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Rosemary Romero
San Jose State University

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RECRUITMENT STRATEGIES OF *ULVA* AND *PORPHYRA* IN CENTRAL CALIFORNIA

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Master of Science

by
Rosemary Romero
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SAN JOSÉ STATE UNIVERSITY

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RECRUITMENT STRATEGIES OF *ULVA* AND *PORPHYRA* IN CENTRAL CALIFORNIA

by
Rosemary Romero

APPROVED FOR MOSS LANDING MARINE LABORATORIES

10/20/09
Dr. Michael H. Graham   Moss Landing Marine Laboratories   Date

James T. Harvey   10/20/09
Dr. James T. Harvey   Moss Landing Marine Laboratories   Date

10/20/09
Dr. Frederick W. Zechman   Fresno State University   Date

APPROVED FOR THE UNIVERSITY

2/5/10
Associate Dean   Office of Graduate Studies and Research   Date

ABSTRACT

RECRUITMENT STRATEGIES OF *ULVA* AND *PORPHYRA* IN CENTRAL CALIFORNIA

by Rosemary Romero

Ephemeral algae are early colonizers of the rocky intertidal zone after a disturbance, although the mechanism of early colonization (including benthic microscopic stages and waterborne propagules) is poorly known. Recruitment of the ephemeral *Ulva* spp. was studied in two types of disturbance manipulations (partial removal of all macroscopic organisms were removed vs. complete removal of all macro- and microscopic organisms) and an un-manipulated control at two tidal heights (high *Porphyra* zone and low *Mazzaella* zone). Replicate disturbances were created in August 2007, November 2007, January 2008, and May 2008 and were monitored until August 2008 on a rocky bench north of Pigeon Point, California. *Ulva* colonization by waterborne propagules (complete removals) was observed throughout the year, whereas *Porphyra* was restricted to spring recruitment, as expected due to temporal cues (changes in photoperiod) regulating propagule availability. Peak *Ulva* responses varied in treatments as a function of timing of clearing, whereas peak *Porphyra* responses varied in locations as a function of timing of clearing. Location and interactions with location (heterogeneity among zones) explained most of the variability in early colonization. Fall and winter clearings experienced opposing responses by *Ulva* and *Porphyra* in each zone. Further experimentation is needed to rule out a negative interaction between *Ulva* and *Porphyra* in fall and winter disturbances.

“After some time, I realized that heterogeneity and instability must not be considered as just a drawback of field data to be neglected ("averaged away" or "seen through by intuition") or circumvented by retreating into the laboratory because they are mere deviations from the "typical" or “representative" case (or even "noise"). On the contrary, heterogeneity and/or instability must be recognized as fundamental features of a natural situation.”

–Den Boer (1968)

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INTRODUCTION

Disturbance is a driving factor in structuring local patterns of diversity in natural communities that are limited by space (Dayton 1971). In the rocky intertidal zone, spatial and temporal variability in natural disturbance results in a mosaic of patches dominated by organisms with varying life histories (Sousa 1984). Initial recolonization of newly available space can occur either from propagules originating beyond the boundaries of the disturbed patches (long-range dispersal) or from other individuals in patches within the system (short-range dispersal) (Levin 1976). Several studies (Dayton 1973, Paine 1979, Sousa 1984) have provided evidence of short-range propagule dispersal (1-3m) by intertidal macroalgae but few have considered species, usually ephemeral species, with the potential for long-range dispersal (Amsler and Searles 1980, Sousa 1984a, Zechman and Mathieson 1985). The mechanisms by which ephemeral species colonize bare space, (including benthic microscopic stages, vegetative propagation, and water-borne propagules) is a critical component to understanding the dynamics of patch colonization.

Patterns of patch colonization and succession are products of the original disturbance and life histories of the colonizing organisms (Sousa 1984b). Members of the genera *Ulva* and *Porphyra* are some of the most conspicuous algae colonizing disturbed substrate on temperate rocky shores (Northcraft 1948, Cubit 1984, De Vogelaere 1991, Kim and DeWreede 1996). These common early colonizers share some common characteristics of opportunistic algae (simple thallus form and rapid growth (Littler and Littler 1980)), yet they utilize two fundamentally different life histories.

Ulva recruitment dynamics

Macroalgal species of the genus *Ulva* (Linnaeus) are simple, green, annual blades that are two cells thick or hollow cylinders that are one cell thick (Hayden et al. 2003). They usually have a perennial holdfast and can live in marine and brackish environments (Abbott and Hollenberg 1976, Lee 1999). *Ulva* species thrive in high nutrient and wave exposed environments, and are tolerant of stressful conditions (Lee 1999). Representatives of the genus exist worldwide in all oceans; ten species are found on the California coast (Abbott and Hollenberg 1976, Druehl 2000). They commonly appear in the rocky intertidal zone after disturbance has removed vegetation, creating newly available substrate (Emerson and Zedler 1978, Sousa 1979b, a, Dawson and Foster 1982, De Vogelaere 1991, Kim and DeWreede 1996). The genus is thus considered an opportunistic weed of rocky intertidal communities. Reproductive characteristics unique to this genus may be responsible for the alga's efficient recruitment after disturbance (Connell 1972, Connell and Slatyer 1977, Littler and Littler 1980).

The life history of *Ulva* spp. consists of an alternation of two morphologically identical macroscopic generations (Figure 1). These generations consist of blades attached to the substrate by a discoid holdfast and differ in ploidy: the gametophyte generation is haploid, whereas the sporophyte generation is diploid. Each cell in the thallus of both generations can become reproductive and release microscopic, flagellated, unicellular propagules. Twenty to sixty percent of overall biomass is allocated monthly to reproduction depending upon the season (Smith 1947, Niesenbaum 1988) and the allocation of biomass to the formation and release of propagules can be greatest when temperatures reach 21°C (Nordby 1977, Nordby and Hoxmark. 1972). Release of propagules, known as fruiting, is often driven by tidal/lunar cycles in intertidal species, with the most conspicuous release occurring within three days of a new or full moon (Smith 1947, Christie and Evans 1962), when temperatures reach seasonal highs (Niesenbaum 1988), and during spring tides (Smith 1947).

Ulva microscopic propagules released from the haploid generation are called gametes, which have an eyespot and two flagella. As reviewed by Smith (1947), *Ulva* gamete eyespots are positively phototactic, therefore both types (+ and -) are attracted to light and gather at the surface, making it easier for + and - gametes to find each other and fuse to form a zygote. Five species of *Ulva* common in the intertidal zone of central California are heterothallic (self-incompatible) but unfertilized gametes can develop into gametophytes parthenogenetically in culture (Smith 1947, Løvlie and Bryhni 1978). Once fertilization takes place, the zygote becomes negatively phototactic, settles to the substrate, and grows into a diploid sporophyte (Graham and Wilcox 2000). *Ulva* zoospores, the microscopic stage released from diploid sporophytes, have four flagella and an eyespot that is negatively phototactic. Zoospores do not undergo fertilization; zoospores must find the substrate and, once attached, grow into a haploid gametophyte. So for *Ulva*, it takes two gametes to make a sporophyte and one zoospore to make a gametophyte (Graham and Wilcox 2000), and both macroscopic stages release propagules into the watercolumn.

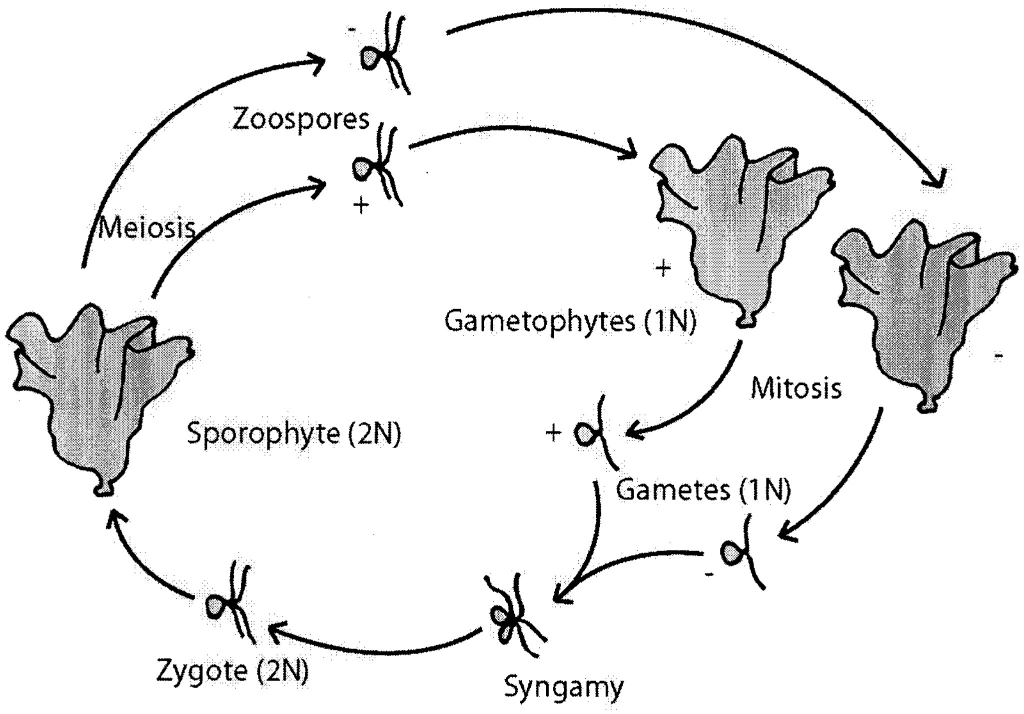

Figure 1. Isomorphic life history of all members of the genus *Ulva*.

Cultures of water samples collected 30 km off the coast of North Carolina resulted in germlings from the "enteromorpha" form of *Ulva* spp. (Amsler and Searles 1980). The genus represented 35% of cultured germlings from samples collected in summer (Amsler and Searles 1980). In another study, propagules of the "enteromorpha" form of *Ulva* spp. were present in water samples collected in estuaries, coastally, and 8 to 24 km offshore in the Gulf of Maine (Zechman and Mathieson 1985). Considering that *Ulva* macrothalli were rarely found offshore, the presence of propagules offshore indicates the potential for long-range dispersal (Amsler and Searles 1980, Zechman and

Mathieson 1985). A proposed explanation for the evolution of biphasic life histories is that the sporophytic generation and zoospores are adapted for dispersal in turbulent environments, whereas the gametophytic generation and gametes are adapted for genetic recombination under calmer conditions (Neushul 1972, Bell 1997). Gordon and Brawley (2004) found that *Ulva lactuca* zoospore and gamete release was stimulated by turbulent conditions, and suggested that the ability for unfertilized *Ulva* gametes to develop parthenogenetically was a way for the genus to increase dispersal potential in conditions unfavorable to fertilization. Positive phototaxis possibly increases the chances of resuspension in the water column (Amsler et al. 1992). The ability of both generations to fruit during periods of increased turbulence and the documented presence of propagules in the water column at great distances offshore, indicate this alga's life history is well suited for post-disturbance recruitment and may partially explain its appearance in areas lacking macrothalli.

In addition to *Ulva's* potential for long-range propagule dispersal, the ability of holdfasts to persist once blades have been removed may explain its swift recruitment of disturbed substrate (Abbott and Hollenberg 1976). The importance of overwintering microscopic stages to the recruitment of macroscopic stages has been documented in recent years (Blanchette 1996, Edwards 2000, Worm et al. 2001). Microscopic gametophytes of the annual macroalga *Desmarestia ligulata* overwinter when the macroscopic thalli are absent, and are the sole source of sporophyte recruitment (Edwards 2000). These microscopic gametophytes can enhance sporophyte recruitment more than a year after their settlement (Edwards 2000). Similarly, recruitment of sporophytes of the annual kelp *Postelsia palmeformis* in mid summer and spring is the result of overwintering under the protection of *Mytilus californianus* (Blanchette 1996). Microscopic gametophytes that settle on rocks beneath *M. californianus* have a greater chance of escaping grazers, leading to greater sporophyte recruitment than settlement to mussel valves (Blanchette 1996). Non-motile cells of *Ulva lactuca* sloughed from senescing plants give rise to new plants in culture (Bonneau 1978), and the presence of the "enteromorpha" form of *Ulva* spp. in the Baltic Sea during spring has been attributed to overwintering microscopic stages (Lotze et al. 1999, Worm et al. 2001).

Porphyra recruitment dynamics

Macroalgae of the genus *Porphyra* are widely distributed annual intertidal seaweeds found in temperate and polar waters (Lee 1999) and utilize a perennial microscopic generation in their life history (Drew 1954). *Porphyra perforata* (from here forward, *Porphyra*) is a member of the genus ranging from Alaska to Baja California that is seasonally abundant in the high intertidal of the California coast (Abbott and Hollenberg 1976, Foster et al. 1988). This species is extremely tolerant to desiccation, and the alga can withstand the loss of up to 90% of its wet weight during emersion (Dring and Brown 1982, Smith 1983). Additionally, this alga is able to persist in a wide range of salinities and thrives in eutrophic waters (Dixon 1973). These abiotic factors combined with seasonal variations in ambient temperature and photoperiod are crucial to the completion of this *Porphyra's* life history.

Porphyra also exhibits a heteromorphic life history, alternating between simple haploid blades (one to two cells thick) and shell-boring microscopic diploid filaments referred to as 'conchocelis' (Figure 2) (Drew 1954, Abbott and Hollenberg 1976, van den Hoek et al. 1995). This alternation of generations is timed to changes in photoperiod with investment in sexual reproduction/conchocelis production during longer photoperiods and investment in gametophyte production during shorter photoperiods (Figure 2) (Waaland et al. 1987, Dring 1988, van den Hoek et al. 1995). Both generations produce non-motile propagules in localized regions of the thallus (Dixon 1973). Release of carpospores by *Porphyra perforata* occurs when photoperiods exceed 12 hrs and at low temperatures coinciding with upwelling periods (Pacheco-Ruíz et al. 2005). Carpospores are the result of sexual fertilization and germinate to produce the diploid filaments of conchocelis. Conchocelis is perennial, continually producing monospores; that give rise to more conchocelis (Conway 1967, Chen et al. 1970). When photoperiods lessen (8-12 hrs of daylight), the production and release of conchospores is triggered at low temperatures (approx. 5°C) (Dring 1967, Chen et al. 1970, Waaland et al. 1987). Conchospores settle, germinate, and become the foliar macrothallus of *Porphyra*, completing the life cycle (Drew 1954, Chen et al. 1970). The macroscopic thallus is rapid growing, ephemeral, and often appears opportunistically in intertidal succession (Northcraft 1948, Dayton 1971, Lubchenco and Menge 1978, De Vogelaere 1991).

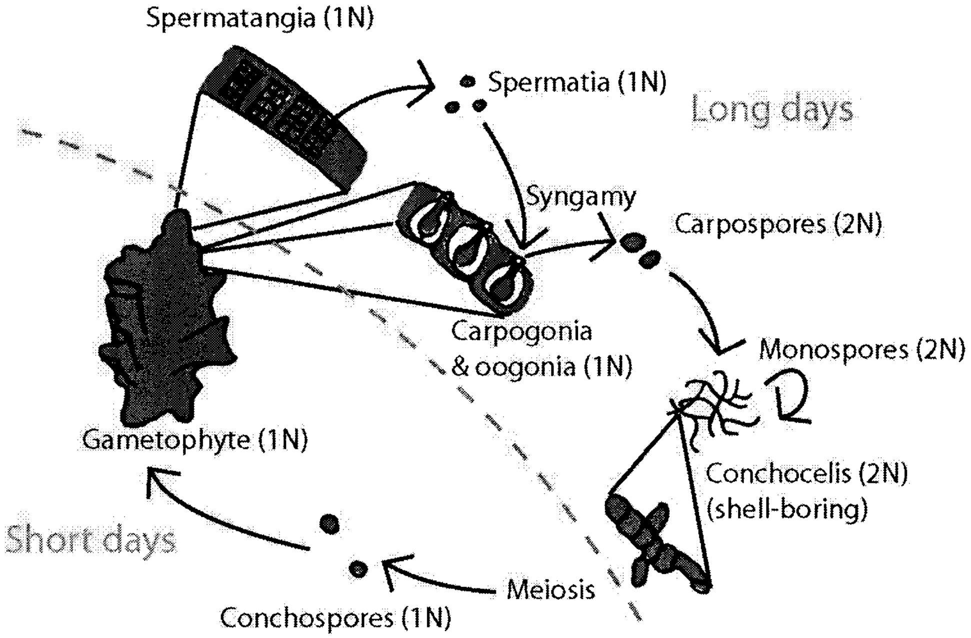

Figure 2. Heteromorphic life history of members of the genus *Porphyra*.

All three types of *Porphyra* microscopic propagules (gametes, carpospores, and conchospores) are non-motile, making them completely dependent on water motion for resuspension, settlement, and mate location (Amsler et al. 1992). Sheath and Hambrook (1990) proposed that turbulance resulting in eddy formation downstream of rocks in freshwater streams increases the probability of gamete fusion in red algae. Propagules of other members of the Bangiophycidae subclass, undergoing the same life history, were observed in summer months throughout the water column (0-20 m), 30 km off shore (Amsler and Searles 1980). The turbulent environment created as tides cycle, waves crash, and presence of propagules in offshore waters combined with a perennial life history stage may explain the colonization success of this alga on intertidal rocky shores.

Several hypotheses exist that explain the evolutionary retention of alternation of generations. In many cases heteromorphic alternation of generations is considered an adaptation to grazing pressure or temporally or spatially fluctuating environments (Lubchenco and Cubit 1980, Littler and Littler 1983, Zupan and West 1988). Conchocelis may provide a perennial seed bank within the substrate awaiting the proper conditions for macrothallus production and ensure the persistence of local populations regardless of dispersal potential.

Ulva vs. Porphyra disturbance response

Ulva and *Porphyra* are rapidly growing ephemeral seaweeds with very different life histories utilizing microscopic stages in similar ways. For an alga (such as *Ulva)* that can produce a vast amount of motile propagules and leave behind a perennial holdfast (post-fruiting), macroscopic recruitment to disturbed substrate can arise from two major sources. The first is recruitment from microscopic stages present on the substrate before the disturbance (fugitives) whose survival is contingent on the increase of available light caused by the removal of competing individuals. This includes propagules that have settled pre-disturbance and holdfasts that have been left behind by senescent thalli. The second is recruitment from microscopic stages in the water column. Similarly, *Porphyra* can recruit from conchocelis, which act as perennial fugitives awaiting shorter photoperiods for the investment in macrothalli. Whereas *Porphyra* does not invest the entire thallus in the production of propagules, and produce non-motile propagules, conchocelis is present and propagating itself year-round. As such, presence of macrothalli is independent of sexual reproduction. Disturbances that coincide in timing with seasonal releases of conchospores can provide opportunities for short-range dispersal of *Porphyra*. *Ulva* recruits throughout the intertidal zone and into the subtidal, whereas *Porphyra perforata* is limited to higher intertidal heights (Cubit 1984, Foster et al. 1988). Thus *Ulva* is capable of long and short-range dispersal throughout the intertidal zone, explaining its blooming potential whereas *Porphyra* is seasonal and may be limited to higher tidal heights and short-range dispersal.

Independent of dispersal potential, the major factors affecting patch colonization include timing of disturbance (in relation to reproductive timing of colonizers) and location of a disturbance (tidal exposure at time of settlement). The resulting heterogeneity of natural assemblages is the product of the diversity of life histories and responses to disturbance regimes (Sousa 1984a). Temporal variation in photoperiod and temperature regulate many seaweed life histories and can dictate propagule availability and survival. This may explain why previous researchers observed different early colonists depending on the timing of experimental clearings (Emerson and Zedler 1978, Hawkins 1981). High intertidal communities experience harsh environmental conditions because they experience the greatest emersion time (with the exception of terrestrial communities). These conditions are magnified by temporal changes in the time of day the substrate is exposed. For this reason, macroalgae in the higher intertidal zone are more regulated by dynamic physical factors (ecophysiology) than biological factors (herbivory, competition) (Cubit 1984). Lower intertidal communities are more diverse (sessile and motile assemblages) and experience less emersion time than high intertidal communities resulting in greater regulation by biological factors than physical factors (MacGinitie and MacGinitie 1949, Denely and Underwood 1979). Differences in submersion and emersion time between intertidal zones can control propagule dispersal, settlement, and survival.

Many studies have examined dispersal potential and abundance of macroalgal propagules present in water samples, but none have directly linked their findings to patterns of recruitment observed on rocky reefs. As such, this is the first study to directly test the contribution of waterborne propagules to recruitment. The contribution of two recruitment strategies, (1) microscopic overwintering stages and (2) waterborne propagules, to post disturbance recruitment of these ephemeral macroalgae were investigated in this study. The responses of these algae to a series of complete and partial removals created in the high and mid-intertidal at a rocky open coast location were compared. Removals were repeated four times in one year to assess temporal variation in responses. A better understanding of how ephemeral algae recruit to disturbed substrate will help elucidate a mechanism of early colonization and recruitment in dynamic environments.

OBJECTIVES

The objective of this study was to test the effect of timing and location of a disturbance on the recruitment mechanism of opportunistic macroalgae. More specifically, I compared recruitment of *Ulva* and *Porphyra* from microscopic stages in the water column to that of microscopic stages left behind after a disturbance (1) four times during the course of one year (August 2007, November 2007, January 2008, and May), and (2) at two different intertidal heights (mid: *Mazzaella flaccida* dominant zone and high: *Porphyra perforata* dominant zone). To test the availability of waterborne propagules to recruitment in space and time I manipulated disturbance severity. I created two types of removals: partial removals in which all macroscopic organisms were removed, leaving microscopic stages on the substrate; and complete removals that included the aforementioned manipulation followed by sterilization of the substrate removing all macroscopic and microscopic stages from the substrate. A third plot type was established (un-manipulated control) in which plots were marked in the same fashion as the removals (see methods section for details on plot marking) but no organisms were removed.

Availability of waterborne microscopic stages was inferred by the presence or absence of recruitment in complete removals. Any recruitment to complete removals would indicate the presence of waterborne propagules. Recruitment to partial removals would result from either or both waterborne propagules and fragments/"fugitive" microscopic stages. Presence of ephemerals in controls would also result from the same propagule sources as partial removals and be representative of natural recruitment patterns. The processes affecting recruitment in these three plot types are outlined in Table 1.

Table 1. Processes affecting recruitment in treatment types.

	Treatment Type		
Recruitment mechanisms	Control (waterborne + fugitives - manipulation)	Partial (waterborne + fugitives + partial manipulation)	Complete (waterborne only + severe manipulation)
	Facilitation	Facilitation	No competition Low herbivory
	High competition High herbivory	Less competition Desiccation (no canopy)	Desiccation (no canopy)

Additionally, a temporal or spatial patterning of these processes could occur as a result of seasonal cycling of physical factors and spatial gradients in biological processes (see Table 2 for summary). Treatments were established four times in one year (August 2007, November 2007, January 2008, and May 2008) to address temporal variability in ambient temperatures, oceanographic regimes (upwelling, oceanographic, and Davidson as defined for the central California coast by Skogsberg 1936, Skogsberg and Phelps 1946, and Bolin and Abbott 1963), photoperiod, and timing of low tides that may influence the survival and/or availability of propagules. Constant recruitment among seasons would indicate that settlement, survival and availability of propagules were independent of temporal variation in these factors. Constant recruitment among intertidal elevations would indicate that recruitment was independent of intertidal elevation. Recruitment differences between zones would indicate that additional processes, biological (grazers, competition) and/or physical (desiccation, emersion) were affecting recruitment. The experimental design (see methods for more detail) allowed for interactions between these factors and treatment to be further investigated. Any variation in treatment effect dependent on either timing or location of the clearing resulted in a significant interaction term with treatment. The inherent differences in how physical factors affect the two zones (see Table 2) increased the probability of these types of interactions.

Table 2. Additional processes affecting post-disturbance colonization that may explain differences associated with spatio-temporal coupling.

		Type of Effect	
Factor		Positive	Negative
Space			
	Porphyra zone	Less competition Less herbivory	Desiccation Emersion
	Mazzaella zone	Submersion Less desiccation	Competition Herbivory
Time			
	temporal patterning of:	Photoperiod Temperature Transport (propagule supply) Tidal cycle	

METHODS

Study Site

The study site was located on an exposed rocky shore north of Pigeon Point, California (N37 10.93 W122 24.08) (Figure 3). The natural system of the study site consisted of three main biological zones (High: *Porphyra* dominant, mid: *Mazzaella* dominant, and low: *Phyllospadix/Laminaria* dominant). Only the high and mid-intertidal zones were of interest in this study. At the onset of the experiment the higher intertidal consisted of flat sandstone and was dominated by *Porphyra perforata* whereas the mid to low intertidal consisted of sandstone outcroppings dominated by *Mazzaella flaccida*. Experimental plots in the *Porphyra* zone were exposed when the tidal height dropped below +2ft above mean lower low water (MLLW) and those in the *Mazzaella* zone were exposed when the tidal height dropped below +1ft above MLLW. This site was exposed to waves (Figure 4) and influenced by seasonal sand inundation. The greatest amount of sand inundation occurred in fall with the *Porphyra* zone experiencing the greatest amount of inundation ($\bar{\chi}$ = 75.0 ± 25.0 SE % cover) and the *Mazzaella* zone never experiencing more than 17.8 ± 8.20 average % cover (Figure 5).

Experimental Design

In this study, I manipulated disturbance severity to test the effect of timing and location of a disturbance on response and recruitment strategy of opportunistic algae. In July 2007, ninety-six 0.5m-diameter circular plots (area = 0.196 m^2) were marked in the center with numbered stainless steal washers affixed to the substrate using a concrete wall anchor and plumbers epoxy. A second concrete anchor was used to mark the edge of each plot. Forty-eight of the ninety-six plots were located in the higher intertidal zone dominated by *Porphyra perforata* (hereafter *Porphyra* zone), whereas the remaining forty-eight were located in the lower intertidal zone dominated by *Mazzaella flaccida* (hereafter *Mazzaella* zone).

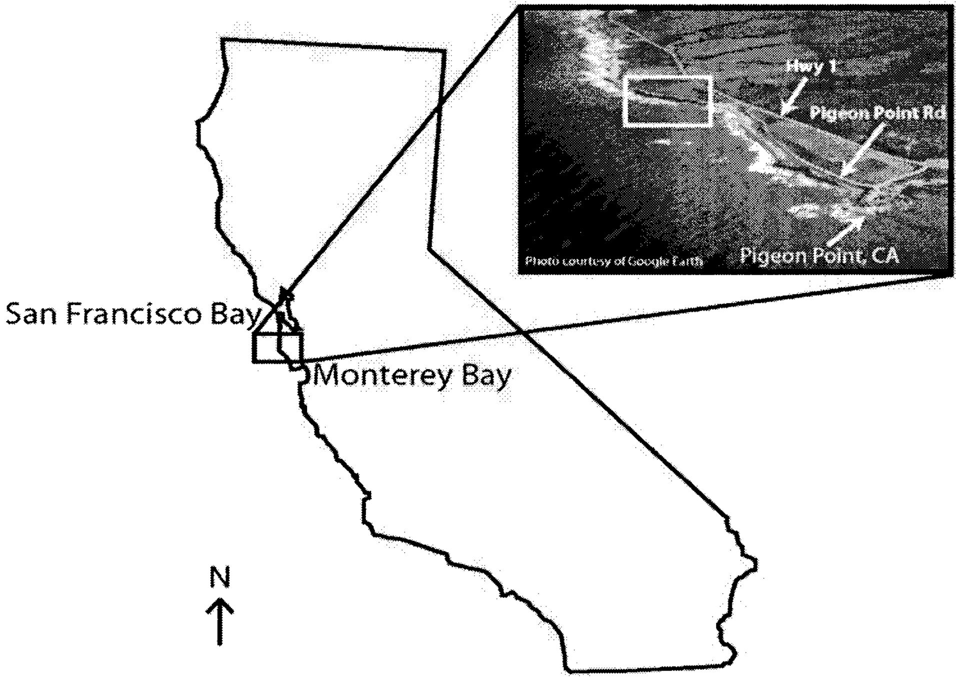

Figure 3. Location of study site, north of Pigeon Point, California at N37 10.93, W122 24.08. Inset is a close up of study site in relation to CA highway 1 and Pigeon Point Rd (Photo Courtesy of Google Earth).

Twelve plots in each zone were randomly assigned one of four clearing dates: August 2007, November 2007, January 2008, or May 2008. Date of clearing and plot types were assigned randomly to the 12 plots in each zone on each date, assuring spatial interspersion (3 plot types x 4 replicates x 2 intertidal zones x 4 dates = 96 plots). All manipulated plots (partial and complete) were removed of all macroscopic organisms by using a wire brush and putty knife. Encrusting red, brown, and non-geniculate coralline algae were scraped and abraded. Complete removal plots were then sterilized with a portable blowtorch to remove any fragments or sporelings left behind by the scraping. Bordering organisms were covered with wet towels to protect them from the flame. The substrate was heated to the point of fracturing and pools to the point of boiling.

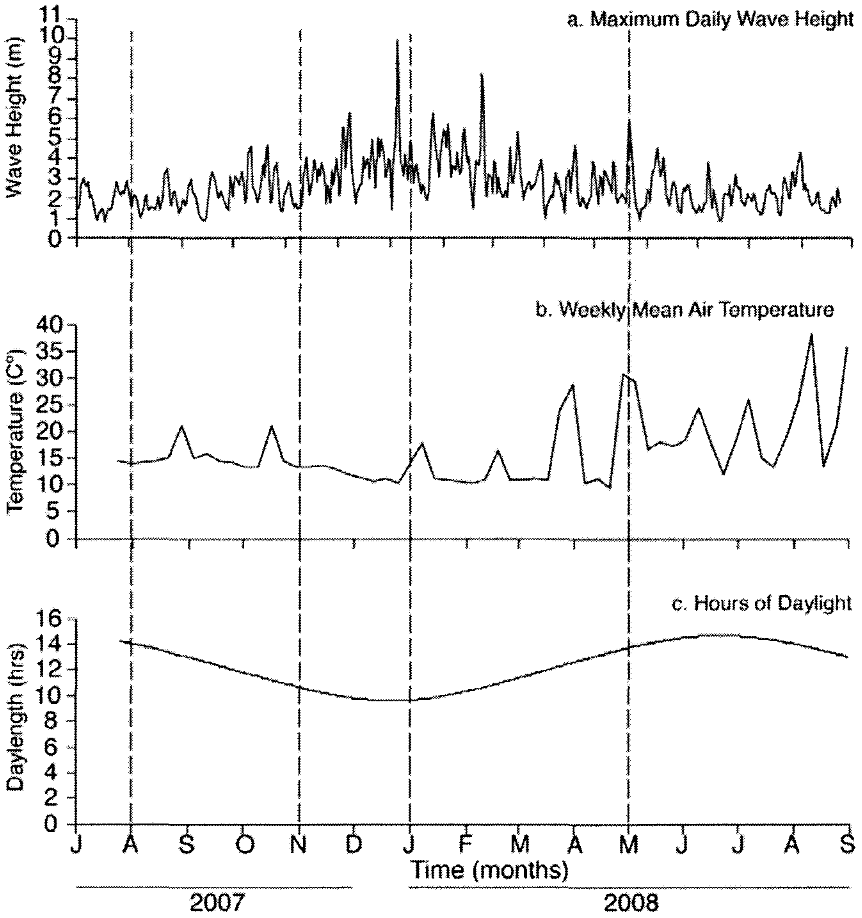

Figure 4. Temporal variability in wave height and hours of daylight. A. Maximum daily offshore wave height from NOAA buoy# 46042 (Monterey Bay). Data from this buoy was used in lue of the closer, Halfmoon Bay buoy (#46012) due to missing data from November 2007 to mid January 2008. Data from the Monterey buoy was correlated to that collected by the Halfmoon Bay buoy (*P*=0.000000). B. Mean weekly air temperature (°C) offshore from NOAA buoy# 46042 (Monterey Bay). C. Hours of daylight for the duration of the study. Dashed lines denote the timing of each experimental clearing.

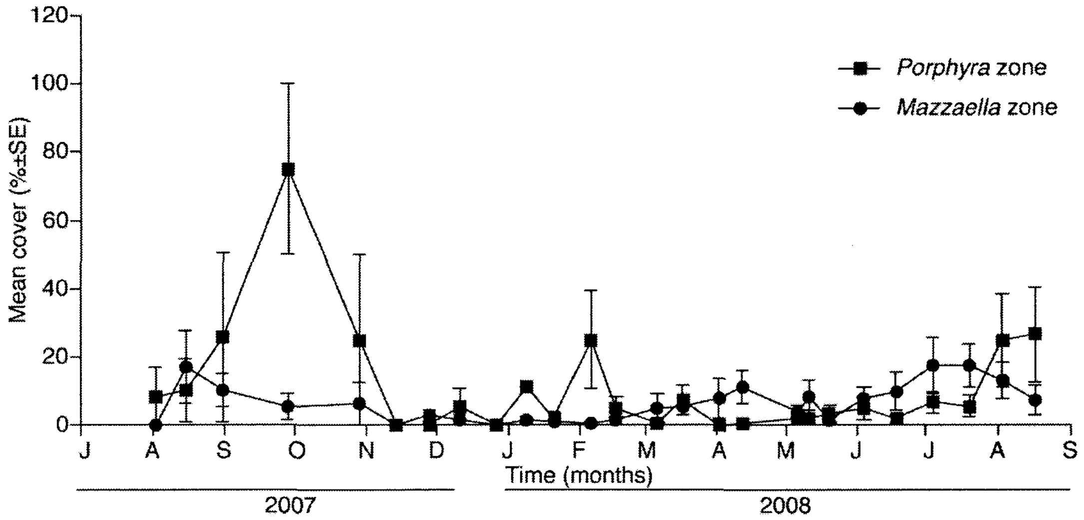

Figure 5. Temporal variability in sand cover (mean ± SE) in all control plots by zone (■=*Porphyra* zone and ●=*Mazzaella* zone).

Monthly Sampling

All plots were sampled before manipulation, in two-week intervals during the first month after clearing, and monthly thereafter. Recruitment was never observed two weeks after the removals were created; therefore monthly sampling was deemed adequate to capture future seasonal changes in recruitment. During each sampling event, abundance was estimated by measuring average percentage cover of all attached macroalgae (canopy and understory, total cover could be >100%), sessile invertebrates, and substrate with a 50-point random point contact (RPC) method (modified from Foster et al. 1991). RPC measurements were collected using a circular sampling hoop with 10 randomly arranged, numbered spokes, each spoke with 5 haphazardly marked points. To avoid sampling the same points over time, the hoop was rotated each sampling period so that a different numbered spoke lined up with the permanent edge marker. Each period, photoquadrats were taken to verify RPC measurements of percentage cover and were used to estimate canopy cover for one plot that was missed on May 20, 2008. Counts of motile invertebrates within ¼ of the plot were used to estimate invertebrate density.

Data Analysis

Ulva and Porphyra response to experimental manipulations

To assess temporal and spatial differences in recruitment resulting from waterborne propagules, peak total percent cover (mean ± SE, n=4) of *Ulva* and *Porphyra* in each plot was compared using a Model I ANOVA (SPSS 16.0, $\alpha=0.10$). Factors included timing (date of clearing), zone (location of clearing), and treatment (plot type). To examine the effect of time and location of a disturbance on *Ulva* recruitment strategy, mean maximum cover per plot for the entire study period (August 2007-August 2008) was compared among treatments for each of four clearing events in both zones. The magnitude of maximum *Ulva* recruitment varied as a function of disturbance timing, location, and severity (i.e. treatment). The assumptions of normality were evaluated by examining residuals, and 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 appropriate, an arcsine transformation was used to normalize the data. With respect to the assumptions of homogeneity of variances, the ANOVA is considered to be robust to differences in variances when replication is equal (Zar 1999). Planned pairwise comparisons among means were tested using Fisher's least significant difference method (Fisher's LSD, SPSS 16.0, $\alpha=0.10$).

Variance components were calculated to evaluate magnitude of effects for significant factors ($P<0.10$) (Winer 1971, Graham and Edwards 2001).

RESULTS

Natural variability of system

The natural system of the study location was dominated by bare space in the high intertidal and macroalgae in the mid-intertidal (Figure 6). Un-manipulated controls located in the higher intertidal community fluctuated temporally between abundant bare rock (October 2007-March 2008) and recruitment pulses of *Porphyra perforata* (so dense a metal detector was needed to locate plot markers) (August 2007 and March 2008-September 2008) (Figures 6a & 7b). Sparse cover of sessile invertebrates and other algae (Figure 6a, see Appendix A for complete list of genera) was observed throughout the experiments with a minor *Ulva* response ($\bar{\chi}$ = 2.50 ± 2.22 % cover ± SE) in summer months (June 2008-July 2008). *Ulva* was absent from high intertidal control plots at the onset of the experiments (August 2007) and was not observed until mid June 2008 (Figure 7a).

The mid-intertidal was dominated by intertidal macroalgae (>100%) throughout the duration of the study (August 2007-August 2008) (Figure 6b.). Abundance of bare rock and sessile invertebrates in control plots located in this zone did not vary greatly during the course of the study. *Ulva* was present in these plots for the duration of the study (Figure 7a). Natural abundance of *Ulva* was greatest during spring and summer (August 2007-September 2007, January 2008-September 2008, $\bar{\chi}$ = 3.00 ± 1.91 % cover ± SE), and decreased during winter (November 2007-January 2008). *Porphyra* was present in the mid-intertidal during spring and summer (March 2008-September 2008), though it rarely exceeded a mean 3.00 ± 1.77 percent cover; maximum was mean 17.3 ± 1.22 (mean ± SE) percent cover in April 2008 (Figure 7b). Species richness (mean ± SD) of biotic cover in the mid-intertidal was almost twice that of the higher intertidal (Figure 8, Appendix A).

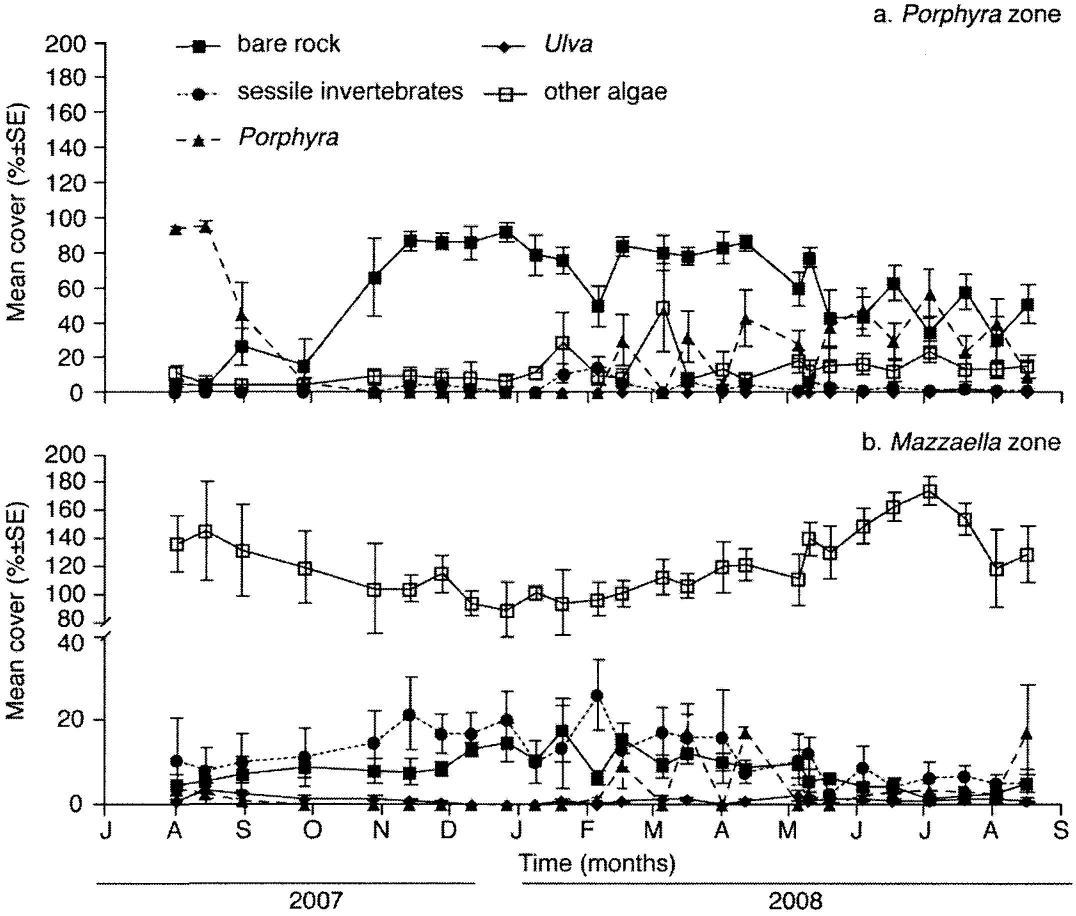

Figure 6. Temporal variability of cover (mean ± SE) in all control plots, August 2007-August 2008, for each zone. a. *Porphyra* zone; b. *Mazzaela* zone. Values are means from each sampling period (■=bare rock, ●=sessile invertebrates, ▲=*Porphyra*, ◆=*Ulva*, and □=other algae). See Appendix A for complete list of macroalgae and sessile invertebrate genera.

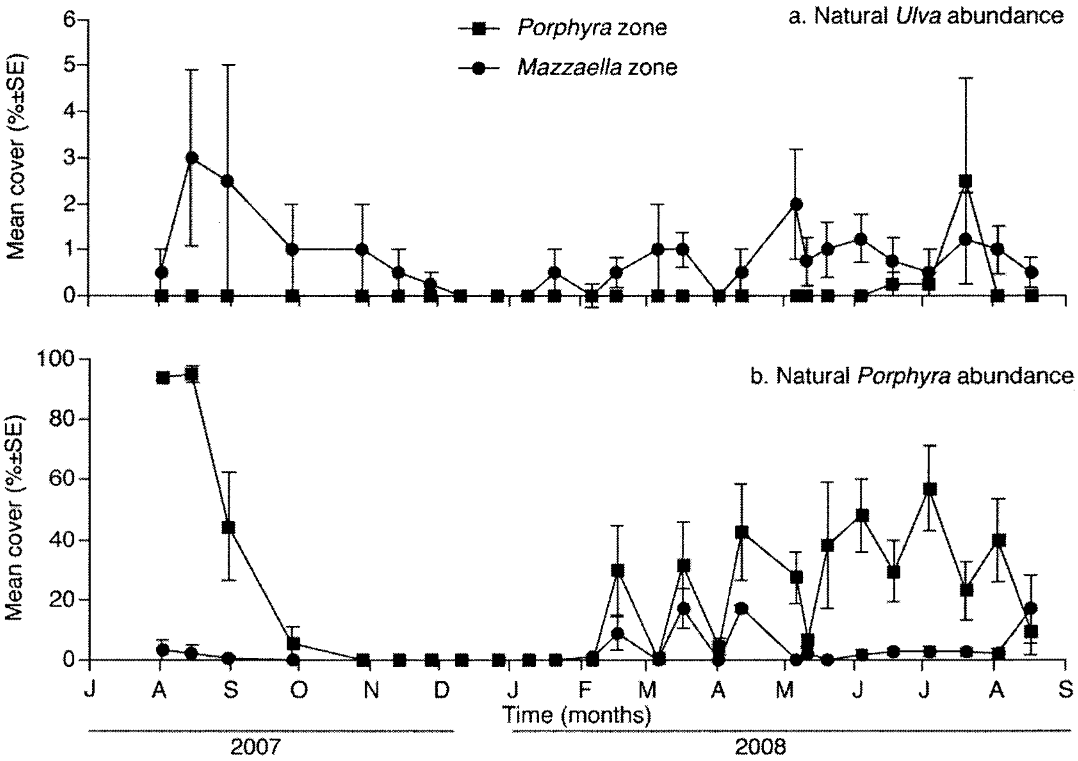

Figure 7. Temporal variability in cover (mean ± SE) of: a. *Ulva* (0≤y≥6) and b. *Porphyra* (0≤y≥100) by zone (■=*Porphyra* zone and ●=*Mazzaella* zone) as captured by un-manipulated control plots. Means represent averages of all control plots sampled on a given sampling period and every sampling period of the study.

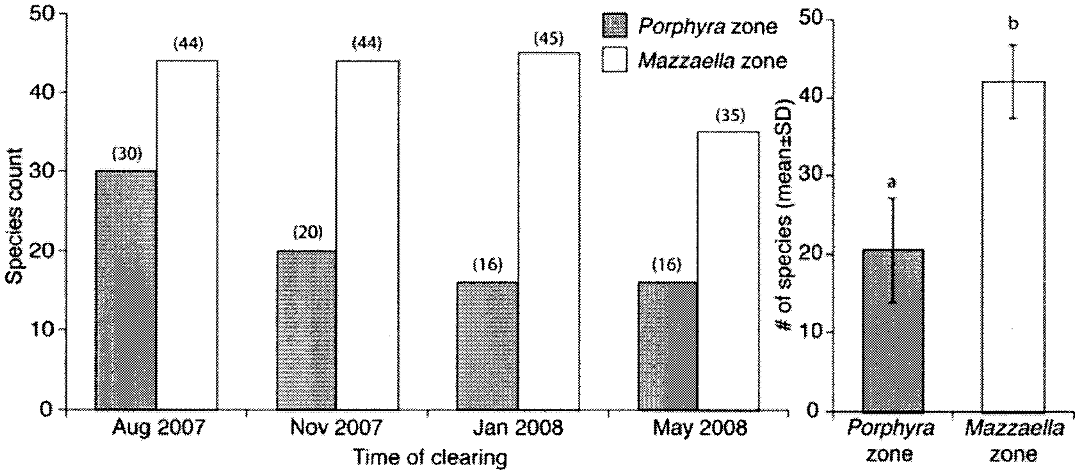

Figure 8. Species richness in all treatment types for the duration of each experiment and average number of species observed in experimental plots for each zone. Letters represent significant differences in average number of species (two-sample t-test, P=0.002).

Ulva response to experimental manipulations

Ulva recruitment pulses were observed seasonally in higher intertidal plots and year-round in lower intertidal plots (Figures 9-10). *Ulva* only recruited to *Porphyra* zone plots during summer (September 2007: partial and July 2008: partial and complete, Figure 9), the greatest response observed was 12.0 ± 12.0 (mean% ± SE) in July 2008. Recruitment pulses were observed year-round in the *Mazzaella* zone (October 2007: complete and partial, December 2007: complete only, April 2008: partial only, and July 2008-August 2008; Figure 10).

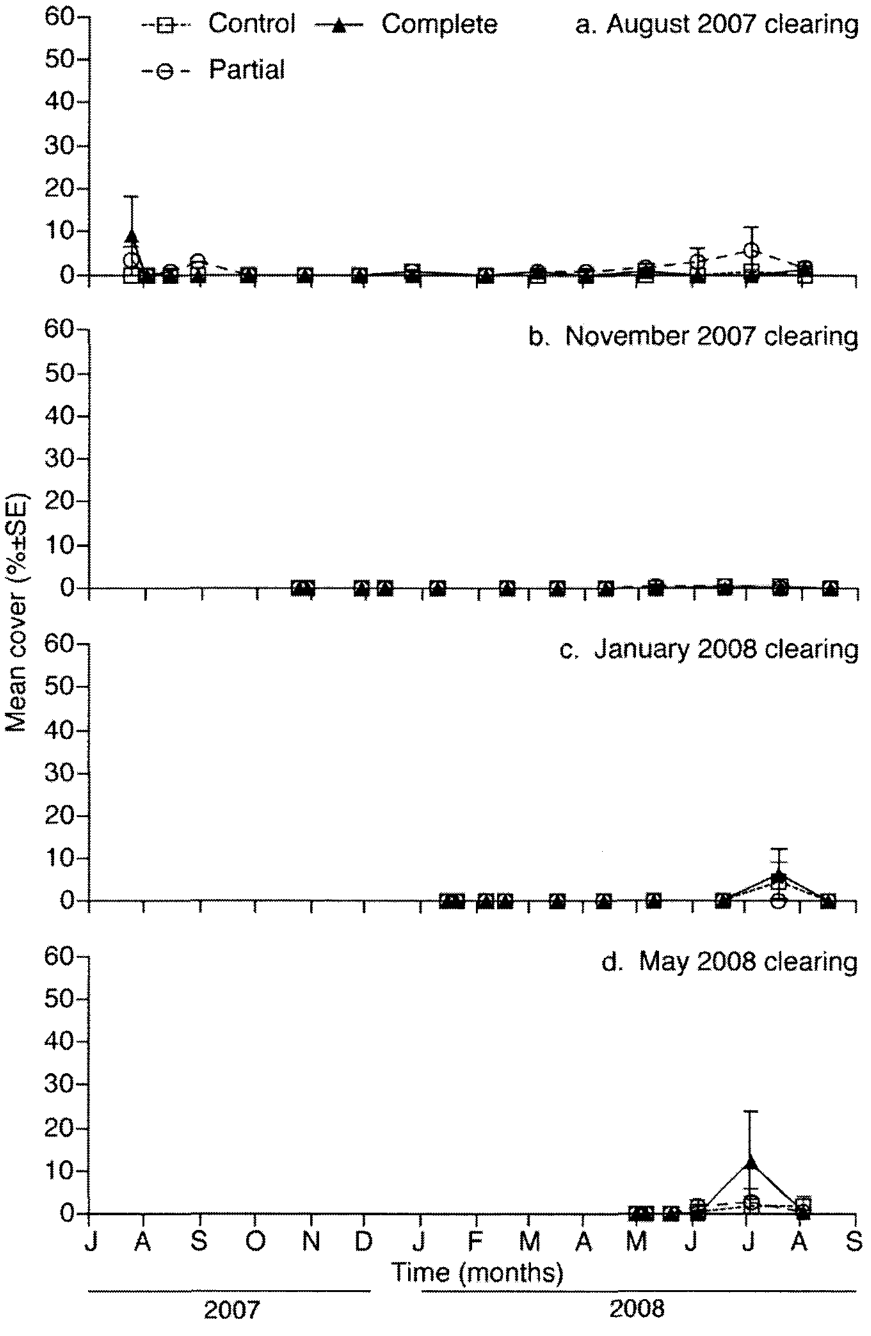

Figure 9. Temporal variability of *Ulva* % cover (mean ± SE) by treatment (□=Control, ○=Partial, ▲=Complete) and time of clearing (a. August 2007; b. November 2007; c. January 2008; d. May 2008) for plots located in the *Porphyra* zone. Initial data point for each panel represents pre-cleared values.

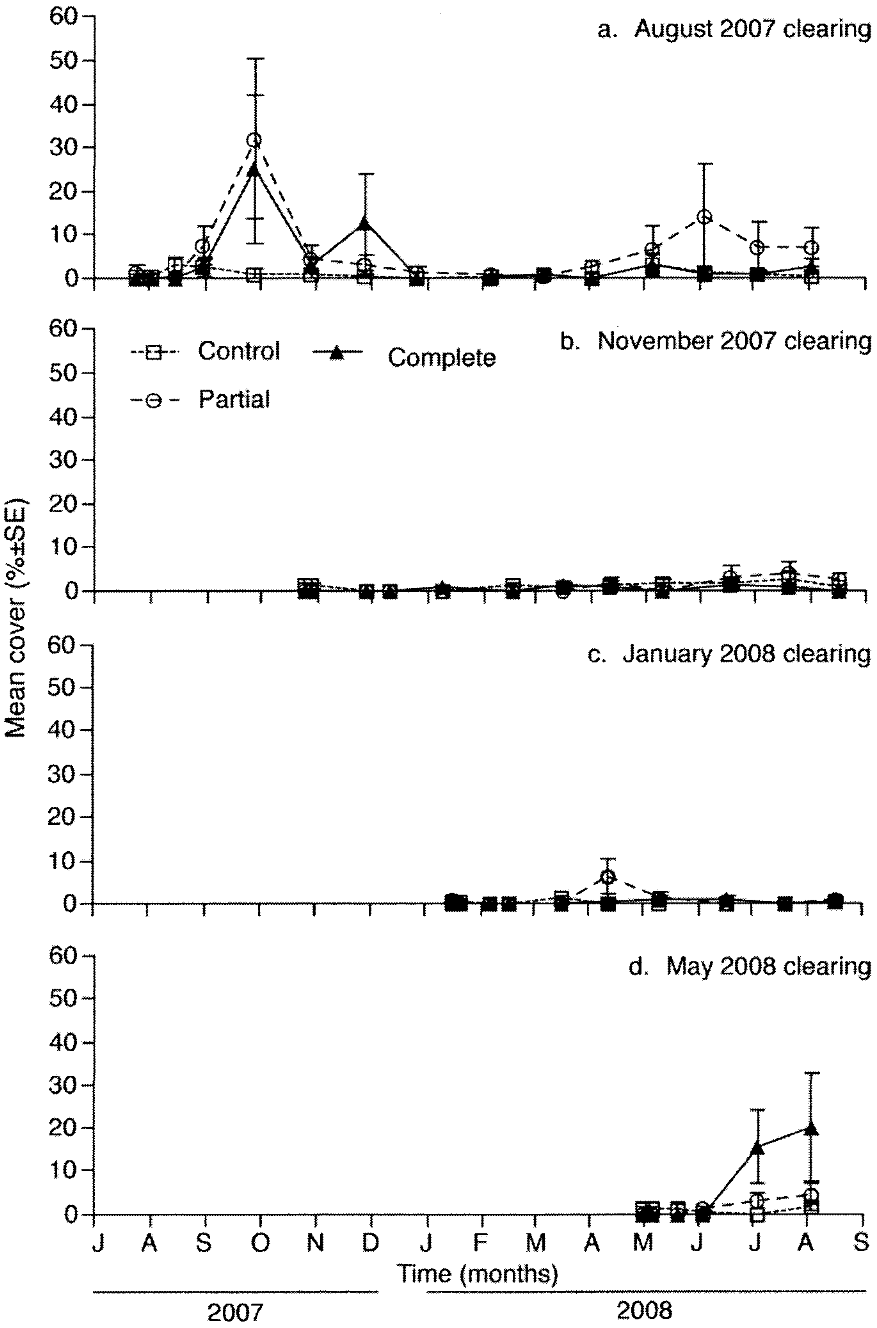

Figure 10. Temporal variability of *Ulva* % cover (mean ± SE) by treatment (□=Control, ○=Partial, ▲=Complete) and time of clearing (a. August 2007; b. November 2007; c. January 2008; d. May 2008) for plots located in the *Mazzaella* zone. Initial data point for each panel represents pre-cleared values.

Maximum *Ulva* cover varied among treatments depending on the timing of the clearings and as a function of location (Figures 11-12, Table 3, Appendix B, $F_{6,72}$=2.02, P=0.074 and $F_{1,72}$=13.8, P=0.000401). There was a significant interaction between timing of disturbance and treatment effects on *Ulva* recruitment (Table 3, Figure 12, for complete ANOVA tables see Appendix B, $F_{6,72}$=2.02, P=0.07) and no significant interactions with zone ($F_{3,72}$=1.96, P=0.13, $F_{2,72}$=0.74, P=0.48, $F_{6,72}$=0.67, P=0.67). Thus, the type of *Ulva* response was dependent on the timing of the disturbance. The timing-treatment interaction explained more of the variability (5.13%) in peak *Ulva* recruitment than the main effects of timing (5.09%) and treatment alone (1.45%) (variance components, Appendix B). The main effect of zone explained more variability in *Ulva* recruitment than the other significant factors in the model (6.32%) (Figure 11, Table 3, Appendix B, $F_{1,72}$= 13.8, P=0.000401). Therefore, the *Porphyra* zone experienced spring and summer *Ulva* recruitment pulses and the *Mazzaella* zone year-round recruitment pulses.

Treatment effects were observed for plots established in August 2007 and May 2008 (Figure 12, Table 3, Appendix B, $F_{6,72}$= 2.02, P=0.074; Fisher's LSD). Peak *Ulva* recruitment to control plots was constant among experiments (i.e. timing); recruitment to manipulations however did vary among experiments. Recruitment to August 2007 complete removals was greater than November 2007 and January 2008 complete removals. *Ulva* recruitment was constant among August 2007 partial and complete removals and greater than controls from that same experiment. Independent of among zone variability, recruitment to partial removals established in August 2007 differed from those established in all other experiments (November 2007, January 2008, and May 2008). Differences also were observed among complete removals and controls established in May 2008. These complete removals experienced greater recruitment than control plots in general (August 2008, November 2007, and January 2008) (Figure 12). Recruitment to partial removals was similar to controls and complete removals (Figure 12, Appendix B). No treatment differences were observed in November 2007 and January 2008; however, recruitment was observed in complete removals created in both of these experiments.

Table 3. Analysis of variance results for maximum *Ulva* and *Porphyra* cover in both zones. *P* values for two-way, model I ANOVA results, timing=time of clearing and treatment. *P* values correspond to panels in Figures 10 & 13; complete ANOVA tables and variance component analyses in Appendix B; post-hoc comparisons are given in the text.

	Response Variable	
Factor	Maximum *Ulva* Cover (Fig. 11)	Maximum *Porphyra* Cover (Fig. 15)
TIMING	**0.006**	**0.000**
ZONE	**0.000**	**0.000**
TREAT	**0.092**	0.292
TIMING*ZONE	0.128	**0.000**
TIMING*TREAT	**0.074**	0.254
ZONE*TREAT	0.480	0.230
TIMING*ZONE*TREAT	0.672	0.839

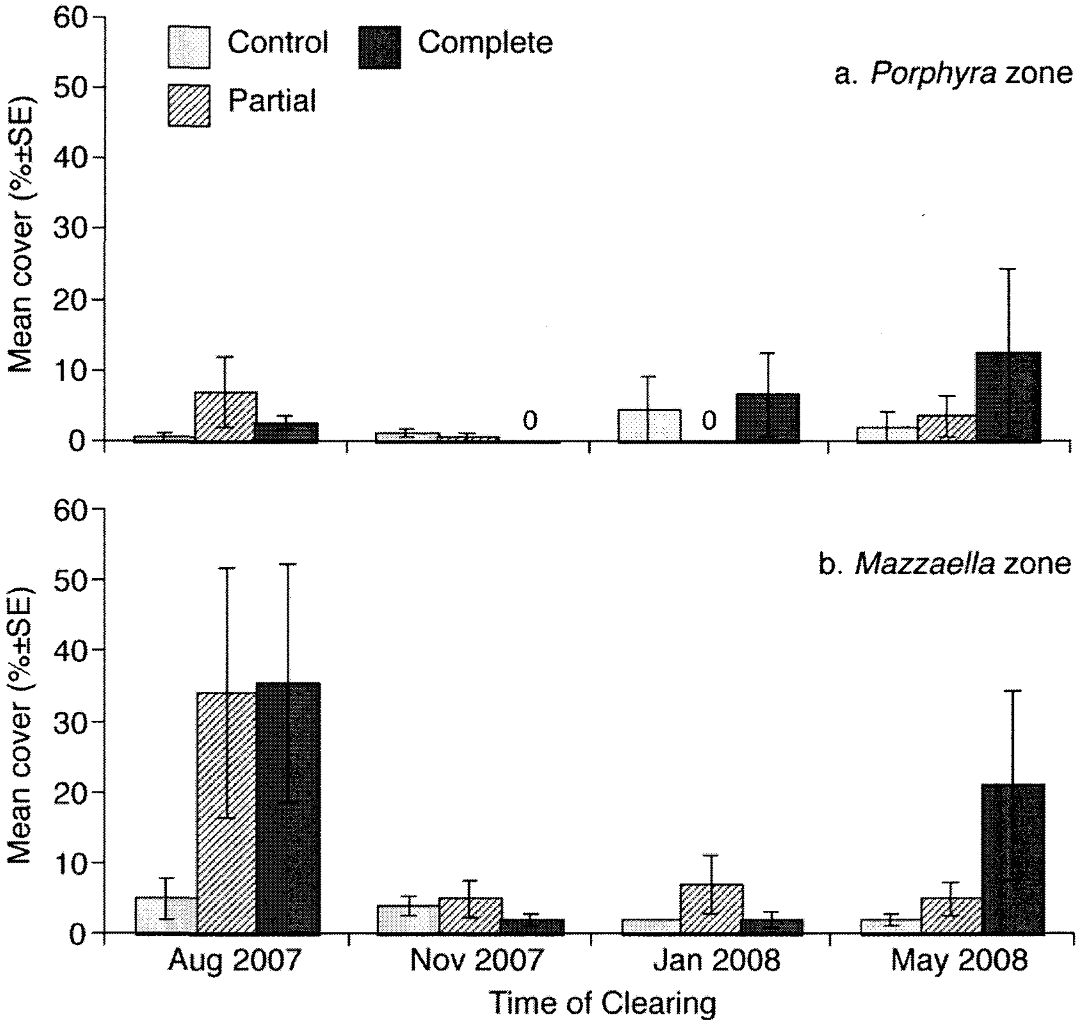

Figure 11. Variability in maximum *Ulva* % cover (mean ± SE) in each treatment compared with unmanipulated controls for all clearing experiments. a. *Porphyra* zone; b. *Mazzaella* zone. These data are not transformed, however, statistical analyses were performed on arcsine-transformed data.

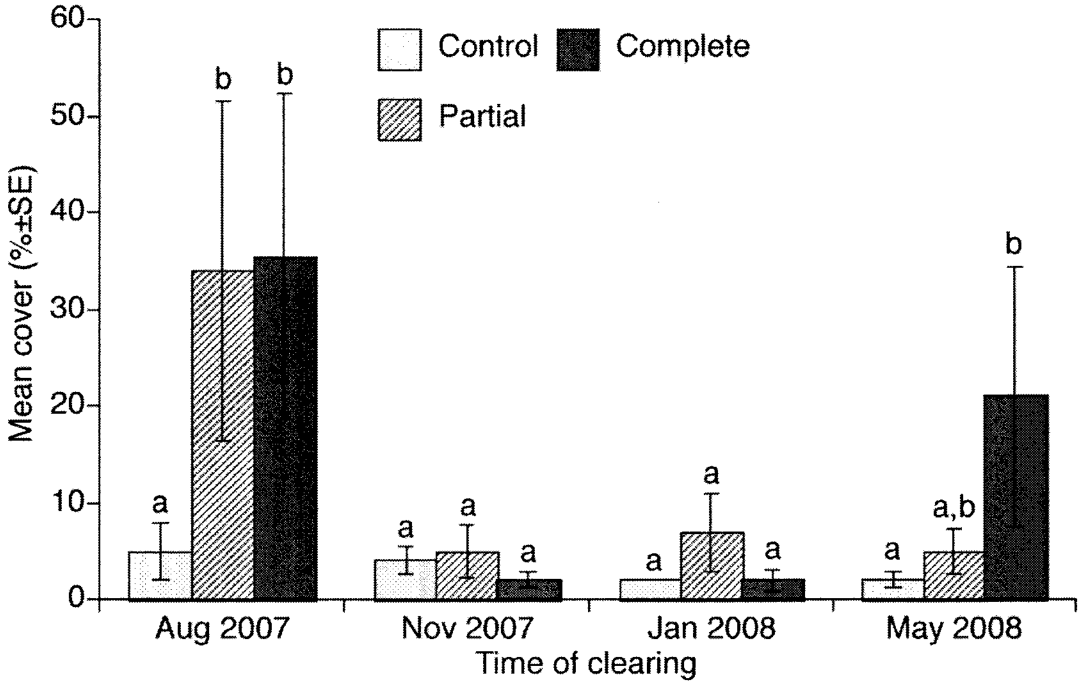

Figure 12. Temporal trends in maximum percent cover (mean ± SE) of *Ulva* in treatments when averaged across zones. No significant interactions with zone were observed. Letters represent significant differences according to the timing-treatment interaction ($F_{6,72}$=2.02, P=0.074). There was a general effect of zone ($F_{1,72}$=13.8, P=0.0004) not represented in this figure. These data are not transformed, however, statistical analyses were performed on arcsine-transformed data.

Porphyra response to experimental manipulations

Temporal variability of *Porphyra* cover was constant among treatments and varied depending on the timing of clearing as a function of location (Figures 13 & 14,). All *Porphyra* recruitment was observed from late winter through summer (September 2007 and February 2008-September 2008, Figures 13 & 14), the greatest response was observed in summer months (June2008 and July 2008; $\bar{\chi}$ = 81.0 ± 8.35% cover ± SE; Figure 13).

While no significant treatment effect was observed, there was a significant interaction between timing of clearing and zone (location) (Figures 15 & 16, Table 3, Appendix B, $F_{3,72}$= 7.41, P=0.000; Fisher's LSD). This indicates that peak *Porphyra* recruitment in the different experiments (timing of clearing) was dependent on the location (zone) of the clearing. Specifically, maximum *Porphyra* recruitment only differed among zones for August 2007 and May 2008 experiments (Figure 16). Spring and summer plots located in the *Porphyra* zone experienced greater maximum cover than *Mazzaella* zone plots cleared at the same time. The timing-location interaction explained 9.42% of the variability in peak *Porphyra* recruitment (variance components, see Appendix B). The main effect of location explained slightly less of the variability in peak recruitment than the interaction (7.44%) and timing alone only explained 4.48% of the variability.

Maximum *Porphyra* recruitment to *Porphyra* zone plots established in August 2007 was greater than maximum recruitment to all other experiments (November 2007, January 2008, and May 2008) (Figure 16, Appendix B for Fisher's LSD results). Maximum recruitment to *Mazzaella* zone plots was greatest for plots established in January 2008 (Figures 15 &16). Sparse *Porphyra* recruitment through time occurred in August 2007 ($\bar{\chi}$ = 20.0 ± 8.40% cover ± SE) and May 2008 *Mazzaella* experiments ($\bar{\chi}$ = 7.00 ± 4.73% cover ± SE; Figure 13).

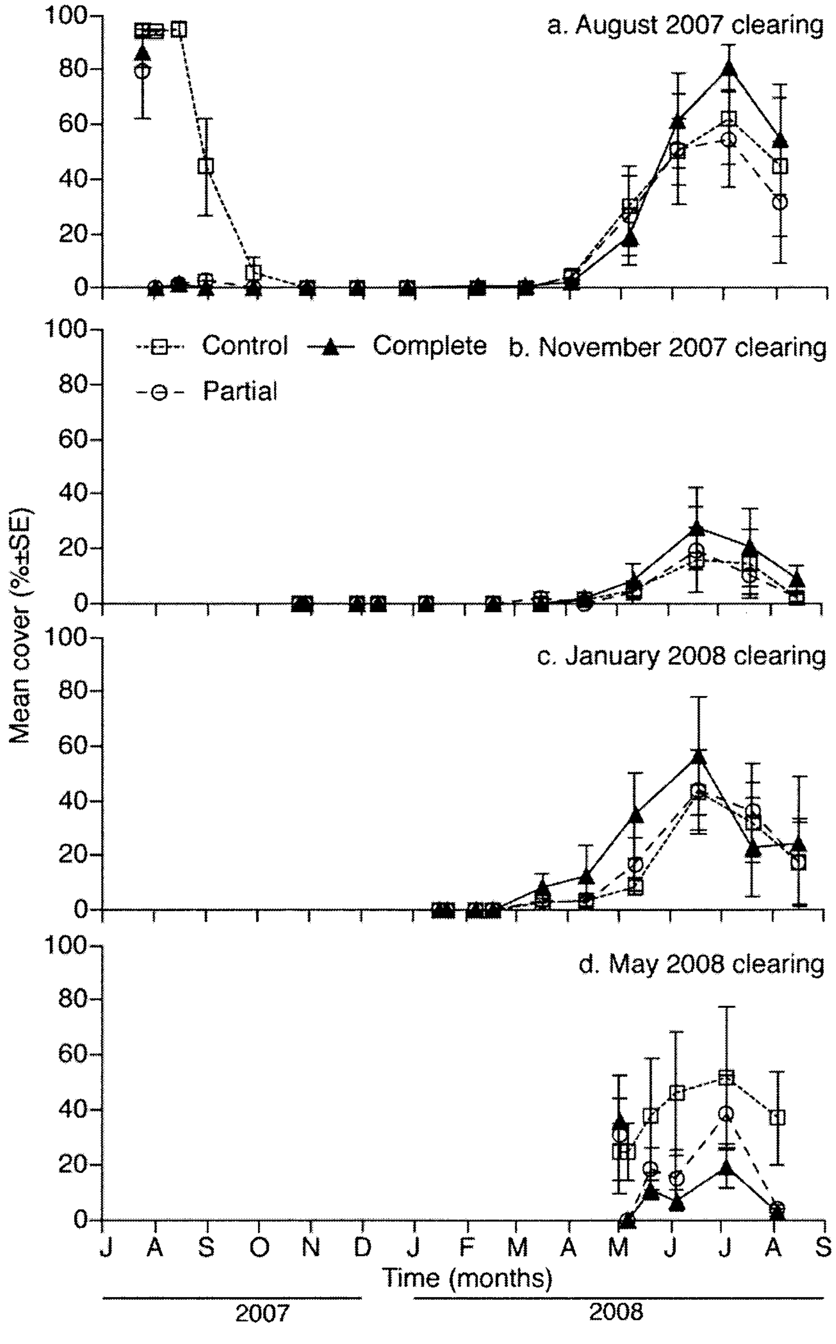

Figure 13. Temporal variability of *Porphyra* % cover (mean ± SE) by treatment (□=Control, ○=Partial, ▲=Complete) and time of clearing (a. August 2007; b. November 2007; c. January 2008; d. May 2008) for plots located in the *Porphyra* zone. Initial data point for each panel represents pre-cleared values.

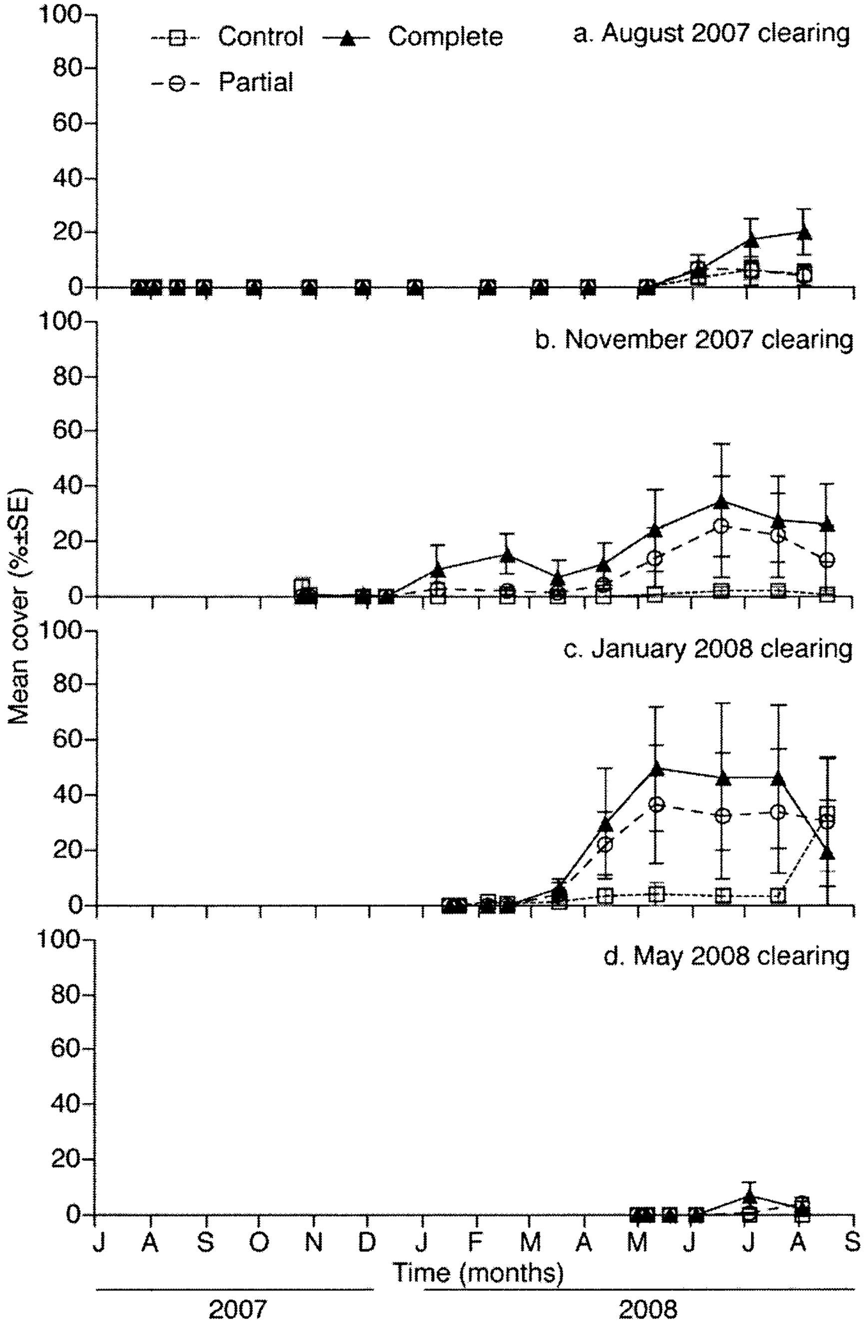

Figure 14. Temporal variability of *Porphyra* % cover (mean ± SE) by treatment (□=Control, ○=Partial, ▲=Complete) and time of clearing (a. August 2007; b. November 2007; c. January 2008; d. May 2008) for plots located in the *Mazzaella* zone. Initial data point for each panel represents pre-cleared values.

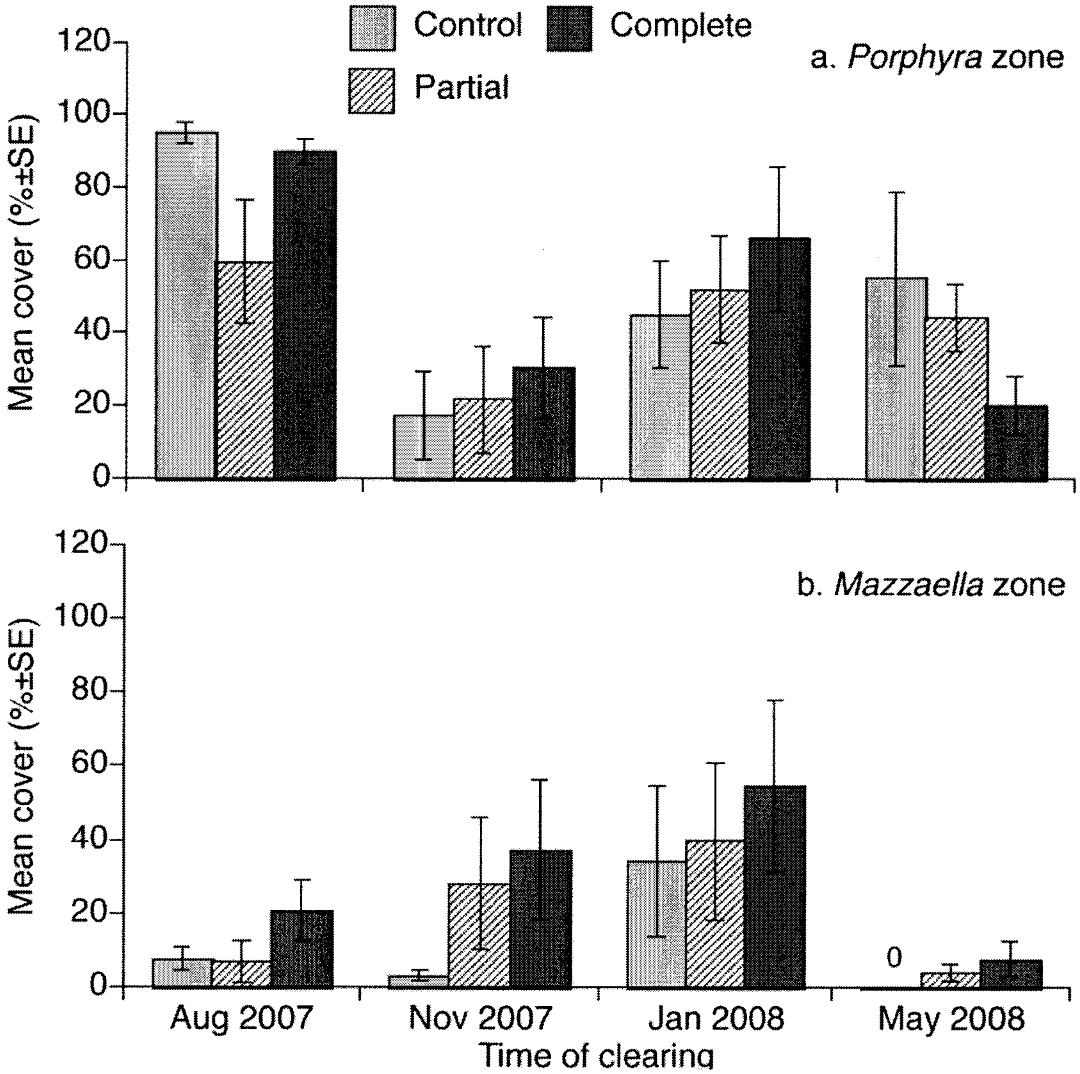

Figure 15. Variability in maximum *Porphyra* % cover (mean ± SE) in each treatment compared with un-manipulated controls for all clearing experiments. a. *Porphyra* zone; b. *Mazzaella* zone. These data are not transformed, however, statistical analyses were performed on arcsine-transformed data. No treatment differences were observed in any particular date or zone.

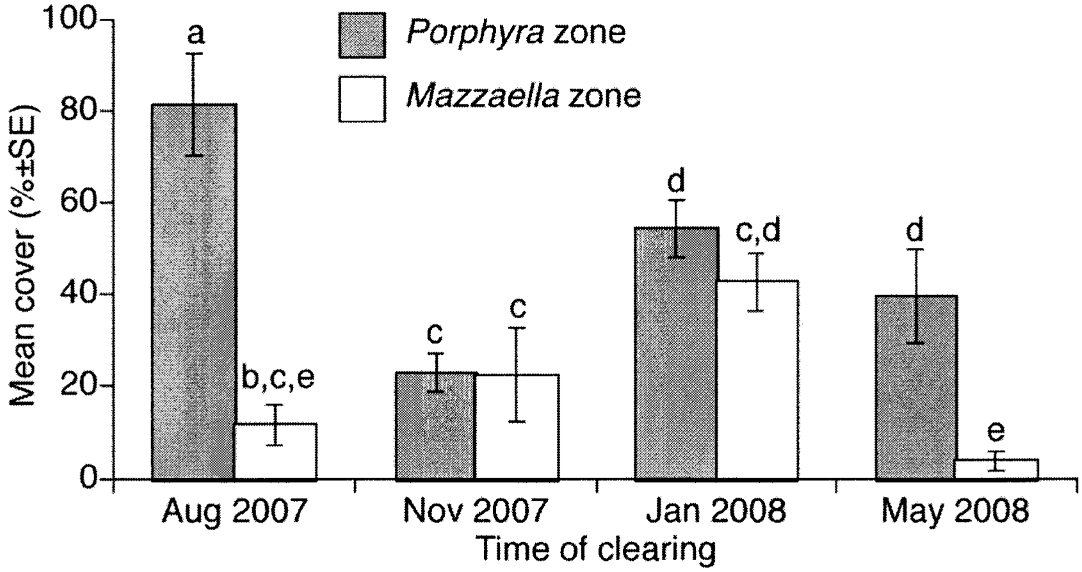

Figure 16. Effect of timing-zone interaction on maximum *Porphyra* percentage cover (mean ± SE). Letters represent significant differences according to the timing-zone interaction ($F_{3,72}$=7.40, P=0.000). Values are averaged across treatment as no treatment effect was observed ($F_{2,72}$=1.25, P=0.292).

Potential interaction between early colonizers

I observed small amounts of *Ulva* cover in high intertidal plots whereas *Porphyra* was a seasonal dominant in the *Porphyra* zone and did well in fall and winter *Mazzaella* zone plots. Additionally, *Mazzaella* zone clearings with the greatest *Porphyra* recruitment experienced the least *Ulva* recruitment whereas those with the greatest *Ulva* recruitment experienced the least *Porphyra* recruitment (Figures 11b & 15b). These opposing responses in recruitment indicated the potential for a competitive relationship between *Ulva* and *Porphyra*. To better understand the relationship between these two seaweeds, *Ulva* percent cover was plotted against *Porphyra* percent cover for every incidence in which either or both of these seaweeds were observed in an experimental plot (Figure 17).

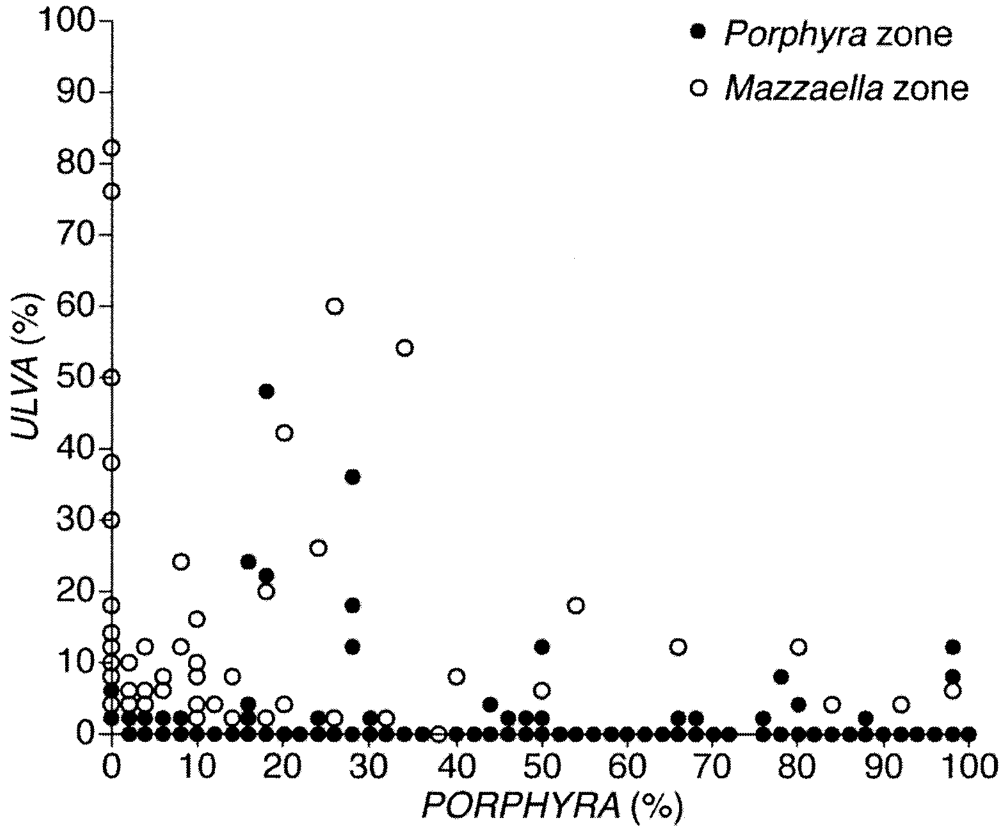

Figure 17. *Ulva* cover (%) as a function of *Porphyra* cover (%) for all experiments in both zones (●=Low zone & ○=High zone). Time of clearing is not indicated as no patterns relating to time of clearing were observed.

The plot clearly shows that in each zone, in clearings created throughout the year, *Ulva* and *Porphyra* could be found in the same plot. In general, incidences of greatest *Ulva* cover occurred at less than 50% *Porphyra* cover and incidences of greatest *Porphyra* cover occurred with low levels of *Ulva* cover (≤20%). This pattern holds true for data from both intertidal zones. A different experimental design would be necessary to rule out competitive interaction between these two seaweeds.

DISCUSSION

I studied the recruitment mechanisms utilized by opportunistic seaweeds within the spatio-temporal coupling that regulates patch colonization. In particular, the importance of waterborne propagules to patch colonization as demonstrated by the presence of both *Ulva* and *Porphyra* in sterilized clearings created throughout the year. Recruitment strategy only affected the magnitude of *Ulva* recruitment and this effect fluctuated depending on the timing of clearing whereas *Porphyra* recruited seasonally regardless of manipulation. The *Ulva* responses were generally affected by location, however, *Porphyra* responses to different locations varied depending on the timing of clearings.

While no effect of treatment was observed in the case of maximum *Porphyra* cover, the effect of treatment on maximum *Ulva* cover varied depending on the timing of a clearing. Lotze (1999, 2000) examined the role of seed banks in propagating blooms of ephemeral seaweeds in the Baltic Sea. She found that overwintering germlings were an important mechanism for early colonization of *Ulva intestinalis* (formerly *Enteromorpha intestinalis*) but that the contribution of this propagule bank varied with season. Seasonal variability was attributed to temporal fluctuations in herbivory and nutrient limitation, with nutrient enrichment counteracting the effects of herbivory (Lotze et al. 2000). Partial clearings created in August 2007 were the only partial clearings that experienced maximum *Ulva* recruitment differing from natural abundances (control plots). The August 2007 clearings were created soon after the beginning of the spring-summer upwelling regime (Skogsberg 1936, Skogsberg and Phelps 1946, Bolin and Abbott 1963).

Increased nutrient availability could have promoted growth from germlings in these partial clearings and contributed to recruitment. This indicates a temporal patterning of biological processes (competition with fragments, herbivory) regulating recruitment of *Ulva* waterborne propagules. Abundance and activity of intertidal gastropod grazers have been correlated with degree of wave action (Lubchenco 1980) with activity greatest in the summer (Lubchenco 1986). Temporal alternations in the relative importance of physical versus biological controls also have been observed in plankton succession of temperate lakes and marine systems (Sommer 1989) and the appearance of spring annuals in terrestrial ecosystems (Fenner 1992).

An *Ulva* response was observed in all disturbance manipulations, with the greatest recruitment occurring in those created in August 2007 and May 2008. Independent of the timing-treatment interaction, the *Ulva* response differed among intertidal zones. Although recruitment of *Ulva* in the *Porphyra* zone resulting from waterborne propagules was only observed in summer, the response of *Ulva* to plots in the *Mazzaella* zone at different times of the year demonstrated that recruitment failures were not the result of seasonal propagule availability (Figures 9 & 10).

Spatial variability (zone) explained the majority of the variability in *Ulva* and *Porphyra* recruitment. The major differences between the two zones were location with respect to MLLW, amount of sand inundation, and biodiversity. The *Porphyra* zone is located closer to shore and thus farther away from MLLW causing it to be exposed for more low tides than the *Mazzaella* zone. The timing of extreme low tides (day vs night; summer vs. winter) varies over the course of a year and among years. Extreme low tides occurred during daytime when increased summer temperatures resulted in abiotic controls (desiccation), whereas extreme lows on foggy nights during winter resulted in biotic controls (mobile grazer activity). The result is a spatio-temporal gradient in exposure time that can lead to fluctuations in the importance of physical vs. biological processes regulating settlement and survival of waterborne propagules and sporelings.

In general, *Ulva* rarely recruited to *Porphyra* zone plots whereas, the greatest *Ulva* responses were observed in spring and summer *Mazzaella* zone manipulations. Unlike the *Mazzaella* zone plots, *Porphyra* zone plots experienced sand inundation immediately following these clearings ($\bar{\chi}$ =25.5 ± 24.8% SE to $\bar{\chi}$ =75 ± 25% SE from September 2007-October 2007 and $\bar{\chi}$ =9.00 ± 6.61 SE to $\bar{\chi}$ =49.0 ± 26.2% SE from June 2008-August 2008) consequently decreasing the amount of substrate available for colonization across all treatments (Figures 18 & 19).

In the case of *Porphyra*, differences in maximum cover among zones observed in summer and spring clearings (Figure 16) coincided with increasing mean tidal elevations during daylight hours (Figure 22). Smith (1983) reported a seasonal alternation in the robustness of *Porphyra* thalli at high and low tidal elevations. When extreme low tides occurred at midday in spring; *Porphyra* thalli at lower tidal elevations were larger, had higher rates of photosynthesis, and more thalli were reproductive than those at higher tidal elevations. Increasing submergence time during daylight hours in fall led to declines in these parameters and eventually in the number of thalli present at lower tidal elevations. Smith also observed a higher incidence of pathogens in thalli collected at the lowest tidal elevations, and proposed that this species' lower tidal limit is regulated by pathogens. This further exemplifies the inherent differences in these two intertidal zones, and indicates that processes regulating settlement and post-settlement survival can vary temporally across intertidal zones and dictate responses by opportunistic algae.

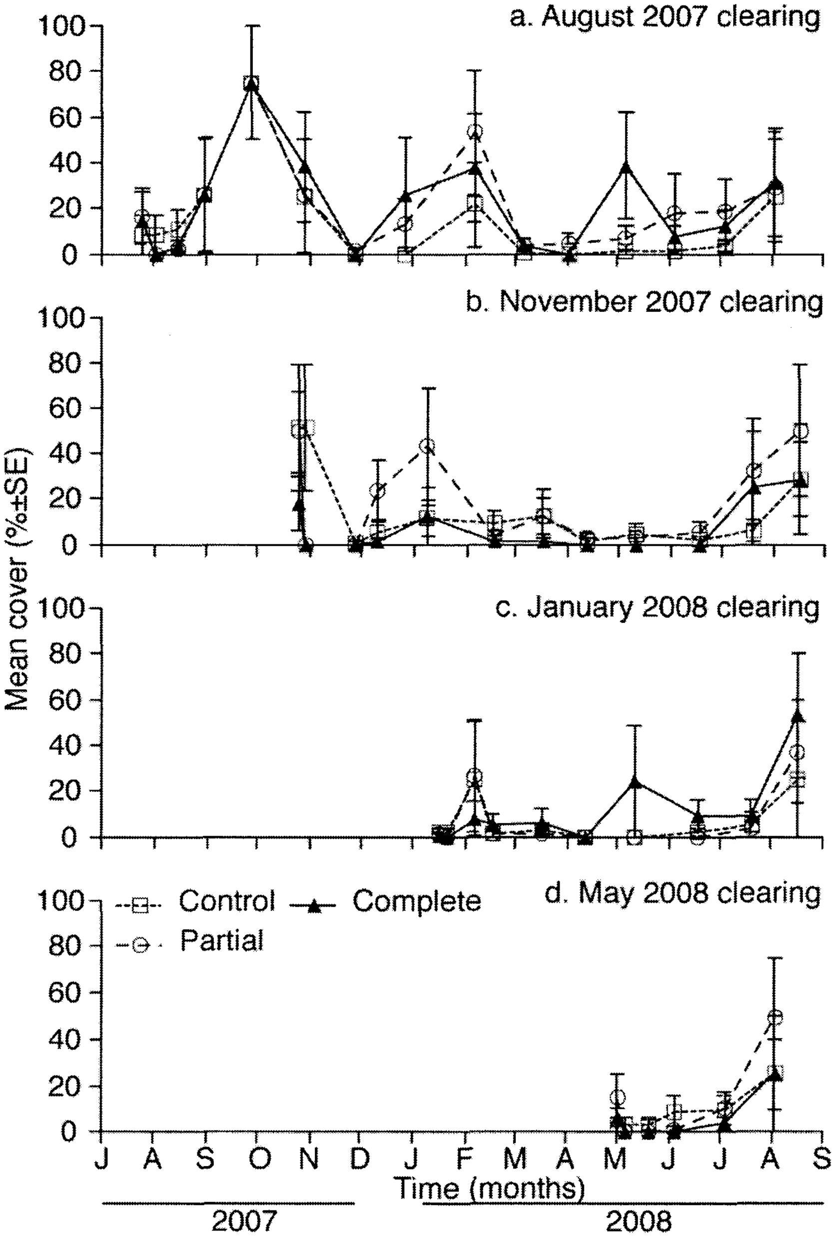

Figure 18. Temporal variability of sand % cover (mean ± SE) by treatment (□=Control, ○=Partial, ▲=Complete) and time of clearing (a. August 2007; b. November 2007; c. January 2008; d. May 2008) for plots located in the *Porphyra* zone.

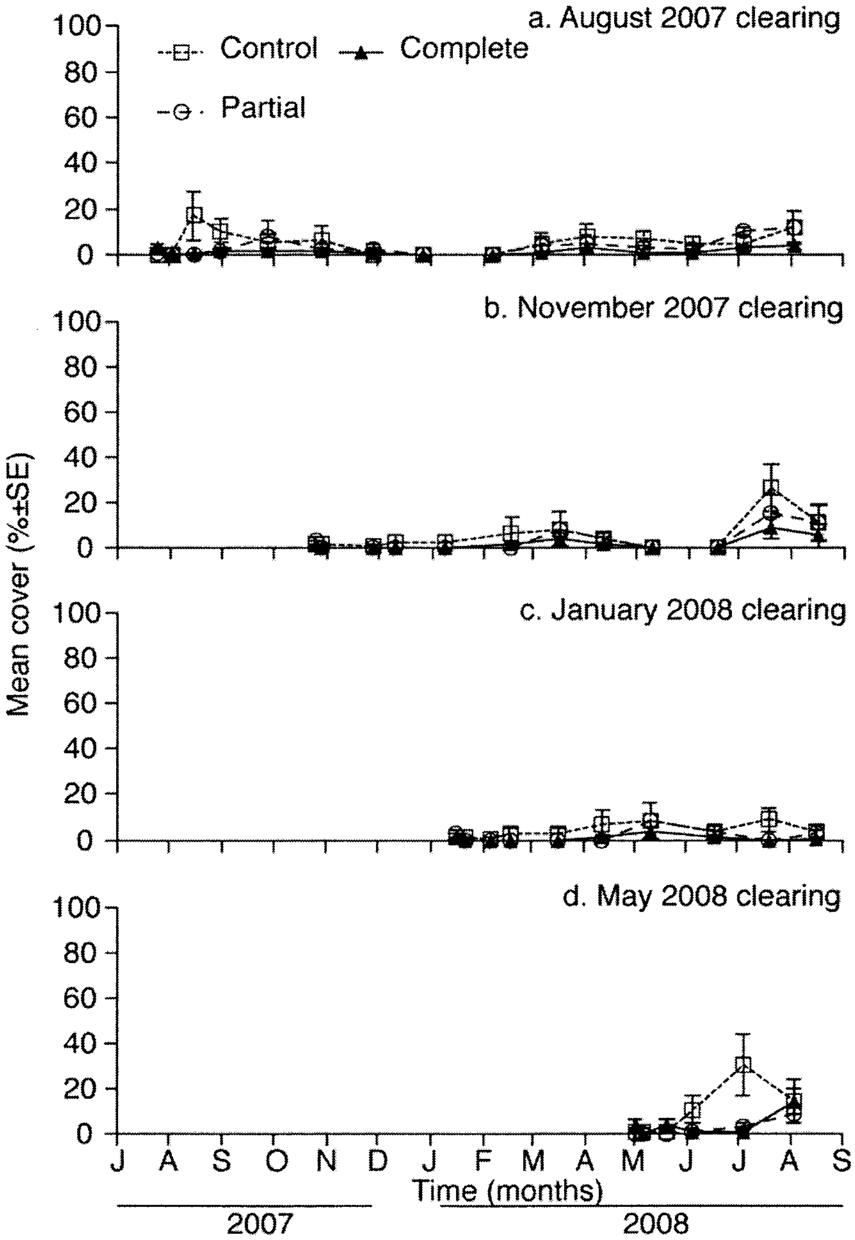

Figure 19. Temporal variability of percentage cover (mean ± SE) of sand by treatment (□=Control, ○=Partial, ▲=Complete) and time of clearing (a. August 2007; b. November 2007; c. January 2008; d. May 2008) for plots located in the *Mazzaella* zone.

Porphyra was locally extinct at this site during late fall and most of winter (Figures 13 & 14). The absence of macroscopic *Porphyra* thalli during fall and winter indicates that the subsequent appearance of macroscopic thalli was most likely the result of settled conchospores. *Porphyra* recruitment was first observed in January 2008 (Figure 14b, in November 2007 *Mazzaella* zone clearings), five months after the August 2007 clearings were created and two months before photoperiod (hours of daylight) reached levels described as optimal for conchospore release by Dring (1967) (Figure 20). During this time many other seaweeds (including *Ulva,* and primarily *Petrocelis* and encrusting coralline) had the opportunity to colonize (via propagules or vegetative encroachment) the August 2007 clearings before decreases in photoperiod cued the release of conchospores (Figure 10a & 21).

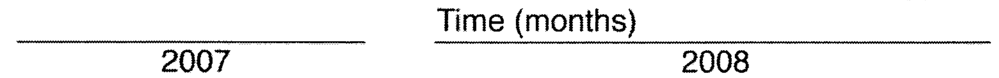

Figure 20. Hours of daylight for the duration of the study with "optimal photoperiod" (8-12hrs) for conchospore release as described by Dring (1967) indicated by the shaded rectangle. Dashed lines represent the timing of each experimental clearing.

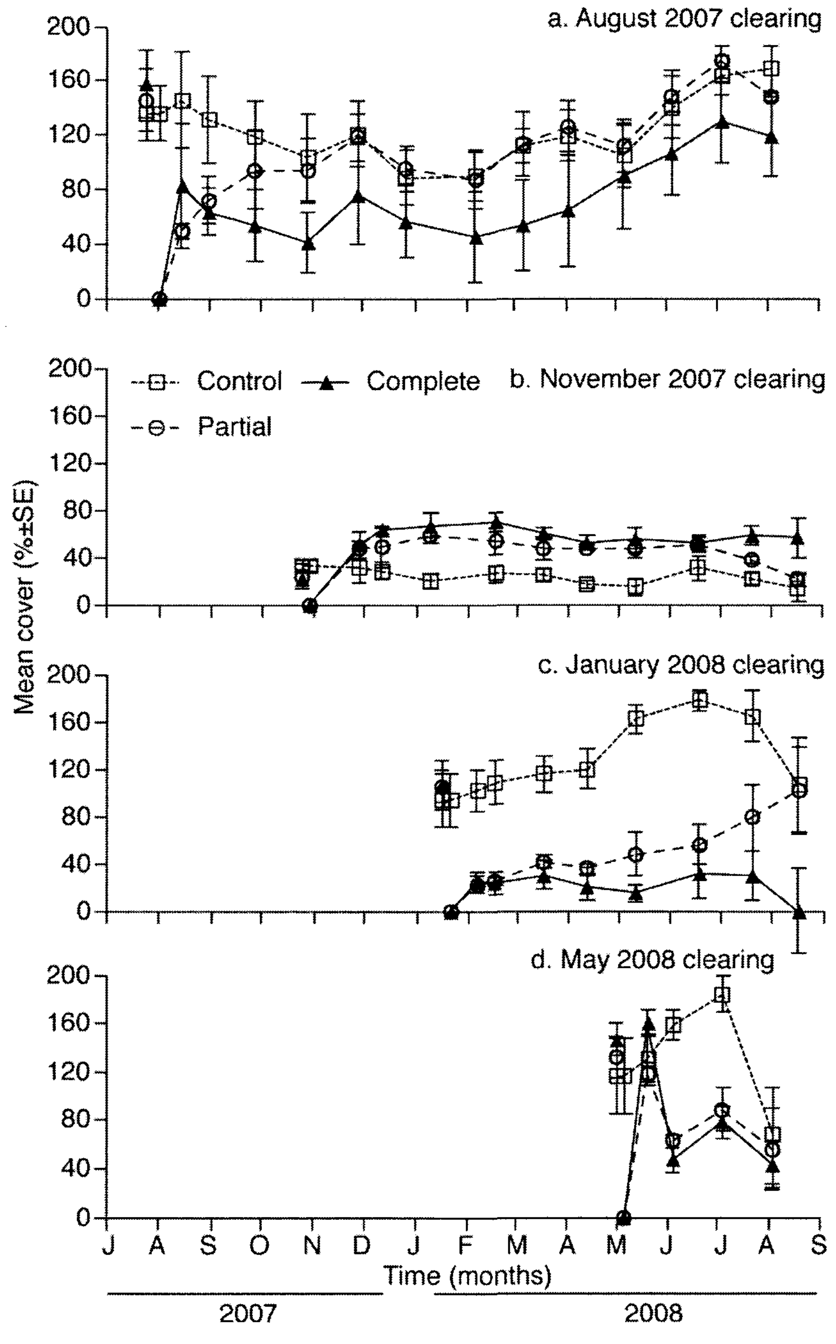

Figure 21. Temporal variability of percentage cover (mean ± SE) of other algae by treatment (□=Control, ○=Partial, ▲=Complete) and time of clearing (a. August 2007; b. November 2007; c. January 2008; d. May 2008) for plots located in the *Mazzaella* zone.

Higher intertidal clearings had greater cover of *Porphyra* than the lower intertidal clearings when differences among zones were observed (Figure 16, August 2007 and May 2008). In fact, often *Porphyra* was the only alga observed in these plots. Conversely, the *Mazzaella* zone was more species rich than the *Porphyra* zone throughout study (Figure 8, Appendix A, two sample t-test, P=0.002). A recent study documented a positive relationship between diversity and algal cover whereas diversity decreased the availability of free space when compared with monocultures (Stachowicz et al. 2008). Increased competition for space resulting from accumulating levels of diverse cover may have contributed to the differences in *Porphyra* cover observed in summer *Mazzaella* zone clearings (Figures 10a & 21).

Photoperiod exceeded the optimal range for conchospore release in March of 2008 which, should have cued conchocelis to decrease production of conchospores and begin propagating more conchocelis (Drew 1954, Dring 1967, Pacheco-Ruíz et al. 2005) (Figure 20). The May 2008 clearings were created four months after the earliest observed *Porphyra* response, just before periods of increased mean monthly tidal elevation at noon and submergence time during daylight hours (Figure 22). Increased submergence during daylight hours has been proposed to increase *Porphyra's* vulnerability to pathogens (Smith 1983) and combined with increased competition and a decreasing propagule supply may explain differences observed between zones in spring and summer clearings.

Establishment of November 2007 and January 2008 plots coincided with the optimal photoperiod for conchospore release (Figure 20). Fall and winter manipulations in the *Mazzaella* zone provided ample substrate for colonization when conchospore availability should have been at its peak. Additionally, these plots experienced lower tidal elevations during daylight hours (Figure 22) when air temperatures are greatest, potentially limiting the establishment of pathogens (Smith 1983). The similarity in *Porphyra* response among zones in fall and winter clearings is likely the combined result of propagule availability, reduced competition, and increased survivorship.

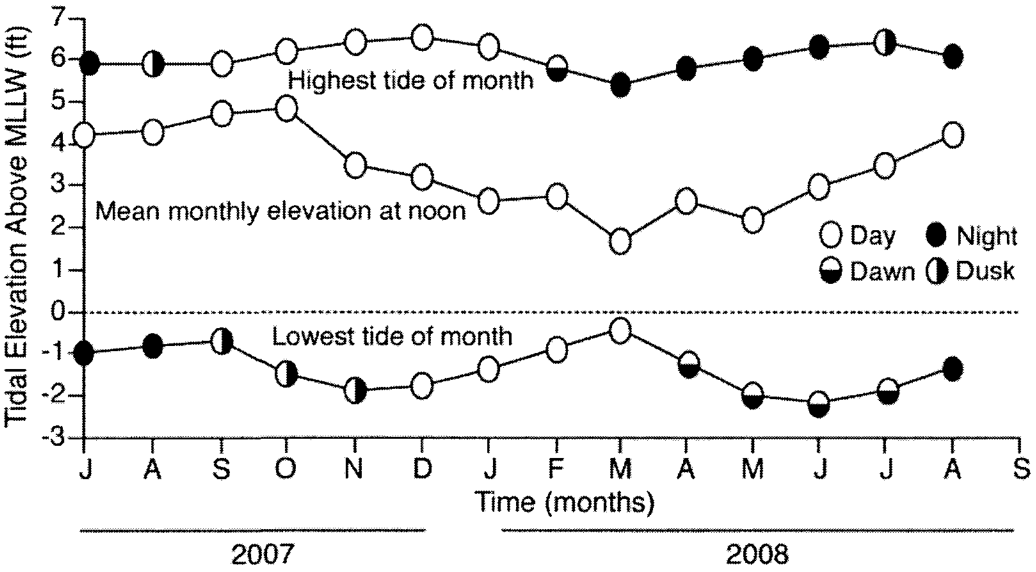

Figure 22. Tidal elevations in feet above mean lower low water (MLLW) of the highest and lowest tides for each month during the study. Also shown are the mean elevations of tides at noon (12:00±0:30min) for each month. Tidal data used to create this figure was obtained from Harbor Master 5.5.8 by Zihua Software, LLC as local NOAA buoys did not collect tide data for the study period.

Several investigations have found that the sequence of succession on rocky reefs is the result of competitive advantages possessed by opportunistic seaweeds and lacking in late successional dominants (Sousa 1979a, Littler and Littler 1980, Connell and Sousa 1983). These same principles can explain the differences among early colonizers observed in this study as supported by the relationship between *Ulva* and *Porphyra* cover (Figure 17). Zone explained the greatest amount of the variability in the model for *Ulva* recruitment (Appendix B). A conspicuous difference between the two zones is the seasonal dominance of *Porphyra* in the high intertidal. The presence of the *Porphyra* foliar phase at the onset of this study indicates the potential for a local "seed bank" provided by the perennial conchocelis phase and can explain why no treatment effect was observed in *Porphyra* recruitment. Local presence of conchocelis may have allowed for *Porphyra* to recruit faster than *Ulva* in clearings that coincided with a decrease in photoperiod (November 2007 and January 2008). *Porphyra* recruited on cue in spring 2008 to all four experiments across both zones. The close proximity of a propagule source could have saturated the study site with *Porphyra* propagules.

The timing of fall and winter clearings also coincided with a decrease in daylight hours and increase in maximum daily wave height (Figure 4). Decreasing photoperiod cues the release of conchospores and increases in water motion can aid in dispersal of propagules (Dring 1967, Sheath and Hambrook 1990, Amsler et al. 1992). The coinciding of available propagules and increase in water motion may have resulted in a competitive advantage for *Porphyra* following fall and winter clearings in the *Mazzaella* zone and may explain why the treatment effect on maximum *Ulva* cover varied with timing of clearing.

Although *Ulva* and *Porphyra* have been identified as early colonizers in countless studies on intertidal succession, they are opportunistic in different ways. *Ulva* responded to clearings created throughout the year, had greater recruitment overall to lower intertidal clearings but utilized recruitment strategies (waterborne propagules, fragments, & sporelings) differently depending on the time of year. Alternatively, *Porphyra* was restricted to a spring response prompted more by a life history cue than a disturbance event.

CONCLUSIONS

Waterborne propagules are an important mechanism for recruitment of early colonizers to clearings created throughout the year. *Ulva* colonization by waterborne propagules was observed throughout the year, whereas *Porphyra* was restricted to spring recruitment, as expected due to temporal cues (changes in photoperiod) regulating propagule availability. Maximum *Ulva* responses varied in treatments as a function of timing of clearing whereas maximum *Porphyra* responses varied in intertidal zones as a function of timing of clearing but was equally abundant in control plots. *Ulva* and *Porphyra* had minimal responses in fall and winter clearings. Further experimentation is needed to rule out a negative interaction between *Ulva* and *Porphyra* in fall and winter disturbances.

Understanding the mechanisms by which organisms recruit can help explain changes in the structure of dynamic communities. This study gives insight into the mechanisms by which some early recruiting species rapidly colonize disturbed substrate. A better understanding of how opportunistic intertidal macroalgae recruit will help to explain future changes in community structure; organisms adapted for recruitment after a disturbance give us an idea of how intertidal communities will look as anthropogenic disturbances increase. Lotze (1999) highlighted the importance of considering all parts of life cycles when investigating the effects of environmental factors (physical and biological) on the population dynamics of macroalgae and organisms in general. In the case of ephemeral species, this aspect is crucial to identifying processes regulating their appearance considering these thalli commonly experience local extinction. Their ability to overcome local extinction makes early colonizers well suited for survival in dynamic environments and may make them best adapted to handle future climate changes.

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Appendices

Appendix A. Detailed list of genera observed in all experimental plots throughout the duration of the study. * indicates genera that were grouped together based on similar ecologic function.

	August 2007		November 2007	
	Mazzaella zone	*Porphyra* zone	*Mazzaella* zone	*Porphyra* zone
Macroalgae	*Amorphous brown blade*	*Acrosiphonia coalita*	*Acrosiphonia coalita*	*Brown crust*
	Analipus japonicus	*Analipus japonicus*	*Analipus japonicus*	*Callathamnion pikeanum*
	Brown crust	*Brown crust*	*Brown crust*	*Chondrocanthus canaliculata*
	Callathamnion pikeanum	*Ceramium spp.*	*Callathamnion pikeanum*	*Cladophora columbiana*
	Ceramium spp.	*Chaetomorpha linum*	*Callophyllis crenulata*	*Cladophora sakaii*
	Chondrocanthus canaliculata	*Cladophora columbiana*	*Chondrocanthus canaliculata*	*Corallina officionalis*
	Cladophora columbiana	*Cladophora stimpsonii*	*Ceramium spp.*	*Cryptosiphonia woodii*
	Cladophora stimpsonii	*Colpomenia peregrina*	*Cladophora columbiana*	*Encrusting coralline*
	Codium setchelii	*Corallina officionalis*	*Cladophora stimpsonii*	*Mastocarpus papillatus*
	Colpomenia peregrina	*Cryptopleura ruprechtiana*	*Codium setchelii*	*Mazzaella flaccida*
	Corallina officionalis	*Cryptosiphonia woodii*	*Colpomenia peregrina*	*Odonthalia fluccosa*
	Cryptopleura ruprechtiana	*Egregia menziesii*	*Corallina officionalis*	*Petalonia faciata*
	Cryptosiphonia woodii	*Endocladia muricata*	*Cryptosiphonia woodii*	*Petrocelis*
	Diatom filaments	*Fucus gardneri*	*Cumagloia andersonii*	*Polysiphonia spp.*
	Egregia menziesii	*Gracilariopsis andersonii*	*Diatoms*	*Porphyra perforata*
	Encrusting coralline	*Mastocarpus papillatus*	*Egregia menziesii*	*Ralfsia*
	Endocladia muricata	*Mazzaella flaccida*	*Encrusting coralline*	*Red Biofilm*
	Fucus gardneri	*Neorhodomela larix*	*Endocladia muricata*	*Red crust*
	Gastroclonium subarticulatum	*Petalonia faciata*	*Fucus gardneri*	
	Gelidium coulteri	*Petrocelis*	*Gastroclonium subarticulatum*	
	Hymenena cuneifolia	*Plocamium cartilagineum*	*Gelidium coulteri*	
	Mastocarpus jardinii	*Polysiphonia spp.*	*Grateloupia setchellii*	
	Mastocarpus papillatus	*Porphyra perforata*	*Mastocarpus jardinii*	
	Mazzaella flaccida	*Ralfsia*	*Mastocarpus papillatus*	
	Mazzaella volans	*Red biofilm*	*Mazzaella flaccida*	
	Microcladia	*Red crust*	*Mazzaella parksii*	
	Neorhodomela larix	*Ulothrix pseudoflacca*	*Microcladia borealis*	
	Petalonia faciata	*Ulva spp.*	*Neorhodomela larix*	
	Petrocelis		*Petalonia faciata*	
	Phyllospadix torreyi		*Petrocelis*	
	Polysiphonia spp.		*Phyllospadix torreyi*	
	Porphyra perforata		*Plocamium cartilagineum*	
	Prionitis lanceolata		*Polysiphonia spp.*	
	Pterosiphonia bipinnata		*Porphyra perforata*	
	Ralfsia		*Pterosiphonia bipinnata*	
	Red biofilm		*Ralfsia*	
	Red crust		*Red biofilm*	
	Rhodoglossum roseum		*Red crust*	
	Rhodymenia callophylloides		*Rhodoglossum roseum*	
	Ulva spp.		*Ulva spp.*	
Sessile invertebrates	*Anthopleura elegantissima*	*Anthopleura elegantissima*	*Anthopleura elegantissima*	*Anthopleura elegantissima*
	*Balanus/Chthamalus**	*Balanus/Chthamalus**	*Balanus/Chthamalus**	*Balanus/Chthamalus**
	Phragmatopoma californica		*Mytilus californianus*	
			Phragmatopoma californica	

Appendix A. Continued

	January 2008		May 2008	
	Mazzaella zone	*Porphyra* zone	*Mazzaella* zone	*Porphyra* zone
Macroalgae	*Acrosiphonia coalita*	*Analipus japonicus crust*	*Analipus japonicus crust*	*Callathamnion pikeanum*
	Analipus japonicus	*Callophyllis crenulata*	*Blue-green film*	*Cladophora columbiana*
	Callathamnion pikeanum	*Cladophora columbiana*	*Chondrocanthus canaliculata*	*Cryptosiphonia woodii*
	Ceramium spp.	*Diatoms*	*Callophyllis crenulata*	*Mastocarpus papillatus*
	Chondrocanthus canaliculata	*Encrusting coralline*	*Cladophora columbiana*	*Neorhodomela larix*
	Cladophora columbiana	*Endocladia muricata*	*Colpomenia peregrina*	*Petalonia faciata*
	Cladophora sakaii	*Mastocarpus jardinii*	*Corallina officionalis*	*Petrocelis*
	Codium fragile	*Mastocarpus papillatus*	*Cryptosiphonia woodii*	*Polysiphonia spp.*
	Codium setchelii	*Mazzaella flaccida*	*Egregia menziesii*	*Porphyra perforata*
	Cladophora sakaii	*Petalonia faciata*	*Encrusting coralline*	*Prionitis lanceolata*
	Colpomenia peregrina	*Petrocelis*	*Endocladia muricata*	*Ralfsia*
	Corallina officionalis	*Plocamium cartilagineum*	*Gastroclonium subarticulatum*	*Red biofilm*
	Cryptosiphonia woodii	*Polysiphonia spp.*	*Hymenena cuneifolia*	*Red Crust*
	Diatom filaments	*Porphyra perforata*	*Mastocarpus jardinii*	*Ulva spp.*
	Egregia menziesii		*Mastocarpus papillatus*	
	Encrusting coralline		*Mazzaella flaccida*	
	Endocladia muricata		*Neorhodomela larix*	
	Fucus gardneri		*Odonthalia fluccosa*	
	Gastroclonium subarticulatum		*Petalonia faciata*	
	Gelidium coulteri		*Petrocelis*	
	Mastocarpus jardinii		*Phyllospadix torreyi*	
	Mastocarpus papillatus		*Plocamium cartilagineum*	
	Mazzaella flaccida		*Porphyra perforata*	
	Mazzaella parksii		*Ptercladia caloglossoides*	
	Microcladia borealis		*Pterosiphonia bipinnata*	
	Neorhodomela larix		*Ralfsia*	
	Petalonia faciata		*Red biofilm*	
	Petrocelis		*Red crust*	
	Phyllospadix torreyi		*Rhodoglossum roseum*	
	Polysiphonia spp.		*Ulva spp.*	
	Porphyra perforata		*Urospora penicilifornes*	
	Pterosiphonia bipinnata			
	Ralfsia			
	Red biofilm			
	Red crust			
	Rhizoclonium riparium			
	Rhodoglossum roseum			
	Silvetia compressa			
	Ulva spp.			
	Urospora dolifera			
	Urospora wormskioldii			
Sessile invertebrates	*Anthopleura elegantissima*	*Anthopleura elegantissima*	*Anthopleura elegantissima*	*Anthopleura elegantissima*
	*Balanus/Chthamalus**	*Balanus/Chthamalus**	*Balanus/Chthamalus**	*Balanus/Chthamalus**
	Phragmatopoma californica		*Phragmatopoma californica*	
	Sponge		*Sponge*	

Appendix B. ANOVA and variance components analysis followed by multiple comparisons' tests describing the effects of disturbance timing (T), location (Z), and treatment (TRT) on response variables that included: a. *Ulva* maximum cover and b. *Porphyra* maximum cover. Omega squared (ω^2) represents the percentage variance explained by each source factor.

a. *Ulva* maximum recruitment

Source	**SS Type III**	**df**	**Mean Square**	**F**	**Sig**	**Variance Component**	**ω^2**
T	0.528	3	0.176	4.438	**0.006**	0.004	5.09%
Z	0.547	1	0.547	13.786	**4E-04**	0.005	6.32%
TRT	0.196	2	0.098	2.467	**0.092**	0.001	1.45%
T*Z	0.233	3	0.078	1.958	0.128		
T*TRT	0.48	6	0.080	2.018	**0.074**	0.004	5.13%
TRT*Z	0.059	2	0.029	0.742	0.480		
T*Z*TRT	0.16	6	0.027	0.673	0.672		
Error	2.855	72	0.040			0.040	47.9%
Total	8.018	96	0.084				

Fisher's LSD evaluation of *Ulva* maximum recruitment, Timing*Treatment (T*TRT)

$\text{Timing}_{(i)}$ $\text{*Treatment}_{(i)}$	$\text{Timing}_{(j)}$ $\text{*Treatment}_{(j)}$	Mean Difference	P-Value
August*Control	August*Partial	-0.310	**0.003**
	August*Complete	-0.270	**0.008**
	November*Control	-0.034	0.735
	November*Partial	-0.012	0.901
	November*Complete	0.038	0.707
	January*Control	-0.028	0.783
	January*Partial	-0.010	0.919
	January*Complete	-0.034	0.734
	May*Control	0.002	0.987
	May*Partial	-0.058	0.565
	May*Complete	-0.213	**0.036**

Timing$_{(i)}$ *Treatment$_{(i)}$	Timing$_{(j)}$ *Treatment $_{(j)}$	Mean Difference	P-Value
August*Partial	August*Complete	0.040	0.687
	November*Control	0.276	**0.007**
	November*Partial	0.298	**0.004**
	November*Complete	0.348	**0.001**
	January*Control	0.283	**0.006**
	January*Partial	0.300	**0.004**
	January*Complete	0.276	**0.007**
	May*Control	0.312	**0.003**
	May*Partial	0.252	**0.013**
	May*Complete	0.097	0.334
August*Complete	November*Control	0.236	**0.020**
	November*Partial	0.257	**0.012**
	November*Complete	0.307	**0.003**
	January*Control	0.242	**0.017**
	January*Partial	0.260	**0.011**
	January*Complete	0.236	**0.020**
	May*Control	0.272	**0.008**
	May*Partial	0.212	**0.036**
	May*Complete	0.057	0.572
November*Control	November*Partial	0.021	0.831
	November*Complete	0.071	0.476
	January*Control	0.006	0.950
	January*Partial	0.024	0.813
	January*Complete	0.000	0.999
	May*Control	0.035	0.723
	May*Partial	-0.024	0.812
	May*Complete	-0.179	**0.076**
November*Partial	November*Complete	0.050	0.617
	January*Control	-0.015	0.880
	January*Partial	0.002	0.982
	January*Complete	-0.021	0.830
	May*Control	0.014	0.887
	May*Partial	-0.045	0.652
	May*Complete	-0.201	**0.047**

Timing$_{(i)}$ *Treatment$_{(i)}$	Timing$_{(j)}$ *Treatment $_{(j)}$	Mean Difference	P-Value
November*Complete	January*Control	-0.065	0.515
	January*Partial	-0.048	0.633
	January*Complete	-0.071	0.475
	May*Control	-0.036	0.720
	May*Partial	-0.095	0.343
	May*Complete	-0.251	**0.014**
January*Control	January*Partial	0.017	0.862
	January*Complete	-0.006	0.949
	May*Control	0.029	0.770
	May*Partial	-0.030	0.764
	May*Complete	-0.186	**0.066**
January*Partial	January*Complete	-0.024	0.812
	May*Control	0.012	0.905
	May*Partial	-0.047	0.635
	May*Complete	-0.203	**0.045**
January*Complete	May*Control	0.036	0.722
	May*Partial	-0.024	0.813
	May*Complete	-0.179	**0.076**
May*Control	May*Partial	-0.059	0.554
	May*Complete	-0.215	**0.034**
May*Partial	May*Complete	-0.156	0.122

b. *Porphyra* maximum recruitment

Source	**SS Type III**	**df**	**Mean Square**	**F**	**Sig**	**Variance Component**	**ω^2**
T	2.809	3	0.936	7.087	**0.000**	0.025	4.48%
Z	4.142	1	4.142	31.35	**0.000**	0.042	7.44%
TRT	0.33	2	0.165	1.25	0.292		
T*Z	2.935	3	0.978	7.406	**0.000**	0.053	9.42%
T*TRT	1.056	6	0.176	1.33	0.254		
TRT*Z	0.396	2	0.198	1.50	0.230		
T*Z*TRT	0.361	6	0.060	0.46	0.839		
Error	9.511	72	0.132				
Total	53.896	96	0.561				

Fisher's LSD evaluation of *Porphyra* maximum recruitment, Timing*Zone (T*Z)

Timing$_{(i)}$ *Zone$_{(i)}$	Timing$_{(j)}$ *Zone$_{(j)}$	Mean Difference	P-Value
August*Porphyra	August*Mazzaella	0.919	**0.000**
	November*Porphyra	0.753	**0.000**
	November*Mazzaella	0.771	**0.000**
	January*Porphyra	0.341	**0.024**
	January*Mazzaella	0.514	**0.001**
	May*Porphyra	0.529	**0.001**
	May*Mazzaella	1.081	**0.000**
August*Mazzaella	November*Porphyra	-0.166	0.267
	November*Mazzaella	-0.148	0.322
	January*Porphyra	-0.577	**0.000**
	January*Mazzaella	-0.405	**0.008**
	May*Porphyra	-0.390	**0.011**
	May*Mazzaella	0.162	0.278
November*Porphyra	November*Mazzaella	0.018	0.904
	January*Porphyra	-0.412	**0.007**
	January*Mazzaella	-0.239	0.112
	May*Porphyra	-0.224	0.136
	May*Mazzaella	0.328	**0.030**

$\text{Timing}_{(i)}$ $^*\text{Zone}_{(i)}$	$\text{Timing}_{(j)}$ $^*\text{Zone}_{(j)}$	Mean Difference	P-Value
November*Mazzaella	January*Porphyra	-0.430	**0.005**
	January*Mazzaella	-0.257	**0.088**
	May*Porphyra	-0.240	0.107
	May*Mazzaella	0.310	**0.040**
January*Porphyra	January*Mazzaella	0.173	0.248
	May*Porphyra	0.188	0.210
	May*Mazzaella	0.740	**0.000**
January*Mazzaella	May*Porphyra	0.015	0.920
	May*Mazzaella	0.567	**0.000**
May*Porphyra	May*Mazzaella	0.552	**0.000**