvetiopsis + *Endocladia*	18.2 (0.1)	76.9 (0.6)	18.2 (3.5)	202.1 (36.0)	15.6 (2.5)	2.3 (0.2)	2.0 (0.2)
Control	18.0 (0.2)	78.3 (0.9)	29.3 (6.2)	116.4 (28.9)	18.0 (3.9)	1.8 (0.3)	1.7 (0.3)

* No data collected because *Pelvetiopsis* was not included in these treatments.

17.9-18.7°C and 74-78%; it was therefore assumed the treatment and plot locations were distributed randomly with regard to temperature and humidity conditions (see Table 8). The directional aspect of the plots was uniformly distributed among treatments, and therefore did not bias the recruitment results associated with the different treatments. Additionally, because inclination did not vary among treatments, it was unlikely to bias the recruitment results (Table 8).

The blocked factor explained 76.6% of the variability in water flow, suggesting that the spatial variability in water flow was highly dynamic, and that changes in water flow across small spatial scales (i.e. distances of 3 m) were likely greater than differences in water flow would be among treatments (variance components, Appendix A). Although exposure to waves was not measured for individual plots, it was assumed to be highly variable throughout the site, and using the blocked experimental design may have helped account for the impact of this variability on *Pelvetiopsis* recruitment.

DISCUSSION

The important and novel result from this study is an understanding of how the amount of biotic cover present on the rock influences *Pelvetiopsis* recruitment. In particular, the facilitative effect of biogenic cover on *Pelvetiopsis* recruitment at low cover levels was highlighted by the appearance of *Porphyra* in the total removal plots. The ephemeral life history of *Porphyra* that was linked to high recruitment in the total removal plots could play a critical part in determining the distribution of *Pelvetiopsis*, particularly in the context of successional responses to disturbance. In this case, it is the occurrence of different algal life histories that has the capacity to positively affect *Pelvetiopsis* recruitment because ephemeral species like *Porphyra* may be more tolerant of stressful environmental variables associated with bare space, thereby modifying the habitat and ameliorating the conditions for *Pelvetiopsis* recruitment. Additionally, the peak recruitment of the foliar phase of *Porphyra* occurs during the winter months (in response to short day lengths, as studied in Baja, California, Pacheco-Ruiz et al. 2005), suggesting that the appearance of *Porphyra* in the months just preceding *Pelvetiopsis* recruitment has the potential to influence *Pelvetiopsis* recruitment on an annual basis.

The ubiquitous effect of biotic cover on *Pelvetiopsis* recruitment is further supported by the observation that the springtime *Pelvetiopsis* recruitment peak was only evident in the single species plots with lower cover, and not in the plots with higher cover levels (see Fig. 5a, 5b). The experimental manipulation of species in the treatments, and subsequent reduction of biotic cover in some treatments, revealed a peak in *Pelvetiopsis* recruitment that would have been missed in a mensurative survey. The magnitude of this effect, where *Pelvetiopsis* was regularly three times higher in treatments with intermediate levels of biotic cover than in very low or very high cover treatments, supports the idea that the dynamics governing the occurrence of optimal habitat (i.e. available bare space in combination with biotic cover) are key to understanding what influences the survival of *Pelvetiopsis* recruits. Other research in temperate intertidal systems has emphasized the importance of so-called "gaps" to successful colonization by fucoid algae (e.g., Worm and Chapman 1998). These results, in combination with the understanding of how *Porphyra* cover facilitates *Pelvetiopsis* recruitment at low levels, help to clarify how cover impacts *Pelvetiopsis* recruitment at a variety of levels.

The relationship between biotic cover and *Pelvetiopsis* recruitment, whereby recruitment is facilitated at low levels of cover and inhibited at high levels of cover, supports the interactive model of how abundance of algal cover affects recruitment proposed in Fig. 1. The relative importance of facilitative and competitive processes to community structure during stressful circumstances has been emphasized in salt marsh ecosystems (where stress occurs along salinity gradients, e.g., Bertness and Callaway 1994), in alpine ecosystems (stress gradients across elevations, e.g., Choler et al. 2001), and in terrestrial forests (temporal stress gradients in water supply among El Niño/La Niña years, e.g., Gutierez et al. 2007). Understanding the balance between positive and negative interactions can help to clarify which factors determine the distribution of *Pelvetiopsis* recruits, and the context of when these factors will be important. For example, consider the prediction that when environmental stress is high, positive interactions will be more prevalent, whereas when environmental stress is reduced, competitive interactions will prevail (e.g., Bertness and Callaway 1994). In the context of this study, environmental stress is highest when biotic cover is low or nonexistent, and therefore facilitation can increase *Pelvetiopsis* recruitment. With increased biotic cover, environmental stress decreases, and recruitment is reduced, likely via competition for bare space, or preemption (e.g., Vadas et al. 1992). Understanding the relative effects of positive and negative interactions on *Pelvetiopsis* recruitment can inform models of population dynamics, and improve predictions of what determines *Pelvetiopsis* distribution.

The effect of individual algal species on *Pelvetiopsis* recruitment was highlighted by 1) similar recruitment among *Pelvetiopsis* plots and *Endocladia* plots, and 2) the striking influence of *Porphyra* cover in the total removal plots. The similarity in recruitment among the single species plots suggests that the individual, specific characteristics of the biogenic structure of *Pelvetiopsis* and *Endocladia* do not affect *Pelvetiopsis* recruitment. However, although there was no detectable difference in *Pelvetiopsis* recruitment between *Pelvetiopsis* and *Endocladia* plots, the *Pelvetiopsis* plots did generally have slightly higher recruitment. This boost in recruitment could be the result of increased propagule supply from the higher cover of adult *Pelvetiopsis* within and adjacent to these plots relative to *Endocladia* plots, or other factors. The influence of propagule supply is further supported by the ANCOVA analysis that identified adult *Pelvetiopsis* proximity as a significant (positive) covariate with *Pelvetiopsis* recruitment. Presence of adult fucoids has been previously shown to have important dramatic effects on population recovery following disturbances, especially in extreme cases like after the Exxon Valdez oil spill in Alaska (DeVogelaere and Foster 1994) as well as in response to experimental disturbances (e.g., Murray et al. 1999, Speidel et al. 2001).

The subtle potential for individual species to influence *Pelvetiopsis* recruitment may be more a function of the presence or absence of biogenic structure than of species' identity. The springtime recruitment of *Porphyra* to the total removal plots had such a strong effect on *Pelvetiopsis* recruitment that it is difficult to overlook how one species can dramatically impact recruitment success for *Pelvetiopsis*. In this case, the influence of *Porphyra* on *Pelvetiopsis* recruitment was likely a function of natural history and reduced environmental stress. The coincidence of the timing of recruitment for *Porphyra* and *Pelvetiopsis* emphasizes how the phenological characteristics of individual species may influence species distributions, and the strong association between the *Porphyra* cover and *Pelvetiopsis* recruitment suggests that there may be some beneficial aspects of *Porphyra* cover to survival of *Pelvetiopsis* recruits.

Researchers have found increased survival of fucoid zygotes outplanted under algal canopies, suggesting that reduced temperature and desiccation stress associated with algal cover may be one mechanism for increased survival (Hay 1981, Brawley and Johnson 1991). The negative effect of temperature stress (including desiccation) on intertidal fucoid survival and distribution is supported by research that indicates the upper distributional limit of fucoid algae increases during cool years, and decreases during warm years (Hawkins and Hartnoll 1985). Additional examples of sensitivity to temperature and desiccation stress include the presence of dehydrin-like proteins in fucoid algae (Li et al. 1998), and reduced survival or growth of embryos under increased desiccation stress (Brawley and Johnson 1991, Davison et al. 1993, Brawley et al. 1999, Ladah et al. 2003). This evidence supports the idea that the increased survival of *Pelvetiopsis* recruits associated with individual species may be more a function of the presence of biogenic habitat than of the morphological or biological characteristics of individual species. Further consideration should be given to the potential for biogenic structure to provide an associational refuge for *Pelvetiopsis* recruits (e.g., Menge 1976, Bertness and Callaway 1994, Stachowicz 2001), whereby recruits are commonly found under algal cover because this habitat protects them from invertebrate grazing by making the recruits inaccessible to grazers (another example of this is recruitment to cracks in rocks).

The significant block effect found in the 2-way ANOVA analysis of cover and invertebrates (as well as a marginal block effect in the recruitment analysis) offers additional evidence that small-scale environmental effects have a substantial effect on intertidal organisms (Underwood 1997).

The effect of algal diversity on *Pelvetiopsis* recruitment was mediated by the relationship between the number of species included in a treatment and its associated total biotic cover. In general, it appears that in stressful systems (i.e. the high intertidal), species occupy more space when grown in combination than when grown individually (see Fig. 5b). At high cover levels, or when bare space is limited (i.e. in the *Pelvetiopsis* + *Endocladia* plots and control plots), *Pelvetiopsis* recruitment was reduced. The importance of competition for limiting resources (in this case bare space) has been well documented, and in this system, it may be that the competitive, negative interactions occurring in the plots with high cover levels and higher diversity overcome the benefits of the presence of biogenic habitat for *Pelvetiopsis* recruitment.

An additional effect of diversity relates to the natural history traits of individual species and is highlighted by the springtime appearance of *Porphyra* during a critical period for *Pelvetiopsis* recruitment. The potential for ephemeral species such as *Porphyra* to modify habitat and influence successional processes is well understood in both terrestrial and marine habitats. In this case, the influence of *Porphyra* on *Pelvetiopsis* recruitment is perhaps best understood in the context of disturbance theory (e.g., Connell and Slatyer 1977, Sousa 1984), whereby disturbance opens up new space, and the ability of later successional species (i.e. *Pelvetiopsis*) to colonize the new space can be enhanced by ephemeral species like *Porphyra*.

The negative relationship between biotic cover and the density of motile invertebrates indicates that if grazers were going to control the abundance of *Pelvetiopsis* recruits, it would be most evident at relatively low cover levels, that is, when grazer numbers are the highest. However, the effect of environmental stress on algae at low cover levels (i.e. higher temperatures and reduced humidity when algae are absent, see Table 5) is likely driving the pattern of reduced *Pelvetiopsis* recruitment at the lowest cover. High densities of invertebrates (i.e. >20 per plot) at low cover levels could further reduce recruitment, but simultaneously high numbers of *Pelvetiopsis* recruits found in plots with high grazer densities suggests that grazers are not the primary determinant of the distribution of *Pelvetiopsis* recruits. The common experimental method of excluding grazers and tracking algal succession in their absence would help to clarify the effect of grazers at known densities since herbivory is not supposed to be important under conditions of high stress. Additionally, it appears that the algae may actually control grazer density by modifying the availability of bare space, this pattern has been previously identified in other systems (Underwood and Jernakoff 1981). In other parts of the world, researchers working in intertidal systems have indicated non-trophic positive interactions to be important in structuring communities, and have shown limited effects of grazers on fucoid recovery (e.g., in New Zealand (*Hormosira banksii* (Turner) Decaisne): Lilley and Schiel 2006, Schiel et al. 2006). In Europe, research indicates a scaled effect of limpets on fucoid algae (e.g., *Ascophyllum nodosum* (Linnaeus) Le Jolis, where growth is unaffected at low limpet densities and inhibited at high limpet densities (Davies et al. 2007).

The results from this study can be integrated to inform a model of the positive and negative factors that influence *Pelvetiopsis* recruitment. This model should focus on total biotic cover, which will have a positive effect at low levels (i.e. 5%-40%) and a negative effect at cover greater than 50%. Adult *Pelvetiopsis* proximity positively affects *Pelvetiopsis* recruitment, with dramatic increases occurring above 10% cover. This factor is likely important in large part due to the limited dispersal potential of fucoid algae evidenced by population genetic differentiation at small (less than 5 m^2) spatial scales (Williams and Di Fiori 1996, Kinlan and Gaines 2003, Coleman and Brawley 2005). Likewise the highest recruitment occurred in plots with mean rock inclination angles >15°, and supports the idea that prolonged desiccation stress may occur on surfaces with low inclination angles. Invertebrate grazer density may negatively affect *Pelvetiopsis* recruitment, but this likely only occurs at high densities (>20 per plot). Finally, the presence and identity of individual species is an important consideration in any study because of the relative capacity for some species to modify stressful habitats (e.g., *Porphyra*), especially following disturbances. The small scale variability in the factors included in this model reinforces the importance of small-scale processes to *Pelvetiopsis* recruitment. Factors not included in the model did not show any striking pattern in relation to *Pelvetiopsis* recruitment; these were aspect, water flow, light availability, and the spatial distribution of reproductive condition.

Additional consideration should be given to understanding the timing of peak recruitment; this study did not adequately characterize reproductive output through time to understand the relationship between reproductive output and peak recruitment. Given that peak recruitment coincided with the timing of the coolest air temperatures at the study site, *Pelvetiopsis* recruitment could be linked to local climatic conditions, especially considering that reduced environmental stress may increase embryo survival (e.g., Brawley and Johnson 1991). In particular, the period of cool temperatures along the central California coast in the springtime is associated with nearshore fog that occurs during upwelling periods. Current research indicates that changes in the timing of upwelling can influence primary productivity of plankton, as well as rocky intertidal communities. For example, delays in the timing of upwelling in Oregon in 2005 due to low wind stress reduced primary productivity and resulted in decreased recruitment of rocky intertidal invertebrates (Barth et al. 2007). The impact of variability in upwelling on nearshore populations of fucoid algae is unknown, however the co-occurrence of peak *Pelvetiopsis* recruitment with the coolest air temperatures suggests that understanding the role of climate in regulating recruitment of fucoid populations could be an avenue for future research. In addition to the influence of nearshore fog, the reduced maximum wave height that occurred during the period of warmer summer temperatures could also have amplified the effect of desiccation on survival of *Pelvetiopsis* recruits.

CONCLUSIONS

The results from this study provide insight to the relative roles of positive and negative factors in determining species distributions in stressful habitats. The interactive effect of biogenic structure on *Pelvetiopsis* recruitment (positive/facilitative effect at intermediate cover levels, negative/competitive effect at very low and high cover levels) characterizes how a combination of positive and negative interactions influences the distribution of *Pelvetiopsis* by impacting small life history stages. While invertebrate grazers have commonly been shown to negatively affect algal community structure, this study indicates that high grazer density and *Pelvetiopsis* recruitment co-occur, and that grazers reduce or prevent *Pelvetiopsis* establishment only at very high densities (greater than 20/0.2 m^2). The ameliorative effect of algal cover on desiccation stress is likely a key component to predicting the survival of *Pelvetiopsis* recruitment. A model that incorporates the balance between positive and negative interactions provides the best explanation for the recruitment patterns evident in this study.

The dramatic influence of algal cover on *Pelvetiopsis* recruitment suggests that algae can structure nearshore ecosystems by modifying environmental conditions for small life history stages at low to intermediate levels of cover. Furthermore, the positive influence of ephemeral species of algae like *Porphyra* on the survival of *Pelvetiopsis* recruits highlights how individual species of algae can influence community structure by modifying successional responses to disturbance (i.e. facilitation). The temporal co-occurrence of *Porphyra* and *Pelvetiopsis* recruitment in the springtime provides additional insight to how algal diversity may contribute to increased ecosystem function.

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APPENDICES

Appendix A. ANOVA and variance components analysis for water flow based on the percentage weight lost from the clod card experiment. Omega squared (ω^2) represents the percentage variance explained by the source factor. Calculations based on Graham and Edwards (2001).

Source	SS	DF	MS	Variance component	ω^2
Block	1151.1	7	164.5	71.3	76.6
Error	239.8	11	21.8	21.8	23.4

Appendix B. ANOVA tables describing the effects of different factors (block, treatment, date, and treatement x date interaction) on response variables that included: a. *Pelvetiopsis* recruitment, b. total biotic cover, and invertebrate densities: c. total *Lottia* spp., d. *Lottia digitalis* + *Lottia paradigitalis*, e. *Lottia scabra*, and f. *Littorina scutulata/plena* + *Litorrina keenae.*

a. *Pelvetiopsis* Recruitment

Source	df	*SS* (Type III)	*MS*	F-ratio	P
BLOCK	9	1399.25	155.472	1.76	0.09
Error	81	7176.45	88.598		
TRT	4	643.6	160.9	1.14	0.45
Error	4	566.96	141.74		
DATE	1	86.49	86.49	0.61	0.48
Error	4	566.96	141.74		
TRT * DATE	4	566.96	141.74	1.60	0.18
Error	81	7176.45	88.598		

b. Total Biotic Cover

Source	df	*SS* (Type III)	*MS*	F-ratio	P
BLOCK	9	7796.84	866.316	3.51	0.00
Error	81	20018.76	247.145		
TRT	4	52835.44	13208.86	16.29	0.01
Error	4	3243.76	810.94		
DATE	1	4.00E-02	4.00E-02	0.00	1.00
Error	4	3243.76	810.94		
TRT * DATE	4	3243.76	810.94	3.28	0.02
Error	81	20018.76	247.145		

c. Total *Lottia* spp.

Source	df	*SS* (Type III)	*MS*	F-ratio	P
BLOCK	9	3577.89	397.543	5.50	0.00
Error	81	5857.01	72.309		
TRT	4	1362.04	340.51	11.04	0.02
Error	4	123.4	30.85		
DATE	1	650.25	650.25	21.08	0.01
Error	4	123.4	30.85		
TRT * DATE	4	123.4	30.85	0.43	0.79
Error	81	5857.01	72.309		

d. *Lottia digitalis+paradigitalis*

Source	df	*SS* (Type III)	*MS*	F-ratio	P
BLOCK	9	1901.84	211.316	6.09	0.00
Error	81	2811.16	34.706		
TRT	4	678.04	169.51	6.00	0.06
Error	4	113	28.25		
DATE	1	196	196	6.94	0.06
Error	4	113	28.25		
TRT * DATE	4	113	28.25	0.81	0.52
Error	81	2811.16	34.706		

e. *Lottia scabra*

Source	df	*SS* (Type III)	*MS*	F-ratio	P
BLOCK	9	760.64	84.516	2.90	0.01
Error	81	2364.36	29.19		
TRT	4	282.44	70.61	6.54	0.05
Error	4	43.2	10.8		
DATE	1	169	169	15.65	0.02
Error	4	43.2	10.8		
TRT * DATE	4	43.2	10.8	0.37	0.83
Error	81	2364.36	29.19		

f. *Littorina scutulata/plena+Littorina keenae*

Source	df	*SS* (Type III)	*MS*	F-ratio	P
BLOCK	8	220.6	27.575	2.759	0.01
Error	72	719.622	9.995		
TRT	4	82.067	20.517	2.962	0.159
Error	4	27.711	6.928		
DATE	1	0.4	0.4	0.058	0.822
Error	4	27.711	6.928		
TRT * DATE	4	27.711	6.928	0.693	0.599
Error	72	719.622	9.995		