Summer 2010

Effects of Competition and Dispersal on the Recruitment of the Annual Kelp Nereocystis luetkeana

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Recommended Citation

Suskiewicz, Matthew, "Effects of Competition and Dispersal on the Recruitment of the Annual Kelp Nereocystis luetkeana" (2010). *Master's Theses*. 3831.
DOI: https://doi.org/10.31979/etd.4wps-e3hp
https://scholarworks.sjsu.edu/etd_theses/3831

EFFECTS OF COMPETITION AND DISPERSAL ON THE RECRUITMENT OF THE ANNUAL KELP *NEREOCYSTIS LUETKEANA*

A Thesis

Presented to

The Faculty of the Department of Marine Science

Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Matthew S. Suskiewicz

August 2010

The Designated Thesis Committee Approves the Thesis Titled

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by

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August 2010

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ABSTRACT

EFFECTS OF COMPETITION AND DISPERSAL ON THE RECRUITMENT OF THE ANNUAL KELP *NEREOCYSTIS LUETKEANA*

By Matthew Suskiewicz

In central California, the role of algal assemblages on the recruitment of the canopy producing annual kelp *Nereocystis luetkeana* was examined by experimentally manipulating canopy and understory algae within 1) a *Macrocysits* bed and 2) a *Nereocystis* bed. *Nereocystis* reproductive material was introduced in some plots to examine the role of dispersal distance on recruitment. *Nereocystis* recruitment at both sites was significantly higher during spring compared to recruitment observed later in the study. Recruitment continued throughout the fall, however, suggesting a broad recruitment window. Recruitment success increased dramatically when understory algae were removed. Presence of a canopy (*Nereocystis* or *Macrocystis*) did not affect *Nereocystis* recruitment, suggesting that *Nereocystis* was not directly competitively inferior to *Macrocystis*. Greater recruitment was observed in areas seeded with *Nereocystis* propagules. Ultimately, recruitment of *Nereocystis* was controlled by understory algal assemblages and by the relatively short dispersal distance of its propagules. Additionally, the broad recruitment window for *Nereocystis* described here suggests that summer recruits can contribute to population resilience to late spring disturbances. This study indicates that given sufficient disturbance to the benthos and ample propagule supply, *Nereocystis* should be able to recruit and colonize new areas, regardless of the presence of *Macrocystis.*

ACKNOWLEDGEMENTS

Obtaining a master's thesis in marine science is an inherently selfish endeavor. It takes an extensive infrastructure, a large community of involved academics, and in the case of this thesis, lots of divers willing to endure cold, turbulent, shark-infested waters for little more than cheese and crackers. Throughout my time here at Moss Landing Marine Labs I have been supplied with a great deal of resources, and have always had a constant supply of academic insight and field help.   Moss Landing Marine Laboratories is a very special place, filled with amazing people.

Dr. Michael H. Graham is a great scientist and was a fantastic advisor. He loves anything that focuses on ecology, kelp, or bacon. Mike both gave me the freedom to work nearly autonomously when I wanted, and he was almost instantly accessible to help me with every problem that I faced. My lab mates, the self-titled "BEERPIGS", are the most critical and analytical group of ecologists I have ever had the pleasure of working with. Their constant evaluation of my thesis at every stage could be maddening, but it has made me a better scientist. And when it came time to collect data, they were always there, willing to do whatever I asked of them, even when they were betting it wouldn't work. I am indebted to Danielle Frechette for multiple edits of this manuscript, and for her patience. Finally, my parents have encouraged my inquisitiveness since before I could walk, and have given me every kind of support possible. I love you both. Thank you.

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Introduction

Nereocystis luetkeana (Mertens) Postels & Ruprecht is a large, conspicuous kelp that forms dense canopies in shallow coastal waters of the Pacific Northeast (Frye 1906). Classified as a spring annual (Abbott and Hollenberg 1976) or as a spring opportunist (Dayton et al. 1984), *Nereocystis* has a heteromorphic life history, with an alternating macroscopic sporophyte stage and a microscopic gametophyte stage. In central California, the macroscopic sporophyte stage is typically first observed in the early spring (McLean 1962, Foster and Schiel 1985), and individual plants can become reproductive shortly before reaching the surface in May (Abbott and Hollenberg 1976). These individuals may form a dense canopy that typically reaches maximum coverage in the fall before being dislodged by the first winter storms of the year (Foster 1982). When present, these large *Nereocystis* beds can form biologically complex, three-dimensional structures. A wide array of invertebrates (McLean 1962) and fish (Bodkin 1988) associate with these beds.

Little direct work in central California has been done on the physical effects that *Nereocystis* beds can exert on their environment and on other algal assemblages. It has been well documented, however, that other algal canopy and understory layers can reduce the light to <1% of surface irradiance (Dayton et al. 1984, Reed and Foster 1984, Clark et al. 2004). Such a drastic reduction in light reaching the benthos reduces or can completely inhibit kelp recruitment, sometimes for several years (Edwards 1998, Clark et al. 2004). Certain kelp species can directly influence the surrounding vegetation via abrasion (Irving & Connell 2006, Hughes in review), shifting the surrounding algae from erect coralline or fleshy species to ones with crustose morphologies. Dense *Macrocystis* beds in southern California can alter the velocity and direction of currents (Jackson 1997), which in turn increases the likelihood that propagules are retained within the centers of large beds (Graham 2003). Currently, it is unclear to what degree *Nereocystis* can alter the physical environment and associated biota, and whether *Nereocystis* can compete and persist in areas occupied by other algal species. As a canopy-producing annual, it can reach great densities, particularly during the late summer, yet it is functionally absent for several months each year (Frye 1906, Foster and VanBlaricom 2001). *Nereocystis* might have a strong and lasting effect on the surrounding biota because it reaches such densities during the summer, or it may have a weak and periodic effect due to its seasonality.

The ecological range of *Nereocystis* stretches from Piedras Blancas in central California to Unimak Island in the eastern Aleutians, Alaska (Miller and Estes 1989). Within this range, *Nereocystis* is found attached to hard substrate, frequently on wave-swept points and rocky outcroppings. These individuals can form large beds where all the adult sporophytes may be removed each winter, but are replaced by new recruits the following spring and summer. This continuance of a kelp patch through multiple generations meets the definition of persistence (Dayton et al. 1984), despite the patch being completely absent for several months each year. Persistence has been defined as the "existence of a patch for more than one generation" (Dayton et al. 1984) and has become a key component in defining the stability of a population and of an entire ecosystem (Connell and Sousa 1983, Dayton et al. 1984).

During winter months, strong southern storms can nearly or completely remove an area of all *Nereocystis* sporophytes (Foster 1982). In order to persist (Dayton et al. 1984), a kelp bed must rely on the successful recruitment of microscopic gametophytes into sporophytes the following spring (see Dixon and Waaland 1985 for synopsis). A single healthy kelp plant such as *Macrocystis* is capable of releasing over 100 million zoospores in a single season (Kritzer and Sale 2006). In *Nereocystis*, meiosis occurs in specialized regions of the blade called sori (Abbott and Hollenberg 1976). Sori first appear on the blade in May and are produced continuously until the plant is ripped out by winter storms (Foster 1982). Haploid, bi-flagellate zoospores are released en mass from these patches into the water column. These releases may be cued by daylight, with the majority of the zoospores being released within a few hours (Amsler and Neushul 1989). These patches then abscize from the blade and fall to the benthos, where some continued, localized release of zoospores may occur (Amsler and Neushul 1989).

Dispersal of kelp propagules is highly variable and episodic (Reed et al. 1988). Zoospores are photosynthetic and can swim in the water column for greater than 72 hours (Reed et al. 1992), greatly enhancing the distance they can be dispersed by ocean currents. However, the adult gametophytes borne from zoospores are sessile and dioecious. Settlement densities in excess of $1/mm^2$ are necessary for successful fertilization and gametogenesis to occur (Reed 1990).

Zoospores which travel outside the kelp bed are more likely to be carried away from the bed (Jackson 1977, Graham 2003) and may not settle in sufficient densities for fertilization to occur (Reed 1990). Kelps readily hybridize and self fertilize (Lewis and Neushul 1995, Druehl et al. 2005), suggesting that a single adult sporophyte could colonize an entire area, but self-fertilization events tend to yield individuals with reduced fitness (Raimondi et al. 2004).

Completion of the gametophyte generation is density-dependent, therefore, zoospores must either settle together in great numbers, or the microscopic gametophytes must survive long enough for another zoospore to settle nearby. The potential longevity of a kelp gametophyte is intensely debated. The sporophytes of kelp annuals frequently are absent for at least a season each year, and it generally is accepted that microscopic stages can persist for at least this long. A series of laboratory (Edwards 1998, McConnico 2002, Carney et al. 2005) and field experiments (Edwards 2000, McConnico & Foster 2005) support this idea. However, it is unclear whether microscopic stages can persist for greater than one year, and it also is unclear what their precise identity (i.e. spore, gametophyte or embryonic sporophyte) may be during these microscopic stages (see Reed et al. 1997, Kinlan et al. 2004, Edwards 2005)

In central California there is a large (~240 km) region of coastline ranging from Piedras Blancas in the south to Año Nuevo Island in the north where the distribution of *Nereocystis* overlaps with the perennial kelp *Macrocystis.* Within this area, these two species often form persistent, monospecific beds that are often adjacent to each other (Crandall 1915, Foster 1982), with the *Nereocystis* beds frequently in shallower water or along more wave-swept points (Kalvass and Larson 2004). This observation of *Nereocystis* persisting only in more hydro-dynamically extreme environments suggests that *Macrocystis* is competitively dominant over *Nereocystis* in all but the most extreme environments. Whereas the greater mass (Faye 1915) and high drag of adult *Macrocystis* plants (Jackson 1997) may explain why *Macrocystis* sporophytes do not persist along these wave swept points but *Nereocystis* sporophytes do persist (Denny et al. 1997), it is unclear what prevents *Nereocystis* from invading areas presently dominated by *Macrocystis*. Numerous studies in central California have demonstrated that a *Macrocystis* bed can form a surface canopy thick enough to reduce surface irradiance by more than an order of magnitude (Edwards 1998, Clark et al. 2004).

Lacking from the literature are targeted, *in situ* experiments designed to examine the ecological role of *Nereocystis* in central California where it coexists with the perennial *Macrocystis*. The importance and relevance of a species is often tied to its stability (Connell and Sousa 1983). For patch-forming, sessile species such as kelps, stability can be measured by considering the persistence, inertia, and resilience of the population over several generations (Dayton et al. 1984). Whereas persistence is the ability of a species to occupy the same location through multiple generations, inertia and resilience consider the ability of a species to colonize new areas, and prevent other species from encroaching, respectively. While many have noted the persistence of *Nereocystis* beds on wave-swept points (Frye 1906, Foster

1982, Dayton et al. 1984, Foster & VanBlaircom 2001), the inertia of these plants to invade nearby *Macrocystis* beds have routinely been called into question (Foster 1984, Dayton et al. 1984); in central California *Nereocystis* is assumed to be competitively inferior, despite any direct experimental studies to test this hypothesis. This is due in part to the difficulties of working in swell exposed areas where *Nereocystis* occurs (Foster 1982), which often are located away from harbors and shore access points (Kalvass and Larson 2004). Manipulative studies of *Nereocystis* largely have been conducted in the laboratory (e.g. Vadas 1972, Duncan and Foreman 1980, Lüning & Freshwater 1988, Amsler & Neushul 1989, Atrium et al. 1994, Denny et al. 1997).

Previous field-based studies of *Nereocystis* either were surveys of extant or historical beds (Crandal 1915, Frye 1915, Scagel 1945, Foreman 1970, Berry et al. 2001 & 2005), or simple quantifications of the marine organisms associated with *Nereocystis* plants (see Andrews 1945, Markham 1969, Bodkin 1986). The majority of recent field-based studies have been conducted in more northerly areas where *Macrocystis* is absent (Maxell and Miller 1996, Carney et al. 2005).

The purpose of this study was to determine if either dispersal of propagules or competition between other species of seaweed could affect the recruitment of *Nereocystis*, and therefore explain why *Nereocystis* only forms persistent beds along wave-swept points in central California. To provide context to the results, the recruitment of the annual, canopy-producing

Nereocystis was compared with three distinct, well studied species of brown seaweeds, each with slightly different life-history characteristics.

Macrocystis pyrifera was chosen because it is a genetically similar (Lane et al. 2006), perennial, canopy producing kelp (Abbott and Hollenberg 1976). Unlike *Nereocystis* it can be present, reproductive, and recruit year-round (Graham 2003). *Macrocystis* may be the most studied of all kelps in this region. Recruitment of *Macrocystis* has been experimentally studied *in situ* (Reed and Foster 1984, Foster and Scheil 1984, Dayton et al. 1984 & 1992, Konar 1996, Reed et al. 2000, Graham 1996, Clark et al. 2004) and under laboratory conditions (Lüning 1988, Reed 1990, Reed et al. 1996 & 1997, Kinlan et al. 2003). Like *Macrocystis*, *Pterygophora californica* is a perennial kelp. However, *Pterygophora* is an understory kelp (i.e. it does not form a surface canopy) and it has a very defined and narrow recruitment window (Reed et al. 1997), similar to what many expect a spring annual kelp such as *Nereocystis* to have. Following the recruitment of both *Pterygophora* and *Macrocystis* allows two perennial kelps with extremes in both their size (canopy and understory) and dispersal windows (narrow and continuous) to be compared with the recruitment of *Nereocystis. Desmarestia ligulata* is not a kelp, but a brown seaweed of the closely related Desmarestiales (Abbott & Hollenberg 1976). Like *Nereocystis*, *Desmarestia* is an annual which can recruit to recently disturbed patches (Edwards 1998), sometimes in such great densities that the emerging adults can prevent all other algae recruitment (Dayton 1992, Clark et al. 2004). Recruitment of this seaweed in central California is thought to be limited essentially to a very narrow window in April. *Nereocystis* in central California is unique, as it is the only canopy forming annual kelp. *Macrocystis*, *Pterygophora*, and *Desmarestia* create a collection of three traits against which to compare the recruitment of *Nereocystis* (Table 1). These three traits are 1) whether the algae forms a canopy, 2) whether it is an annual or a perennial, and 3) whether it has a limited or broad recruitment window.

A dense canopy of *Macrocystis* fronds can reduce surface irradiance to the benthos by greater than an order of magnitude (Clark et al. 2004), which in turn can limit or even completely prohibit the recruitment of many species of kelp (Reed & Foster 1984, Dayton et al. 1992, Edwards 1998). It is uncertain whether a *Nereocystis* canopy can create the same magnitude of effect that a developed *Macrocystis* canopy can have. Perennial kelps have the potential of being present for several years, whereas a kelp with an annual life-history by definition is absent for a portion of each year. Whether *Nereocystis*, an annual, can affect subsequent algal recruitment at all is undetermined, and if so, during which months of the year. Finally, the duration of the "recruitment window" of a sessile species can have a lasting and broad impact on ability of that species to persist in an area, and recover following a disturbance. In species with limited recruitment windows, recruitment occurs during a brief period of time, often swamping similar species (Reed et al. 1990), but requires a temporally reliable pattern of disturbance. Broad or continuous recruitment windows do not rely on such temporal disturbance but require either a prolonged microscopic stage (Dayton 1985) or a continuous release of nearby zoospores (Kinlan et al. 2004).

The objective of this study was to examine *Nereocystis* recruitment. Specifically, three questions were addressed. 1) Does *Nereocystis* have a limited or broad recruitment window? 2) Is *Nereocystis* competitively inferior to *Macrocystis*; (i.e. is the presence of a *Macrocystis* bed enough to prevent colonization of *Nereocystis* into these areas)?, and 3) Is recruitment of *Nereocystis* into a nearby *Macrocystis* bed limited by the dispersal distance of its propagules; given a sufficient supply of zoospores, can *Nereocystis* successfully recruit into an existing *Macrocystis* bed?

While this approach focuses on direct observation of only one stage of a kelp's complex life history, by examining recruitment a great deal can be inferred. Successful recruitment requires completion of the microscopic stages. Areas with lower observed recruitment may either have had lower settlement of propagules, or the new cohort of emerging sporophytes did not grow and survive long enough to be counted. Regardless, in an annual population of sessile individuals, recruitment failure will cause that population to become extinct.

Methods

In order to effectively test the three questions outlined previously, two field sites were necessary. One site was located within a persistent *Nereocystis* bed where propagule supply was assumed to be at maximum, and the second site within a *Macrocystis* bed not far from reproductive *Nereocystis* adults. Whereas the methods described below are similar for both sites, each location allowed different aspects of the research questions to be addressed. The site within a *Nereocystis* bed provided a baseline of natural *Nereocystis* recruitment, it tested the effect of a *Nereocystis* canopy on its own recruitment and by tracking recruitment throughout a season, it would be possible to determine whether the recruitment window was limited to a very narrow time or year or more broad and continuous. Having a site within a persistent *Macrocystis* bed allowed a parallel set of questions to be addressed. It has been suggested that *Nereocystis* may be competitively inferior to *Macrocystis*. By removing the *Macrocystis* canopy this idea of direct competitive dominance can be addressed. Also, it has been hypothesized that the recruitment of *Nereocystis* into new areas may be limited in part by the dispersal distance of its propagules. Experimental plots within a *Macrocystis* bed almost certainly have fewer *Nereocystis* propagules than those located directly within a *Nereocystis* bed, and the observed recruitment can be used to determine if the ability of *Nereocystis* to colonize new habitat may be limited by dispersal distance.

The two sites were selected for this experiment, Big Creek Marine Reserve (hereafter BCMR) and Stillwater Cove (hereafter SWC). In addition to having large, persistent *Nereocystis* and *Macrocystis* beds (respectively), these two locations each offered a large, relatively flat area of hard substrate with minimal sand cover at 8-10m MLLW and reasonable access to divers. Specific site locations were selected in Fall 2007, corresponding to the expected maximum kelp canopy cover (Donnellen 2003). With the exception of deploying site markers and initial surveys of the biota in 2007, all field work was conducted between February and November 2008.

Big Creek Marine Reserve (BCMR)

BCMR was located 4 miles north of Lucia along the Big Sur Coastline (36º 04.166'N, 121º 35.919'W – Figure 1). It was composed of granitic rock from the Santa Lucia range and consisted of a mixed canopy within the cove and large *Nereocystis* beds to the north and south of the cove.

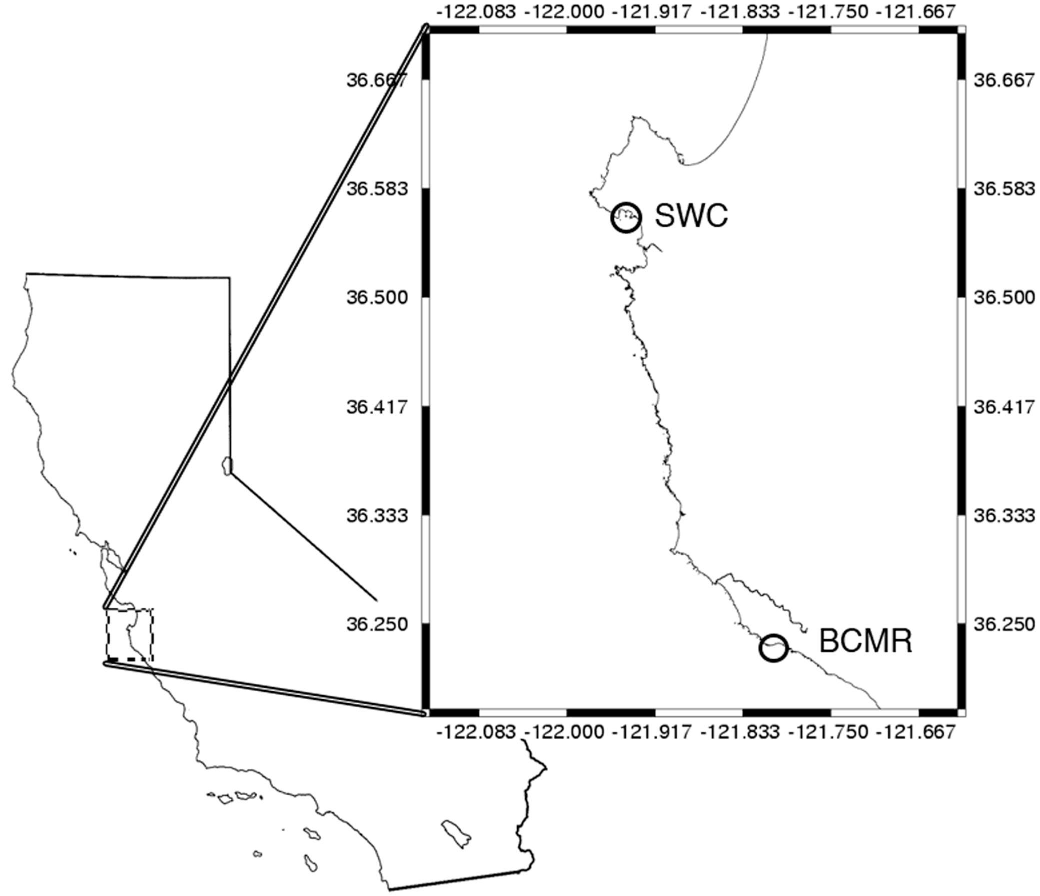

Figure 1: Location of study sites.

Experimental plots were established in 2007 inside the annual *Nereocystis* bed located to the south of the cove. Criteria for site selection were the presence of a dense *Nereocystis* canopy (in Fall of 2007), a predominance of low relief rock outcrops at a depth of 8-10m MLLW, and very limited sand cover. To minimize the input of *Macrocystis* propagules, all plots were established at least 200 meters from the nearest *Macrocystis* bed to the north, and these plots ran roughly parallel to the shore. Ten plots, each 10 meters in diameter, were established in the fall of 2007 and marked by a surface float attached to a stainless steel eye-bolt in the center of each plot. The edge of each plot was at least 10 meters from the edge of any adjacent plots. Within each plot, six subplots (1 meter in diameter) were created by haphazardly selecting areas of exposed bedrock with low relief and minimal incline. These haphazardly selected subplots were marked by a lag-bolt in the center of each plot and then randomly allocated using a six-sided die into either scraped plots or control plots (each n=3). Subplots were at least two meters from one another, from the center marker buoy, and from the edge of the plots to maintain independence from understory and algal turf assemblages.

In the fall of 2007 the following was done within each plot. The three subplots randomly allocated as "scraped" were cleared by divers on SCUBA of all macroscopic algae using a combination of knives and paint scrapers. *Pterygophora californica* thalli were cut within 5 cm of the holdfasts and removed from the plots completely. The remaining holdfasts were left in place because removing them can result in fragmentation of the underlying rock, and because they can serve as recruitment substrate for other kelp species including *Nereocystis luetkeana* (Kennelly 1987). Encrusting corallines and invertebrates were left relatively unmolested. The corresponding 3 unmanipulated subplots were marked in a manner similar to the "scraped" subplots but were otherwise left unchanged. This process was repeated for all 10 plots. To aid in underwater navigation a lead-line connected the center bolts of each plot, anchored in places by destroyer chain and eye-bolts. Great care was taken to ensure that the lead-line would not cross into any "scraped" or "unmanipulated" subplots, even under heavy surge. Five out of the ten plots were randomly selected as "no canopy" plots. Beginning in April of 2008 and continuing throughout the experiment, any canopy-forming kelp species were cut by divers and allowed to drift away, before they could reach the surface and form a canopy. In the remaining five plots a canopy was allowed to form naturally.

This pattern of randomly allocated factors arranged within one of two blocking factors created a "split plot" design. In this case, the presence or absence of a canopy was the blocked factor. Within each canopy treatment there were two replicated, randomly assigned treatments: a "scraped" treatment where all fleshy algae were removed, and an "understory" treatment where the algal assemblages were permitted to develop unperturbed. This "split-plot" design was chosen because the two assemblages being considered, canopy & understory, operate at very different spatial scales. Canopy producing kelps in 10 m depth can shade a large area of the benthos (see Dayton et al. 1984), which required the large 10 m diameter plots. However, the significantly smaller understory and turf algae physically affect much smaller areas, allowing these treatments to be split and replicated within the blocked, canopy factor.

This split-plot design created four distinct treatments: understory/with canopy, understory/no canopy, scraped/with canopy and scraped/no canopy. Because adult *Nereocystis* and *Macrocystis* sporophytes can become very large and have the potential to physically shade a very large area it was necessary to group the subplots towards the center to reduce edge effects by creating a large 'buffer zone' between the edge of the plots and the sampled subplots.

All scraped plots were surveyed each month, beginning in March 2008, which was before the first anticipated annual kelp recruits (pers. obs, but see Edwards 1998 and McConnico 2003). After each sampling, all fleshy algae within the "scraped" subplots were carefully removed to ensure their physical presence would not influence subsequent recruitment.

All subplots were sampled once per season by divers on SCUBA. Within the scraped plots, divers identified, measured, recorded and then removed all kelp recruits and *Desmarestia* recruits within a 1 m diameter circle around the center marker bolt (0.79 m^2). After each scraped plot was sampled, all fleshy algae besides juvenile kelps were removed by hand to ensure the potential recruitment area remained comparable throughout the experiment. Juvenile kelps too small to be identified (generally <6 cm TL) were measured but allowed to persist until the next sampling period, when they had presumably either grown enough to be visually identified to species or been removed by natural disturbances. *Desmarestia* spp. recruits were easily identifiable as soon as they were large enough to be counted (Edwards 1998). Sampling was similar in the unmanipulated control plots, however no fleshy algae were removed, and the plots were allowed to develop naturally throughout the experiment.

Second only to the canopy forming *Nereocystis*, the most conspicuous alga within the southern kelp bed at Big Creek was the perennial kelp *Pterygophora*. The density of *Pterygophora* was estimated during the fall of 2007 by counting all individuals within 2 x 10m band-transects (n=3). During the initial establishment of the scraped plots the 5 *Pterygophora* plants closest to the center bolt were chosen to estimate average size and age. In the field TL of the thallus was recorded, and a short segment of the stipe located ~5 cm above the holdfast was removed to be used for age analysis. Age was determined by cross-sectioning the stipe and counting the rings (methods of Hymanson et al. 1990).

Algal cover was measured in May and June 2008 using a simple Random-Point-Contact (RPC) method. A rigid PVC bar, 0.5 m in length, was haphazardly placed across the center bolt of the "understory" subplots. This rigid bar had a string with five knots serving as "points". At each point the diver would pull the string taut above and below the bar and record whatever species fell under those two points. The bar would then be rotated 90º and the process repeated, giving a total of 20 random points in each subplot. Because the "scraped" plots were routinely disturbed and removed of fleshy algae, only the unmanipulated "understory" plots were sampled using this method.

Stillwater Cove (SWC)

The SWC study site was located near Carmel, just south of the Monterey Peninsula (36.5570 N, 121.9400 W – Figure 1). It was characterized by a dense

Macrocystis canopy throughout the cove, with a sparse *Nereocystis* canopy just north of the cove. The cove opened to the south and was relatively protected from the northwest swells common to the coast of central California coast. During winter, the less frequent southern swells remove most of the *Macrocystis* canopy (Foster 1982, Reed and Foster 1984). The large understory assemblages were dominated by *Pterygophora californica*, with *Cystoseira osmundacea* and *Chondracanthus corymbiferus* also present. A dense turf assemblage of geniculate coralline algae covered most available rock substrate (see Reed and Foster 1984). Patches of sand frequently intruded over the bedrock. Criteria for site selection were the presence of a dense *Macrocystis pyrifera* canopy (during Fall 2007), a predominance of low relief rock outcroppings at 8-10 m and limited sand cover.

The experimental design at SWC utilized a split-plot design similar to the design used at BCMR. Twelve plots were established within the kelp forest at SWC. Six of these twelve plots were randomly chosen to be “no canopy” treatments. All canopy-forming kelps were removed from these plots in March 2008, and divers periodically removed any new juvenile, canopy forming kelps as well as the reproductive fronds of *Cystoseira osmundacea*. This prevented a canopy from forming within these plots during the experiment. A canopy was allowed to form naturally in the remaining six “canopy” plots.

Within each plot, six subplots were established, each 1 m in diameter. During the fall of 2007, three of the subplots within each plot were randomly selected as “scraped” treatments, and were cleared by divers using a combination of knives and paint-scrapers. The remaining subplots were marked but otherwise left as an unmanipulated "understory" treatment.

This split-plot design created four distinct treatments in SWC: Understory/with canopy, scraped/with canopy, understory/no canopy, and scraped/no canopy are equivalent to the same four treatments created inside the *Nereocystis* bed at BCMR. In addition to these four treatments shared between the two study sites, an additional factor was created at SWC to test whether recruitment of *Nereocystis* was limited by dispersal and successful settlement. A total of six plots (three canopy and three no-canopy) were 'seeded' with reproductive *Nereocystis* sori during the fall of 2007. Ripe sori from several different reproductive *Nereocystis* sporophytes were collected from a population located about 0.5 km from the experimental plots. These sori were mixed together to reduce selfing and placed into mesh bags. The mesh bags, weighted by large granite cobble, were placed directly on top of all six subplots (scraped and understory). These mesh bags were allowed to sit on the bottom for ~72 hours before being retrieved by divers. This 'spore seeding' was repeated twice during Fall 2007, and was similar to the method used by Dayton et al. (1984). This "seeding" of substrate served to determine whether successful zoospore settlement was limiting subsequent recruitment. However, when analyzing *Nereocystis* recruitment this doubled the number of treatments (i.e. "seeded, scraped/no canopy" and "not seeded, scraped/no canopy") and reduced the sample size by half.

Pterygophora density was estimated during Fall 2007 utilizing the same methods used at BCMR (2 x 10 m band transect, n=3). Basic algal cover was measured during May 2008. Algal cover was determined by a simple Random-Point-Contact method. A rigid PVC bar, 0.5 m in length, was haphazardly placed across the center bolt of the "understory" subplots. This rigid bar had a string with five knots serving as "points". At each point the diver would pull the string taut above and below the bar and record whatever species fell under those two points. The bar would then be rotated 90º and the process repeated, giving a total of 20 random points in each subplot. Because the "scraped" plots were routinely disturbed and removed of fleshy algae, only the unmanipulated "understory" plots were sampled using this method.

Statistical Methods

All data were analyzed using SPSS v.16.0.1 statistical package for Mac. Species studied had known recruitment strategies that varied from continuous to extremely limited in time. The primary interest was in the effect of the canopy and understory on recruitment of *Nereocystis* rather than in the difference in recruitment of one species between months. Whenever recruits were observed in all treatments a Split-level ANOVA (type III) was used (Appendix X). The assumption of normality was confirmed using a Kolmogorov-Smirnov test , whereas the assumption of equal variances was assessed by examining the residuals. When the assumption of equal variances was not met, the data was log-transformed. In the cases where one or more treatments failed to yield any recruitment a one-way ANOVA was used, because a split-level ANOVA cannot be run when one or more treatments yields a value of zero. When a one-way ANOVA demonstrated a significant difference between treatments, a post-hoc LSD test was used to determine which treatments differ.

Results

Big Creek Marine Reserve

The algal assemblages at BCMR were dominated by two kelps, the perennial understory kelp *Pterygophora* and the annual canopy producing kelp *Nereocystis*. The densities and large individual sizes of these two species far exceeded the abundance of all other macroalgae. Adult *Pterygophora* density as measured in Fall 2007 was 9.2 individuals/m^2 (+/- 1.7 SE). While only a subsample of plants were directly measured, many of these individuals exceeded 150 cm TL, with one individual observed to be 210 cm. The understory canopy created by the *Pterygophora* plants was dense, often approaching 100% cover; it was difficult or impossible to see the substrate or any turf algae from directly above these plants. Stipe ring counts indicated that the average age of these *Pterygophora* plants was 3.9 years (+/- 1.7 SE, n=30).

Being an annual, it's unsurprising that *Nereocystis* went from low to high densities within a few months. While a few sporadic and highly battered individuals were observed from the surface to have overwintered, not a single *Nereocystis* sporophyte was observed during a survey dive in March 2008 within the ten, 10 m diameter plots (0 individuals in 790 m^2). By the August sampling, the density of *Nereocystis* adult plants within the five canopy treatments had reached 0.29/m^2 (+/- 0.05 SE), or about one plant every 3.5/m^2.

RPC data conducted within the "understory" treatments in June 2008 showed that most of the substrate was covered by sessile invertebrates or encrusting algae.

These encrusting species covered 68% of all available space (Figure 2). Geniculate corallines dominated all erect algal species (16% total cover). Non-calcified, fleshy red algae accounted for 9% of all surface cover, and kelp holdfasts and *Desmarestia* each occupied 6%. A few other species of brown algae (namely *Costaria costata*) were observed but were rare and patchy, and were not captured by the RPC method. The sessile invertebrate and encrusting algae categories were combined because a heavy layer of silt and low light under the *Pterygophora* canopy made identification of each species extremely difficult.

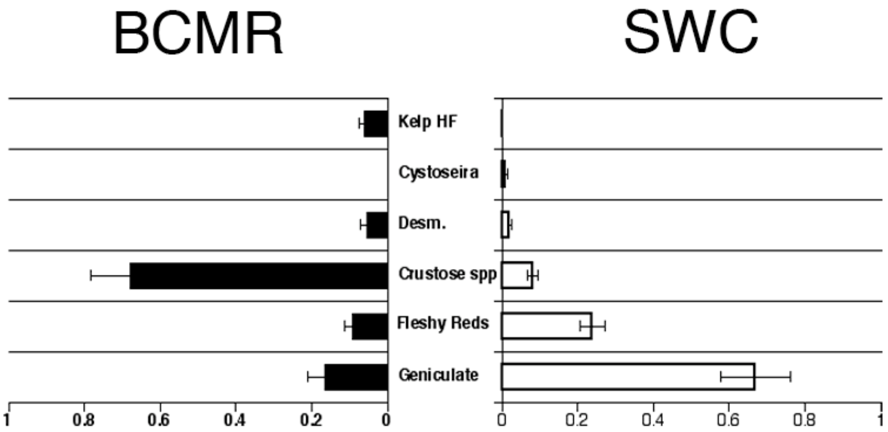

Figure 2: Total Percent Cover of algal functional groups between BCMR and SWC, Spring 2008 (mean of all 12 plots/site, with n=3 samples taken within each plot, +/- SE)

The *Nereocystis* canopy at Big Creek Marine Reserve developed predictably in 2008, first reaching the canopy in May and growing increasingly dense through the summer and into the fall (pers. ob.). *Nereocystis* recruits were observed in all treatments both in June and August of 2008, with recruitment greatest during the spring (Figure 3). Recruitment in June ranged from 17.5/m^2 +/- 4.2 SE inside the "scraped, with canopy" treatments to 1.1/m^2 +/- 0.6 SE inside the "understory/no canopy" treatments. During the June sampling, recruitment was significantly different and an order of magnitude greater in scraped plots than in plots where the understory had been left alone ($p<0.001$, Table 1). The presence of a canopy had no discernible effect on recruitment ($p=0.361$), despite numerous plants that had reached the surface within each plot. While overall recruitment was lower in August compared to June, the patterns of recruitment during August mimicked those seen earlier in the season. In August, recruitment was again greatest within scraped subplots ($p<0.001$).

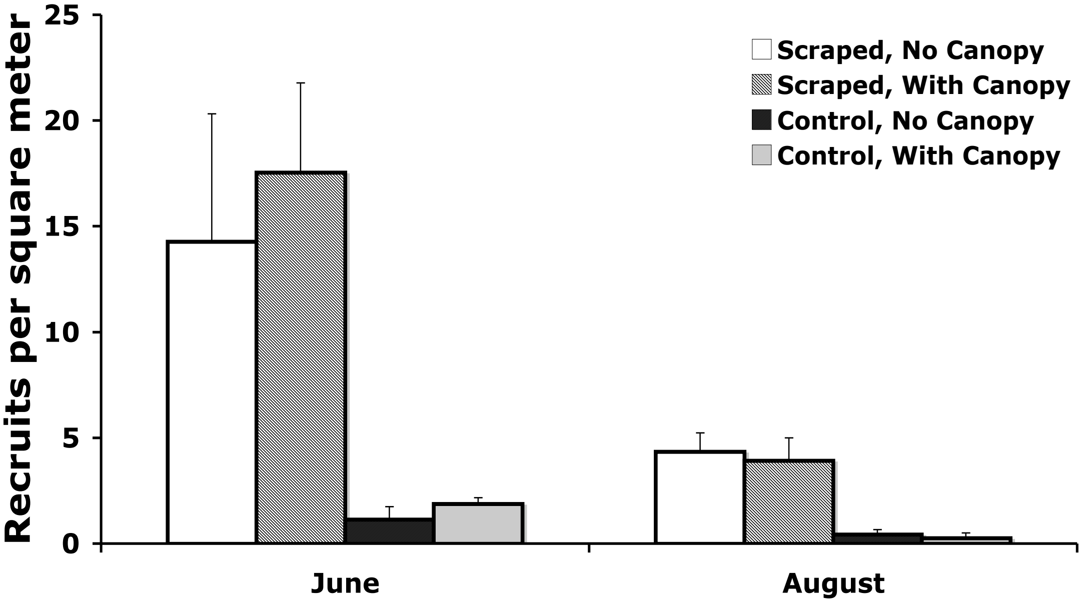

Figure 3. *Nereocystis* recruitment at BCMR sampled in 2008 (mean +/- SE, n=6).

There was no significant effect of the *Nereocystis* canopy on *Nereocystis* recruitment, and the interaction between canopy and understory was also not significant (p=0.361 in June and p=0.512 in August), suggesting the canopy never became dense enough to retard recruitment.

Recruitment of *Macrocystis pyrifera* at the Big Creek site was low throughout the experiment, with the number of recruits at or below 1/m^2 across all treatments and sampling periods (Figure 4). This low level of recruitment was consistent with an area with few nearby adult *Macrocystis* sporophytes.

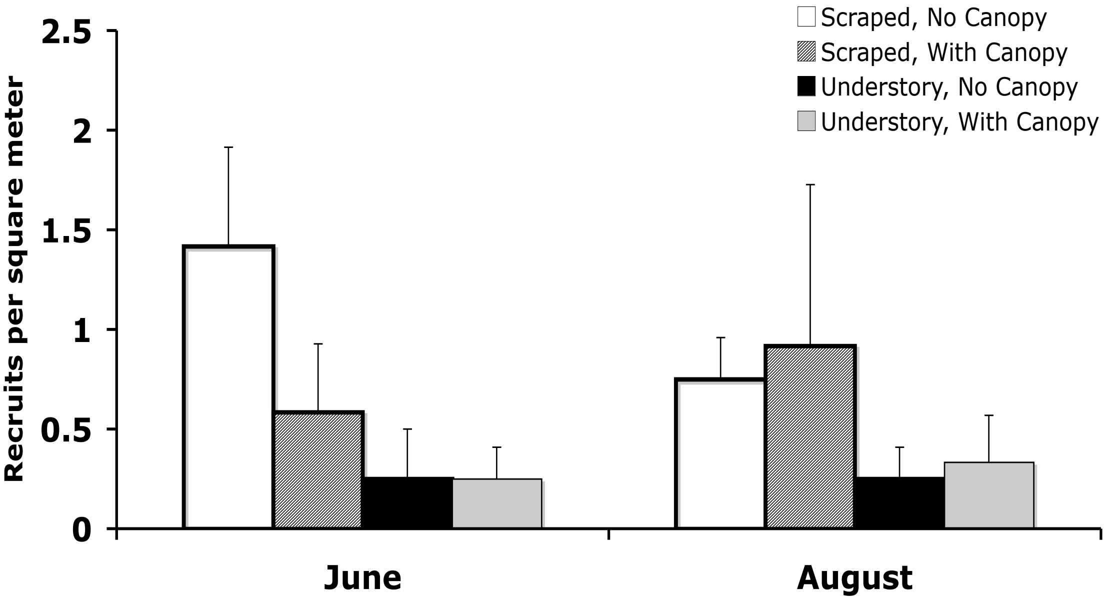

Figure 4: *Macrocystis* recruitment at BCMR sampled in 2008 (mean +/- SE, n=6).

During the June sampling, *Macrocystis* recruitment was significantly greater within scraped plots (p=0.005, Table 2). This difference was less distinct during the August sampling (p=0.051). As with *Nereocystis* recruitment, canopy had no significant effect on *Macrocystis* recruitment during the experiment.

Whereas *Desmarestia* had most of its recruitment during the June sampling, *Pteryogorphora californica* showed the opposite pattern (Figure 5). Recruitment of *Pterygophora* was very low during June, with the largest number of recruits occurring in "scraped/no canopy" plots (1.8 recruits/m^2, +/- 0.62 SE).

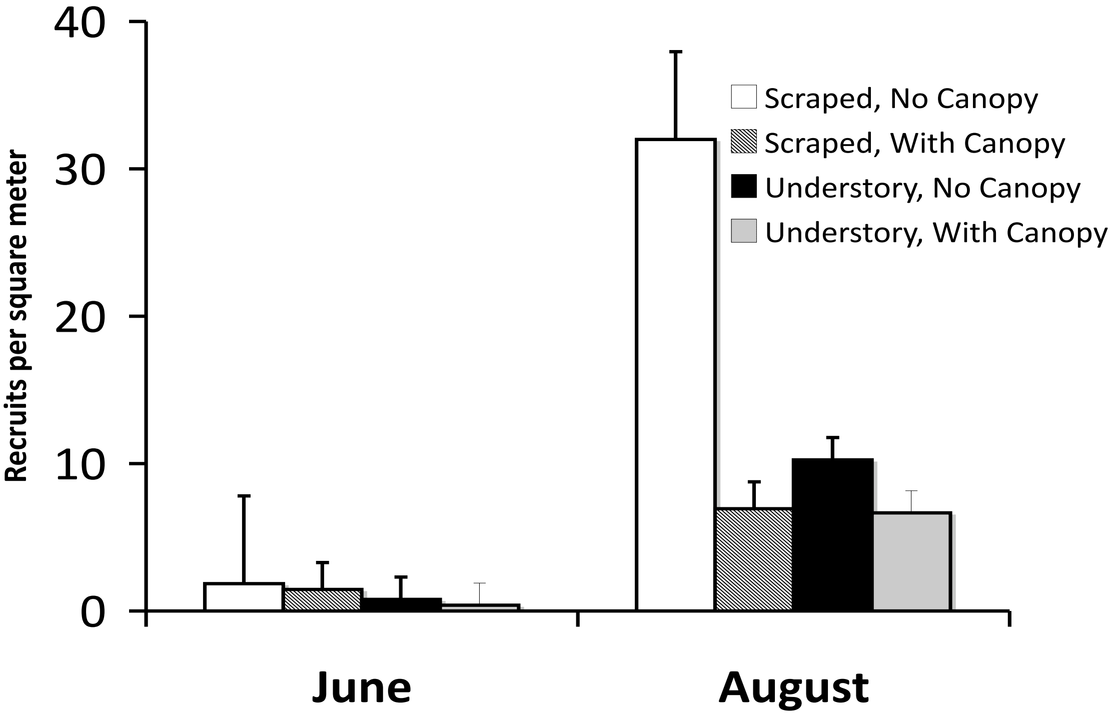

Figure 5: *Pterygophora* recruitment at BCMR sampled in 2008 (mean +/- SE, n=6). Scraped plots showed significantly greater recruitment than plots where the understory algae had been left intact (p=0.027, Table 3), however the presence of

the canopy was deemed non-significant during June (p=0.369). August recruitment of *Pterygophora* was more than an order of magnitude greater than June recruitment. During the August sampling period, the “scraped, no canopy” plots had at least twice the density of recruitment compared to any other treatment. Scraped plots had significantly greater recruitment than plots where the understory was left intact (p=0.001), and plots where canopy had been removed also showed significantly greater recruitment (p=0.001). Additionally, there was a strong interaction between canopy and understory with greatest recruitment occurring in locations where both had been removed (p=0.001). This pattern of August *Pterygophora* recruitment and a strong interaction between understory and canopy layers is consistent with other studies conducted in central California (e.g., Reed et al. 1996).

Desmarestia ligulata had the greatest recruitment per square meter of any Phaeophyceae during this experiment, with over 50 individuals/m^2 in some treatments during June (Figure 6). Recruitment was greatest during the June, and was greatest in the scraped plots (p<0.001, Table 4). August recruitment did occur within all plots, but recruits were not nearly as abundant as during the June sampling. Unlike *Macrocystis* and *Nereocystis, Desmarestia* recruitment was negatively influenced by the presence of a canopy in August (p=0.021). The effect of the newly formed spring canopy in June was less certain (p=0.130).

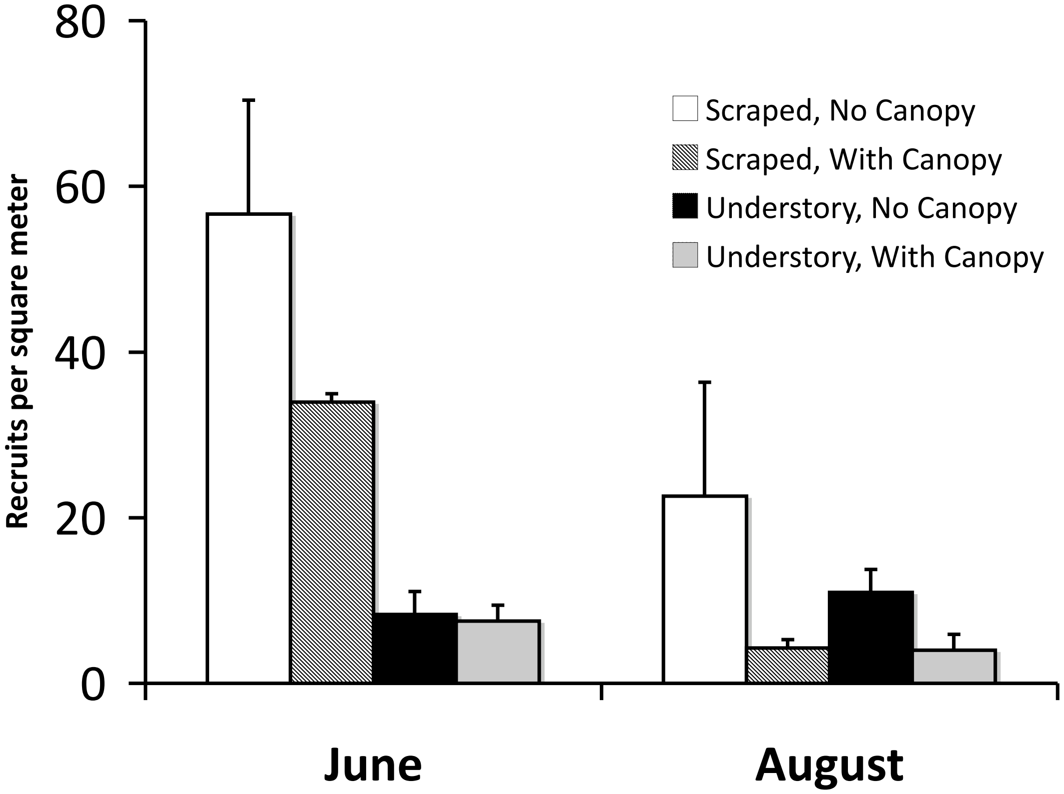

Figure 6: *Desmarestia* recruitment at BCMR sampled in 2008 (mean +/- SE, n=6).

Despite having fewer total recruits, there was a significant interaction between canopy and scraped plots during the August sampling period. This interaction can be explained by the fact that the majority of the recruits were observed in the "scraped, no canopy" treatment.

Table 1: Split-Level ANOVA (Type III) on the effects of Canopy and Understory on the recruitment of *Nereocystis* at BCMR. Months analyzed separately.

Date	**Source**	**df**	**MS**	**F Value**	**P**
May	Canopy	1	132.02	0.940	0.361
	Understory	1	4318.02	30.372	**<0.001**
	Canopy*Understory	1	62.02	0.436	0.512
August	Canopy	1	2.82	0.413	0.538
	Understory	1	312.82	45.871	**<0.001**
	Canopy*Understory	1	1.35	0.198	0.658

Table 2: Split-Level ANOVA (Type III) on the effects of Canopy and Understory on the recruitment of *Macrocystis* at BCMR. Months analyzed separately.

Date	**Source**	**df**	**MS**	**F Value**	**P**
May	Canopy	1	1.67	1.020	0.342
	Understory	1	13.07	8.553	**0.005**
	Canopy*Understory	1	0.60	0.393	0.534
August	Canopy	1	0.15	0.069	0.799
	Understory	1	6.02	3.989	**0.051**
	Canopy*Understory	1	3.75	2.486	0.121

Table 3: Split-Level ANOVA (Type III) on the effects of Canopy and Understory on the recruitment of *Pterygophora* at BCMR. Months analyzed separately.

Date	**Source**	**df**	**MS**	**F Value**	**P**
	Canopy	1	2.40	0.906	0.369
May	Understory	1	17.07	5.176	**0.027**
	Canopy*Understory	1	0.00	0.000	1.000
	Canopy	1	3081.67	29.885	**0.001**
August	Understory	1	1815.00	13.256	**0.001**
	Canopy*Understory	1	1728.07	12.621	**0.001**

Table 4: Split-Level ANOVA (Type III) on the effects of Canopy and Understory on the recruitment of *Desmarestia* at BCMR. Months analyzed separately.

Date	**Source**	**df**	**MS**	**F Value**	**P**
	Canopy	1	2076.82	2.621	0.144
May	Understory	1	20944.02	27.482	**<0.001**
	Canopy*Understory	1	1804.02	2.367	0.130
	Canopy	1	2406.67	6.225	**0.037**
August	Understory	1	508.07	6.228	**0.016**
	Canopy*Understory	1	481.67	5.681	**0.021**

Stillwater Cove

Prior to this experiment, the *Macrocystis pyrifera* bed at SWC suffered from an abnormally large series of swells the proceeding winter, including a storm event from December 1st through December 4th, 2007. This storm recorded sustained coastal swells in central California in excess of 30 feet (see Lewitsky et al. 2008 for partial review). As a consequence of this storm and the abnormally severe winter, absolutely no mature *Macrocystis* plants were present in or around the experimental plots when the experiment began in March 2008. By May, *Macrocystis* plants within the "canopy" treatments had reached the surface and begun to form a canopy. During the May sampling the number of *Macrocystis* sporophytes which had reached the canopy was 6.2 per plot (0.08/m^2). By July that number had increased to 9.1 individuals per plot (0.12/m^2). This density in July was consistent with the density reported in mature *Macrocystis* beds in the literature (Dayton et al. 1992), suggesting that, at least numerically, the *Macrocystis* population at SWC had recovered in about 7 months.

Overall, the algal assemblages at the two sites were very different. Excluding the canopy forming kelps, BCMR was dominated by large, dense *Pterygophora* plants growing above a variety of encrusting species. *Pterygophora* density measured during the fall, 2007 was significantly lower at SWC than BCMR (2.7 plants/m^2 +/-0.7 SE at SWC vs. 9.2 plants/m^2 +/- 1.7 SE at BCMR, $p<0.001$). Additionally, *Pterygophora* plants sampled at SWC (98 cm TL, +/- 3.9 SE) were significantly shorter than those at BCMR (152 cm TL, +/- 6.5 SE at BCMR. t-test; $p<0.001$, $n=30$)

Beneath the *Pterygophora*, the most abundant algae were geniculate corallines, which covered 66.9% of all available substrate (see Figure 2). Fleshy red algae also was common, with (23.8% of available cover). Unlike at BCMR, where the vast majority of the substrate was covered by encrusting corallines and sessile invertebrates, at SWC these species accounted for just 8.1% of all available space. The remaining algal cover was occupied by *Desmarestia* (1.9%) and the perennial fucoid *Cystoseira* (0.08%). Geniculate corallines and fleshy red algae combined accounted for about a quarter of the algae present. In contrast, SWC had about one third the density of *Pterygophora*, but over 90% of the substrate was covered by either fleshy or calcified corallines.

Overall *Nereocystis* recruitment was very low at SWC, never averaging more than 1.3 recruits/m^2 during any of the months sampled (Figure 7). Throughout all sampling periods, recruitment was only observed inside the two scraped treatments; no recruitment occurred inside plots where the understory algae had been left unmanipulated. This complete lack of recruitment within plots where the understory algae had been left in tact demonstrates competitive exclusion by understory algae on *Nereocystis* recruitment. Because recruitment only occurred within scraped plots, only the “scraped/canopy” and “scraped/no canopy” treatments were considered during analysis.

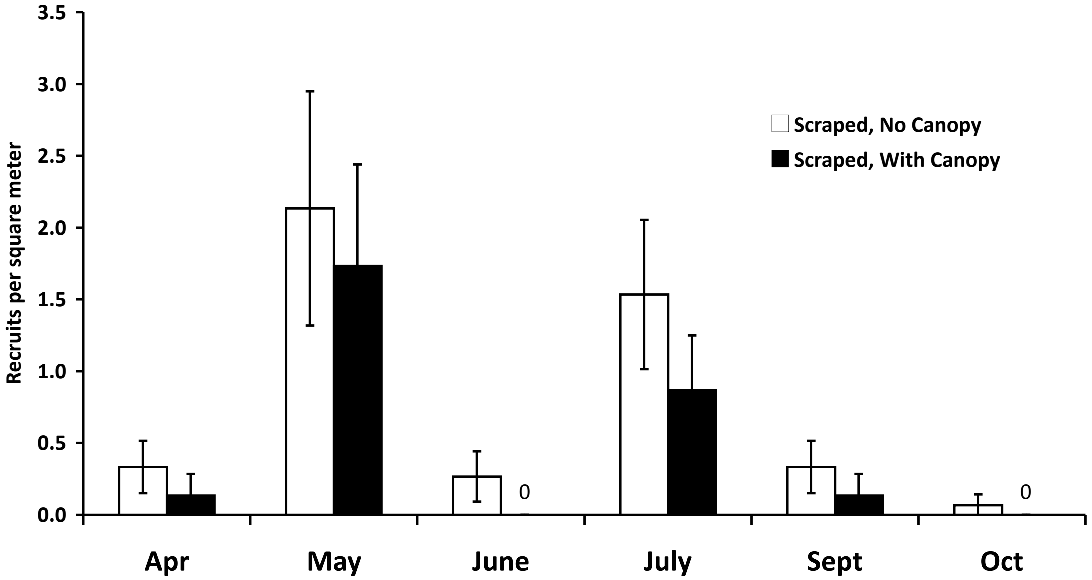

Figure 7: Recruitment of *Nereocystis* at SWC (mean +/- SE, n=6). Because *Nereocystis* recruitment was observed only within treatments where the understory had been removed, only the scraped plots are compared here.

During the fall of 2009, 32 of the small plots at Stillwater Cove were seeded with *Nereocystis* sori to examine the role of available propagules on subsequent recruitment, creating the following possible treatments: “seeded/no canopy,” “seeded/with canopy,” “unseeded/no canopy” and “unseeded/with canopy.” An independent t-test run between the two seeded treatments (p=0.400) and the two unseeded treatments (p=0.283) showed no significant difference between the “canopy” and “no canopy” treatments, regardless of whether they had been seeded or not (Table 5). A univariate ANOVA showed no significant interaction (p=0.379, Table 6) between canopy and seeded treatments. Therefore, to increase sample size when comparing the seeding effect, all seeded plots were pooled, as were all unseeded plots, eliminating the “canopy” and “no canopy” distinctions when comparing the effect of seeding plots on *Nereocystis* recruitment.

The greatest number of recruits were observed during May, with a second peak of recruits in July. In five out of the six months sampled, plots that had been seeded with *Nereocystis* sori the previous year yielded more *Nereocystis* recruits than plots that received no added reproductive material. Of these five, recruitment was significantly greater at the beginning of the survey, and during the final two months. The only month in which seeded plots did not have greater recruitment was during June, which showed anomalously low recruitment in both treatments, and marginally greater recruitment in the unseeded treatment.

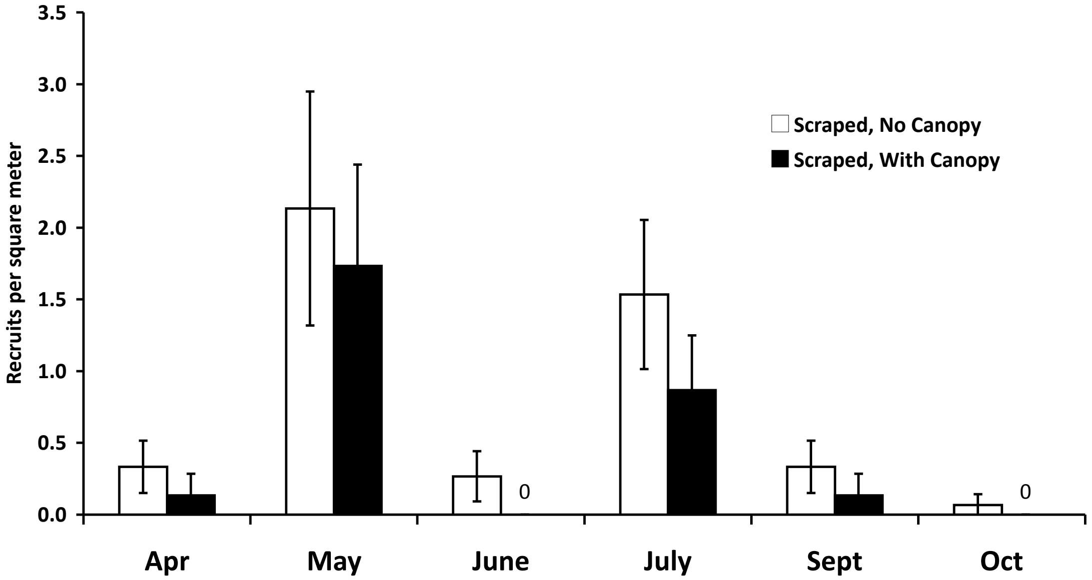

Figure 8: Recruitment of *Nereocystis* at SWC between plots seeded with additional zoospores in Fall 2007 and control ("unseeded") plots. This graph includes plots where the understory had not been removed, even though no recruitment occurred within either the "seeded, understory" or "not seeded, understory" treatments (mean +/- SE, n=5).

The "background" level of *Nereocystis* recruitment at Stillwater Cove (e.g. the recruitment which occurred in plots un-augmented by sori the previous year) was also analyzed. For this analysis only "un-seeded" plots were utilized. Because no recruitment ever occurred in the two "understory" treatments, an independent-samples T test was used to compare the two remaining treatments: "unseeded/with canopy" and "unseeded/without canopy." Recruitment was observed during all six sampling periods, demonstrating that *Nereocystis* can recruit during the spring, summer and fall without external propagule sources. Despite lower recruitment overall, the pattern of recruitment was similar to the recruitment of seeded plots, with two peaks of recruitment occurring in May and again in July (see Figures 7 & 8). Once the seeded plots were taken out of the model, the role of the *Macrocystis* canopy became apparent. During the first two months the canopy had no discernible effect on *Nereocystis* recruitment at SWC. However, every month from June onward had significantly greater *Nereocystis* recruitment within the "no canopy" treatment, with no recruitment occurring in the canopy treatment during the final two months of sampling (Table 6).

Recruitment of *Macrocystis pyrifera* in SWC was higher than *Nereocystis luetkeana* during all months sampled (Figures 7 & 9), with recruitment showing two peaks, the first in May and the second in July.

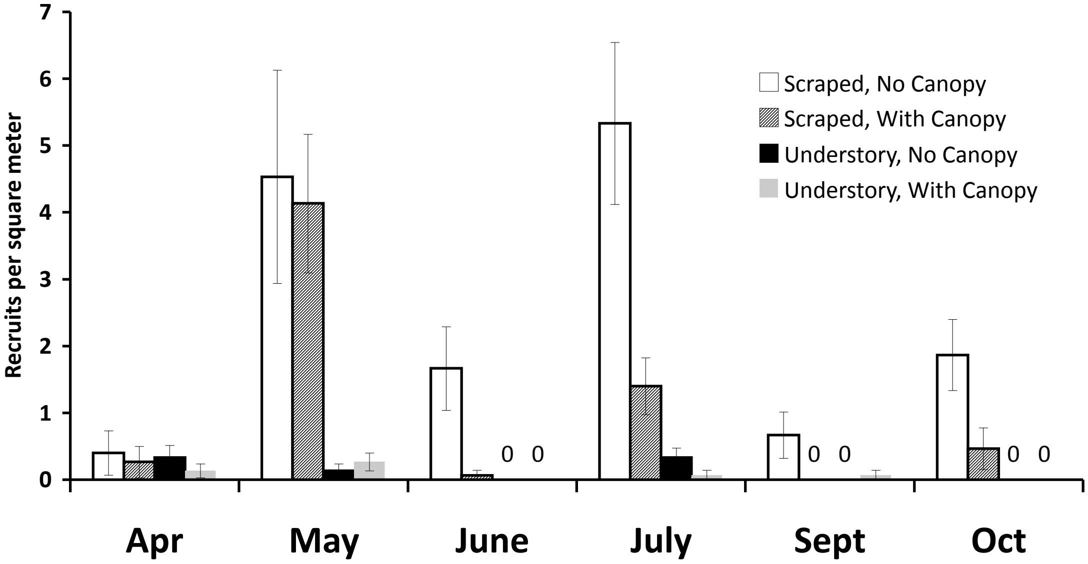

Figure 9: Recruitment of *Macrocystis* at SWC in 2008 (mean +/- SE, n=6)

During all months sampled, the “scraped/no canopy” plots showed the greatest recruitment, and “understory/canopy” treatments had either the lowest recruitment or were not significantly different than the lowest treatment for that month (Table 7a). Because recruitment was not observed in some month/treatment combinations, certain months were analyzed using a one-way ANOVA (Table 7b). April showed the lowest recruitment overall, with no significant difference between any of the treatments. Recruitment of *Macrocystis* increased about an order of magnitude in May, with significantly greater recruitment within the scraped plots. The canopy clearings showed no significant difference compared to controls during the month of May. June showed a marked decrease in overall recruitment. The “scraped/no canopy” treatment had significantly greater recruitment than all the other treatments, however the remaining treatments were not significantly distinct from one another, and only a single recruit was observed in any of these other treatments in June (n=45). July showed a second spike in *Macrocystis* recruitment, with the “scraped/no canopy” plots again showing the greatest recruitment. Both the scraped and canopy treatments were significant along with an interaction between these factors. July was the only month sampled where each treatment was significantly different from the others. Recruitment was significantly greater in the “scraped/no canopy” treatment than in the three other treatments, which were not statistically distinguishable from each other and showed decreased recruitment relative to the previous month. Recruitment continued through October, and followed a pattern very similar to September.

The first recruits of *Pterygophora californica* were not observed in Stillwater Cove until May, and recruitment was dominated by a single large event during the month of July (Figure 10). The four recruits observed during the May sampling were all within the "scraped/no canopy" treatment and, curiously, were all found in the same single plot. Despite the low statistical certainty of these four clustered recruits, the May sampling shows a similar pattern seen in subsequent months, with the "scraped/no canopy" treatment receiving the bulk of new *Pterygophora* recruits.

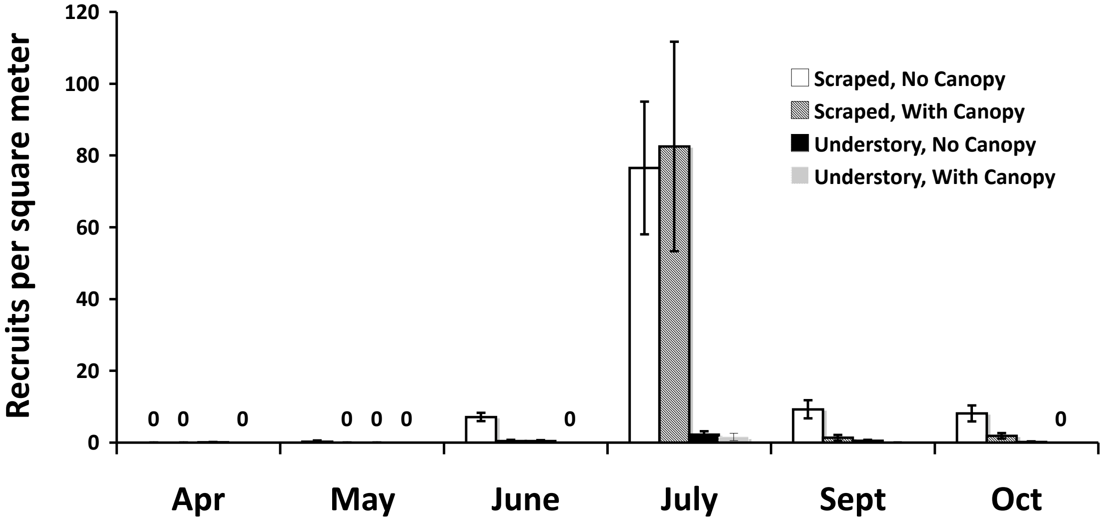

Figure 10: *Pterygophora* recruitment at SWC in 2008 (mean +/- SE, n=6)

In fact, during June and October the "scraped/no canopy" treatments have significantly greater recruitment than the other three treatments, and the remaining three treatments are not significantly different from each other (Table 8a). *Pterygophora* recruitment in July was significantly greater in scraped plots, but was not affected by the presence of the same *Macrocystis* canopy that had negatively effected *Macrocystis* recruitment. However, recruitment in September showed that both the canopy and understory were significant, along with the interaction of these two treatments.

Desmarestia ligulata recruits were observed in all treatments and during all months sampled in Stillwater Cove. Overall recruitment was greatest during the spring and slowly decreased towards the fall (Figure 11). With the exception of *Pterygophora* recruitment in July, *Desmarestia* showed greater recruitment than any other brown macroalgae in this study. In all months recruitment was highest in the “scraped/no canopy” treatment and was generally lowest in the “understory/canopy” treatment (i.e. there was never another treatment which was statistically lower, Table 9).

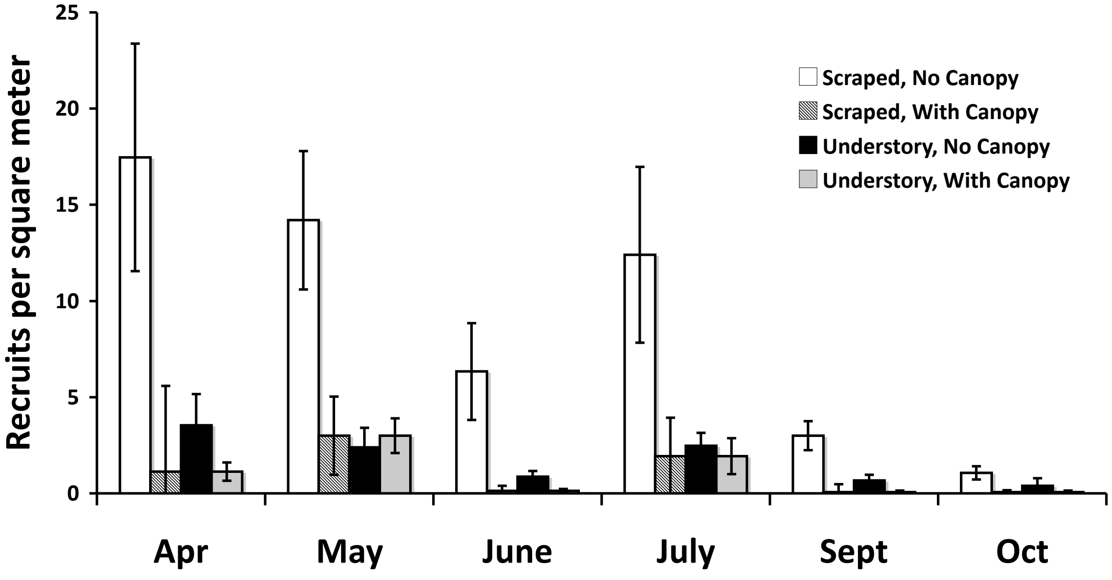

Figure 11: *Desmarestia* recruitment at SWC in 2008 (mean +/- SE, n=6)

The highest values of recruitment for *Desmaresita* occurred in the April "scraped/no canopy" treatment (17.4 recruits/m^2 +/- 8.1 SE), and often occurred in discrete patches within the plot (pers. ob.). Scraped plots had significantly greater recruitment than control plots, but in April the canopy treatment was not significant. The same observations occurred in May, where scraped plots had significantly greater recruitment, and canopy was not a factor. In June the average recruitment for each plot was lower than it was in either April or May, however for the first time in this study the canopy treatment had a significant effect on *Desmarestia* recruitment; plots where the canopy had been removed had greater recruitment than plots where the *Macrocystis* canopy had been allowed to develop normally. Likewise, there was a significant interaction between the Canopy and Understory factors, suggesting an additive effect of the algal layers on recruitment. July continued to show significantly higher recruitment within scraped plots, but the role of the canopy was less obvious than in the previous month. By September the recruitment of *Desmarestia* within the "scraped/no canopy" treatment was about 17% of where it was in the spring, and the other treatments showed an even lower percentage of maximum recruitment. However, both the understory treatment and the canopy treatment were significant, as well as the interaction between these two algal layers. By October recruitment was very low with many plots showing no recruits at all, but the absence of a canopy and the absence of understory algae (scraped plots) continued to show a significant positive relationship

Table 5: Independent Samples t-Tests comparing recruitment of *Nereocystis* in SWC between plots seeded with additional zoospores and plots with no additional input of reproductive material (all treatments pooled).

Date	**df**	**F**	**t**	**P**
April	58	7.314	-1.407	0.009
	36.094		-1.297	
May	58	2.245	-0.876	0.139
	37.046		-0.813	
June	58	2.632	0.786	0.110
	55.01		0.886	
July	58	0.001	0.084	0.975
	48.515		0.083	
September	58	8.994	-1.407	0.004
	27.834		-1.211	
October	58	2.81	0.814	0.099
	35		1	

Table 6: Independent Samples t-Test. Recruitment of Nereocystis at SWC between Canopy and No-Canopy treatments. To avoid possible a potentially counfounding factor, only non-seeded plots were used in this analysis.

	df	**F**	**t**	**P**
April	34	2.154	0.702	0.151
May	34	0.669	0.275	0.419
June	34	40.8	-2.545	**<0.001**
July	34	3.006	-1.04	**0.092**
Sept	34	28.333	-2.129	**<0.001**
October	34	9.973	-1.435	**0.003**

Table 7a: Split-Level ANOVA (type III) on the effects of Canopy and Understory on the recruitment of *Macrocystis* at SWC. Months analyzed separately.

	Source	**df**	**MS**	**F**	**P**
April	Canopy	1	0.417	0.633	0.449
	Understory	1	0.15	0.254	0.616
	Canopy*Understory	1	0.017	0.028	0.867
May	Canopy	1	0.267	0.023	0.884
	Understory	1	256.267	24.767	**<0.001**
	Canopy*Understory	1	1.067	0.103	0.750
July	Canopy	1	66.15	9.885	**0.014**
	Understory	1	150.417	33.17	**<0.001**
	Canopy*Understory	1	40.417	11.118	**0.002**

Table 7b: One-Way ANOVA on the effects of Canopy and Understory on the recruitment of *Macrocystis* at SWC. Months analyzed separately. A post-hoc Fisher's LSD test was used to determine which factors were significant for all three months.

	Source	df	MS	F	P
June	Between Groups	3	10.156	8.849	**<0.001**
	Within Groups	56	1.148		
	Total	59			
Sept.	Between Groups	3	1.572	4.344	**0.008**
	Within Groups	56	0.362		
	Total	59			
Oct.	Between Groups	3	1.572	4.344	**0.008**
	Within Groups	56	0.362		
	Total	59			

Table 8a: Split-Level ANOVA (type III) on the effects of Canopy and Understory on the recruitment of *Pterygophora* at SWC. Months analyzed separately.

	Source	df	MS	F	P
July	Canopy	1	109.35	0.043	0.841
	Understory	1	90404.02	25.076	**<0.001**
	Canopy * Understory	1	163.35	0.045	0.832
Sept	Canopy	1	256.27	5.694	0.044
	Understory	1	365.07	22.005	**<0.001**
	Canopy * Understory	1	216.6	13.056	**0.001**

Table 8b: One-Way ANOVA on the effects of Canopy and Understory on the recruitment of *Macrocystis* at SWC. Months analyzed separately. A post-hoc Fisher's LSD test was used to determine which factors were significant for June and October.

		df	**MS**	**F**	**P**
May	Between Groups	3	0.267	1	0.400
	Within Groups	56	0.267		
	Total	59			
June*	Between Groups	3	176.31	41.300	**<0.001**
	Within Groups	56	4.269		
	Total	59			
Oct*	Between Groups	3	218.328	13.864	**<0.001**
	Within Groups	56	15.748		
	Total	59			

Table 9: Split-Level ANOVA (type III) on the effects of Canopy and Understory on the recruitment of *Desmarestia* at SWC. Months analyzed separately.

	Source	**df**	**MS**	**F**	**P**
April	Canopy	1	228.15	0.619	0.454
	Understory	1	2318.817	17.413	**<0.001**
	Canopy * Understory	1	33.75	0.253	0.617
May	Canopy	1	6.667	0.111	0.748
	Understory	1	1664.267	30.975	**<0.001**
	Canopy * Understory	1	24.067	0.448	0.507
June	Canopy	1	153.6	8.098	**0.022**
	Understory	1	135	7.229	**0.010**
	Canopy * Understory	1	91.267	4.887	**0.032**
July	Canopy	1	86.4	2.544	0.149
	Understory	1	976.067	11.806	**0.001**
	Canopy * Understory	1	52.267	0.632	0.430
Sept	Canopy	1	33.75	14.727	**0.005**
	Understory	1	30.817	12.585	**0.001**
	Canopy * Understory	1	12.15	4.962	**0.031**
Oct	Canopy	1	6.017	6.224	**0.037**
	Understory	1	2.017	2.584	0.115
	Canopy * Understory	1	1.35	1.73	0.195

Discussion

Nereocystis luetkeana is an extremely large and conspicuous alga commonly found along rocky, wave swept shorelines in central California. Considered a canopy-forming annual with a limited recruitment window, the factors controlling the recruitment of this kelp have largely been inferred from studies of other Phaeophyceae, including *Macrocystis pyrifera, Pterygophora californica*, and *Desmarestia ligulata*. However, there is reason to question these extrapolations: *Macrocystis* is a canopy forming kelp, but it is a perennial with well-established, year round recruitment potential. *Pterygophora* has been shown to have a very limited recruitment window, but it too is a perennial and does not grow to the surface. *Desmarestia* is an annual with a surmised spring recruitment period, but it is neither a kelp nor a canopy-forming alga. Finally, the recruitment potential of brown seaweeds, and of kelps in particular, has been frequently linked to a short dispersal distance. A short dispersal distance, coupled with the limited persistence of microscopic stages proposed by Reed (1990) could be strong factors in the persistence and expansion potential of an annual kelp.

To best quantify the recruitment potential of *Nereocystis*, two experimental sites were used: one within a *Nereocystis* bed (with a presumably large propagule bank), and one inside a *Macrocystis* bed at Stillwater Cove. To further address the propagule supply question, select experimental plots within Stillwater Cove were supplied with reproductive material, or "seeded," the year prior. Not only did this allow comparison of *Nereocystis* recruitment between sites and degrees of propagule supply, but it also permitted direct comparison of recruitment between different species of algae. Similarities in recruitment could suggest similarities in life-history strategies and ultimately may help describe why *Nereocystis* persists in certain locations and fail to expand into other, apparently suitable locations.

Recruitment of *Nereocystis* was highest within the *Nereocystis* bed at Big Creek Marine Reserve, lending credence to the idea that recruitment was influenced, at least in part, by propagule supply, and that the benthos at Stillwater Cove has not been saturated with *Nereocystis* zoospores. Indeed, the plots "seeded" with *Nereocystis* sori the previous year generally had greater recruitment. The exception to this trend was during the June sampling, when seeded plots had a slightly lower density of recruits; however the certainty of this relationship was not robust ($p=0.11$, table 2a). Additionally, even within seeded plots the level of recruitment at Stillwater Cove was about an order of magnitude lower than the maximum recruitment at Big Creek Marine Reserve.

These data suggested that, while seeding did increase the density of microscopic gametophytes at SWC, they were still far from reaching saturation. It has been estimated that a single *Nereocystis* plant can release between 10^9 and 10^{12} spores over the course of a single season (Neushul et al. 1976), with survivorship presumably extremely low. The amount of reproductive material placed into each mesh bag was not precisely measured, but included a single soral patch from five different adults. It was a reasonable assumption that these five soral patches offered several orders of magnitude less propagules than the reproductive output of a large sporophyte integrated over an entire season. This 'seeding' method was chosen because of its ease of execution and previous, successful use in the scientific literature with the perennial kelp *Macrocystis* (e.g. Dayton et al. 1984).

The marginal increase in recruits within seeded plots throughout this experiment may be due to a combination of limited contact time (~72 hours) or possibly the competency of the selected sori. This idea of reduced competency has been shown for other annual kelps in central California. Despite the presence of reproductive blades during several months, *Alaria marginata* has been shown to have reproductive output change several orders of magnitude in a single month (McConnico and Foster 2005). It is possible that *Nereocystis*, another annual kelp, also demonstrates such a wide range of reproductive output, and that the selected sori were simply not very fecund.

Finally, it is possible that sufficient propagules from the mesh bags successfully settled onto the benthos, but another, untested factor prevented the large recruitment pulse seen at Big Creek from occurring at Stillwater Cove. *Pterygophora* has been shown to reduce recruitment of other species of kelp via interspecific competition, most likely related to pheromone swamping (Reed 1990). Given the high density of *Pterygophora* sporophytes and recruits at both sites, it seems unlikely that *Pterygophora* would retard *Nereocystis* recruitment at one site and not at another. A more reasonable suspect would be *Macrocystis*, which was abundant at Stillwater Cove and rare at Big Creek Marine Reserve. The implications of interspecific competition of gametophytes and propagule saturation on the persistence of two habitat forming, canopy producing kelps warrants further investigation.

On a community level, a dense *Nereocystis* canopy did not retard its own recruitment. The scientific literature is replete with examples of a dense *Macrocystis* canopy retarding the *Macrocystis* recruitment (Dayton et al. 1984, 1992, Foster and Scheil 1984, Reed and Foster 1984, Clarke et al. 2004). This influence on recruitment is most often attributed to physical shading, with the canopy capable of reducing surface irradiance to ~1% of surface irradiance (Edwards 1998, Clark et al. 2004). However, during the experiment *Macrocystis* recruitment under the *Nereocystis* canopy showed no significant difference when compared to recruitment in plots where the *Nereocystis* canopy had been removed. In fact, during the August sampling the greatest density of recruits occurred in the "scraped, with canopy" treatment, although this was not statistically distinguishable from the "scraped, no canopy" treatments.

The role of the *Nereocystis* canopy cannot be fully discounted, because it did reduce the recruitment of both *Pterygophora* and *Desmarestia* during the August sampling. In both of these species, the treatments with no canopy yielded greater recruitment than the treatments that allowed the canopy to form naturally. Also, of the four treatments the "scraped, no canopy" treatment yielded >50% of all the observed recruits for both *Desmarestia* and *Pterygophora*. This suggested that the interaction between the removal of the understory and the removal of the canopy was driving the pattern of recruitment for these two seaweeds. Because we did not see this interaction with the *Nereocystis* recruitment, it appeared that *Nereocystis* behaved more like the canopy-producing perennial *Macrocystis* than either the spring annual *Desmarestia* or the understory perennial *Pterygophora*.

Two explanations can describe why *Macrocystis* recruitment was not negatively influenced by the *Nereocystis* canopy. First, *Nereocystis* likely never developed sufficient density to reduce the average benthic irradiance enough to retard gametogenesis. Previous studies on the fertility of female gametophytes relative to quantum irradiance have shown *Macrocystis pyrifera* requires less light than *Pterygophora* (Lüning and Neushul, 1978). The morphology of *Nereocystis* may help to explain why it does not reduce surface irradiance as easily as *Macrocystis.* A *Macrocystis* sporophyte is composed of blades on numerous stipes. When these fronds reach the surface they remain on the surface due to the pneumatocysts present at the base of each blade. In contrast, *Nereocystis* has a single, larger pneumatocyst, and as a result its blades tend to hang vertically in the water column instead of spreading outward.

The second explanation regarding why the *Nereocystis* canopy did not negatively influence the recruitment of either *Macrocystis* or *Nereocystis* may be canopy light "flecking." Swell and water motion can cause even a dense canopy to part and allow for flecks of light to reach the benthos (Wing et al. 1993). In a terrestrial rain forest, this "flecking" from the canopy can contribute up to 80% of the total light flux (Kusar and Coley 1993). Some species of seaweed seem better able than others to utilize these ephemeral increases in light (Brawley and Johnson

1991); it is possible that both *Macrocystis* and *Nereocystis* are capable of utilizing flecking better than *Pterygophora* or *Desmarestia.* Because of its exposed coastline and broad subtidal bench, BCMR may facilitate "flecking" more than at Stillwater Cove.

The *Nereocystis* bed at Big Creek Marine Reserve has a naturally high level of physical disturbance. The understory is dominated by the perennial *Pterygophora*. These plants are older, larger, and have a higher density than those found at SWC. However, beneath this subcanopy of *Pterygophora* plants the benthos is dominated (68%) by bare rock and crustose species. The low percent cover of fleshy algae beneath the *Pterygophora* layer suggest that these species are frequently dislodged, most likely via strong winter storms. The remaining crustose species appeared to be good recruitment surfaces for all of the kelps.

All four species recruited into the "understory, with canopy" treatment during both of the sampling seasons, suggesting that natural disturbance created enough bare space for recruitment to occur, even without any experimental manipulation. Within these control plots, recruits were often observed clustered in small areas of bare rock, which most likely resulted from a large kelp plant being ripped out the previous winter.

Recruitment, particularly by *Nereocystis*, was also observed directly on the stipes of adult *Pterygophora* plants. However, none of these recruits survived long enough to reach the canopy; the constant motion of *Pterygophora* in the swell appeared to dislodge these recruits as they grew. The presence of *Desmarestia* recruits inside the "understory, no canopy" treatment suggested that even this light-adapted (Clark 1996) annual had micro-habitats free of shading and physical abrasion from other algae. Interestingly, despite recruiting in fairly significant numbers within unmanipulated plots (several per m^2), *Desmarestia* was never observed to form the extremely dense sub-canopy assemblages seen in other experiments (Dayton et al. 1984, Edwards 1998, Clark et al. 2004). This presence of the juvenile stage but complete lack of adult dominance may be attributed to both the "whiplash" effect of the numerous large *Pterygophora* plants and to the frequent large swells that could dislodge the more delicate *Desmarestia*. Since recruits were removed from the scraped plots immediately after counting, it is uncertain whether these cleared areas would yield the classic dense *Desmarestia* mat observed elsewhere. However, visual surveys of large pilot clearings the previous year showed only a moderate abundance of *Desmarestia* adults.

As expected, *Pterygophora* recruited primarily during the summer, and recruitment was greatest in plots where both the canopy and the understory algae had been removed. While some recruits were observed during the spring sampling, the summer sampling yielded about 17x more. *Pterygophora* plants were prolific at Big Creek, often completely obscuring the substrate and forcing divers to bury themselves under their sub-canopy to sample each quadrat. Perhaps the most surprising thing about the *Pterygophora* recruitment data was that the maximum recruitment at BCMR was less than half of the maximum recruitment seen at Stillwater Cove, despite the greater abundance of adult sporophytes at Big Creek.

However, maximum recruitment at SWC occurred in July, which was almost a full month before Big Creek could be sampled. The reason for this delay was the Basin Complex Fire which burned 210 square miles and closed access to Big Creek Marine Reserve for 37 days, making July sampling impossible. Juvenile recruits have been shown to have a high mortality in their first month since detection: Dayton et al. (1984) estimated that ~16% of recruits were dislodged during a very benign month in July 1974. The lower recruitment observed at BCMR during this study could very well be attributed to the natural loss of recruits and the late sampling.

Desmarestia ligulata had the highest number of recruits at BCMR, and yet it was never observed to form the kind of dense, persistent adult populations that the other three species formed in the area. Recruitment during the spring exceeded 56 individuals/m^2 in the "scraped, no canopy" treatment. Even within the unmanipulated "understory, with canopy" treatment, recruitment of *Desmarestia* exceeded 7 per m^2, yet adult *Desmarestia* thalli were noticeably absent during the following sampling period, suggesting those recruits had been removed naturally. *Desmarestia* was also the only species sampled that was influenced by the presence of the *Nereocystis* canopy during both sampling periods. This is not particularly surprising considering *Desmarestia* has been classified as a light-adapted, spring annual (or even "ephemeral") seaweed. However, just the presence of this inverse relationship demonstrates that the *Nereocystis* canopy did become dense enough by June to have some effect on the seaweed assemblages.

Perhaps less expected was the recruitment of *Desmarestia* during the summer. Numerous studies have documented the potential for *Desmarestia* to recruit into disturbed areas in very high numbers during the early spring (Dayton et al. 1984, 1992, Reed and Foster 1984, Edwards 1998, Clark et al. 2004), at times forming dense assemblages capable of blocking the recruitment of most species of algae. However, the presence of new recruits in August, particularly in the unmanipulated “understory, with canopy” treatments was surprising. As with *Nereocystis*, it appeared that these “spring annuals” are not strictly limited to recruiting during the spring. A wider recruitment window could benefit the population in highly disturbed systems, where space could become available even during the summer months. Given the short time-frame between recruitment and sexual maturity, an August recruitment cohort could easily reach sexual maturity before the seasonal winter storms arrive. Whether these recruits arose from propagules released the previous season, or from plants that had recruited that spring, sexually matured and released propagules of their own is uncertain. *Desmarestia* gametophytes grown in laboratory conditions have been shown to reach macroscopic size in <40 days, (Edwards 1996), with the first recruits typically observed in early April (Edwards 1998). Following that time-line it is conceivable that a recruitment class could emerge in April, become reproductive by early June and release propagules which then would be macroscopic by August. It is also probable that the recruits observed in August originated from propagules released the previous season, and had simply not completed the microscopic gametophyte stage before the June sampling. Plants are continuously reproductive once reaching maturity and typically persist through until winter storms remove them, although some individuals can overwinter (Abbott and Hollenberg 1976). This wide window of propagule release from the previous generation may explain the correspondingly large window in recruitment.

Sampling at SWC offered fewer challenges than at BCMR due to its location, launch pier, and boat access during most of the year. As a consequence, it was sampled much more frequently than the BCMR site, which in turn created allowed for a monthly comparison of recruitment. *Nereocystis* recruitment at SWC was greatest in May, and showed a curious double-peak of recruitment in May and July. Overall plots seeded in 2007 with reproductive material yielded greater recruitment in 2008, and no recruits were ever observed in the plots where the understory algae had been left in tact. These data showcase a few differences between BCMR and SWC. First, the low overall recruitment suggested that propagules were either not arriving in sufficient numbers, or they were not surviving the microscopic life history stage. Second, the RPC surveys showed that, while the species compositions were similar, the availability of bare rock and custose corallines was significantly higher at BCMR than at SWC. Finally, the low recruitment even within the "scraped, seeded" plots suggests that the propagules released from a nearby, healthy adult population integrated over time may far exceed those which release from a few sori placed directly over the benthos.

As mentioned earlier in this discussion, the increased recruitment within seeded plots suggested that propagule supply was at least partly responsible for the lower recruitment of *Nereocystis* observed at SWC. Additionally, the presence of recruits very late into the season offered distinct evidence that *Nereocystis* was not limited to a narrow recruitment window. As with *Desmarestia*, the potential for an extremely fast-growing annual to recruit later in the season could be beneficial, particularly in the highly disturbed areas where it commonly persists. *Nereocystis* recruits can grow and become sexually mature in less than two months (Abbott and Hollenberg 1976), and individuals frequently persisted until the first large winter storm, and occasionally over-winter. The July recruitment pulse seen at SWC could provide the necessary propagules should a late spring storm remove the recruits observed in April and May.

After removing the seeded plots from the analyses, it was evident that *Nereocystis* recruitment was negatively effected by the presence of a dense *Macrocystis* canopy. During the summer and fall, recruitment was greater within "no canopy" plots, but not during the two spring months sampled. The likely reason why April and May did not show any reduced recruitment within canopy plots was that the canopy did not develop until late April. Large storms during the previous winter removed the canopy entirely, and no plants were observed to have reached the surface until the first sampling in May. In all, almost three quarters of the total *Nereocystis* recruitment (74.3%) in unseeded plots occurred during these first two months, suggesting that a particularly stormy winter may favor subsequent recruitment and recovery of a *Nereocystis* population.

The source of the double peak evident in the *Nereocystis* and *Macrocystis* recruitment at SWC was a source of great conjecture. Viewed in one manner there were two distinct 'pulses' of recruitment for both *Macrocystis* and *Nereocystis*, occurring in May and in July. Viewed a different way, recruitment was high during the spring and early summer, with simply a bad recruitment month in June. As discussed earlier, given the life-history and rapid growth of these two species it could be possible that April recruits could become reproductive by May, release propagules and, 40-60 days later observe recruitment from those propagules in July. However, since all *Nereocystis* occurred within scraped plots and were removed after sampling, (and no adult *Nereocystis* plants were observed nearby), this pattern could not explain the double-peak shown for *Nereocystis* recruitment. It is possible that June was simply a poor month for recruitment. It has been suggested that this decrease in June recruitment could be due to interspecific competition between microscopic stages, with *Pterygophora* a likely culprit.

Nereocystis luetkeana appears to be able to recruit and thrive in patches currently occupied by the dense perennial *Macrocystis*. However, its ability to do so seems dependent on two processes: sufficient disturbance to the benthos to create bare space, and the successful arrival and settlement of propagules, which appear to have a very short dispersal distance akin to other kelps. The presence of *Macrocystis* adults can retard recruitment later in the season, but as *Nereocystis* recruits more heavily in the spring this competitive dominance over the new recruits is likely of little importance. Instead, it is the density of understory seaweeds and the presence of nearby source of reproductive material that determines which species will persist in an area.

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