Hello Darkness: Light adaptations in red algae reinforce patch dynamics in temperate reef commmunitIES

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dedication

For my holdfast, Colin, who swam with a GPS over his head to collect the waypoints

For my mamma, Liza who taught me what a strong woman looks like

For my pops and first dive buddy, Brian, who always understood my passion

For my brother, Devin, who frequently calls just to talk… and coax me into some adventure

For my best friend, Claire, for keeping me curious and always asking the right questions

For the San Diego BEERPIGS chapter, who were the wildest deck of cards

And most importantly, for my sweet pup Ed Ricketts, for being there for it all

“We must remember three things," he said to them. "I will tell them to you in the order of their importance. Number one and first in importance, we must have as much fun as we can with what we have. Number two, we must eat as well as we can, because if we don't we won't have the health and strength to have as much fun as we might. And number three and third and last in importance, we must keep the house reasonably in order, wash the dishes, and such things. But we will not let the last interfere with the other two.”

-John Steinbeck, *The Log from the Sea of Cortez*

ABSTRACT OF THE THESIS

Hello Darkness: Light Adaptations in Red Algae Reinforce Patch Dynamics in Temperate Reef Communities

by

Tristin Anoush McHugh

Master of Science in Biology with a Concentration in Ecology

San Diego State University, 2017

The organization of algae on temperate rocky reefs is dynamic and stochastic, and may be a result of variable oceanographic conditions paired with the algae’s unique life history characteristics. Evidence suggests that algal assemblages are stratified by functional groups, adaptive characteristics, and morphology; each layer has the potential to shade the layer below it and thereby dramatically influence kelp forest community composition. Alternatively, removal of canopy layers has been shown to elicit positive responses in understory assemblages due to increased irradiance at the benthos. Loss of individual algae can occur from disturbances of varying frequencies and magnitudes that can physically remove them from the benthos and thereby alter benthic irradiances. This study addresses gaps in knowledge about the role of red algal ecophysiology in this process through field and laboratory experiments in two geographically distinct locations of California. Specifically, I investigated whether red algal benthic cover is altered under different canopy manipulations (i.e. levels of disturbance), and if the elicited responses by the algae are due to differences in their photophysiology. Counter to expectations, red algal benthic cover in Point Loma and Carmel Bay, CA did not differ among levels of disturbance. In addition to this lack of responses to the experimental canopy manipulations, no differences in red algal photophysiology (measured in oxygen evolution) were detected during laboratory incubations under different irradiances. Rather, simple patchiness in red algae communities accounted for most of the variation observed in both locations, suggesting that community organization likely results, at least in part, from individual species’ life history characteristics, their ecologies, and stochastic processes. This study contributes to a new line of inquiry pertaining to the processes dictating red algal assemblages on temperate rocky reefs, which suggests that photophysiology does not appear to explain observed differences in red algal benthic cover, as had previously been hypothesized, and does not support photophysiology as a mechanism for that organization.

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**INTRODUCTION**

Coastal marine habitats dominated by canopy-forming primary producers (e.g. kelps) are complex ecosystems that are generally characterized by having several distinct macrophyte layers (Reed and Foster 1984, Dayton et al. 1984). Although structurally taller canopies can gather more light for photosynthesis and consequently exert a competitive dominance over those beneath them, these heightened canopies are more susceptible to physical removal by large disturbance events such as winter storms (Reed and Foster 1984, Dayton et al. 1984). Consequently, disturbances that remove these canopies generally elicit direct positive responses in understory primary producers (Dayton et al. 1984, Reed and Foster 1984). In addition, depending on the strength of the physical disturbance, patch gaps (e.g. Dayton et al. 1984) can be minimized or eliminated and lead to homogenization of community composition by opportunistic species (Edwards 1998).

Despite these observations, the responses of understory species to canopy loss under different levels of disturbance remains unknown. Equilibrium hypothesis suggests that maximum species diversity, ecosystem stability, and local coexistence are all reached at intermediate levels of disturbance with regard to their frequency, magnitude, and timing (Connell 1978). For example, if disturbances are infrequent and weak, diversity can be lost due to monopolization of space by species exhibiting competitive dominance through resource allocation, or their life history characteristics (Eggling 1947, Lubchenco and Menge 1978, Souza 1979, Connell 1979). Conversely, if disturbances are frequent and strong, organisms able to colonize quickly are able to proliferate and can sometimes outcompete dominant competitors (Dayton 1971, Connell 1973, 1976). The frequency of disturbances has generally been defined by ecologists as being either “infrequent” or “frequent”. “*Infrequent”* disturbances are defined as events that occur on an annual basis and typically result in the system returning to its ‘pre-disturbance state’ following the perturbation (Bender 1984, Dayton et al. 1984, Dayton 1985, Dayton et al. 1992). In contrast, “*frequent”* disturbances have generally been defined as recurring seasonal events that prevent community assemblages from returning to equilibrium by altering competitive hierarchies among the species (Mac Arthur 1958, Levins 1968, Bender et al. 1984). Further, the magnitude of disturbances, “*strong”* or *“weak”,* within forest ecosystems has direct implications for community recovery and composition (Dayton et al. 1984, Reed and Foster 1984, Edwards 1998, Clark et al. 2004). While *“Weak”* disturbances may only remove canopies, *“Strong”* disturbances have the ability to remove most or all individuals from a system. Consequently, the frequency (*Frequent* or *Infrequent*) and magnitude (*Weak* or *Strong*) to which a disturbance persists can have contrasting consequences for forest community composition, especially in systems where habitat-forming species are primary producers that organize as layers within the ecosystem.

Much like terrestrial forests, kelp forests are dynamic and complex due to variable abiotic conditions paired with a variety of species’ unique life history characteristics (Abbott and Hollenberg 1974, Schiel and Foster 2015). Kelp forests along the coast of California, in particular, can generally be divided into five stratified categories; **1) surface** **canopies**supported primarily by *Macrocystis pyrifera,* **2) sub-canopies** supported primarily by the stipitate kelps *Pterygophora californica* and *Eklonia arborea,* both of which occur up to 1-2 m above the substratum, **3) understory algae** prostrate canopies supported primarily by the kelp *Laminaria farlowii* and the annual brown alga *Desmarestia ligulata,* both of which lie on or <1m above the substratum, **4) red algae** supported by a diverse array of filamentous and foliose red and erect coralline algae, and **5) encrusting coralline algae** that adhere to the benthos and function as part of the substrate (Reed and Foster 1984, Dayton et al. 1984, Tegner and Dayton 1987, Schiel and Foster 2015). Each layer has the potential to shade the layer below it and exert a direct negative effect on that subsequent layer. Further, each layer may also impact the entire community through competition for space during settlement and recruitment events (Reed and Foster 1984, Dayton et al. 1984, Clark et al. 2004, Edwards and Connell 2012). In addition, seasonal fluctuations in abiotic conditions strongly impact the timing of benthic succession as well as algal growth and abundance (Edwards 1998, Schiel and Foster 2015). This interaction between biotic and abiotic factors creates a dynamic environment for species that photosynthesize (Dayton et al. 1984, Reed and Foster 1984, Clark et al. 2004); however, the effects of disturbances on kelp forest ecosystems vary depending on their frequency and magnitude (Connell 1978, Souza 1979).

Winter storms typically disturb kelp forest ecosystems through large swell and surge that physically remove surface canopies (Seymour et al. 1989). This process has been observed to subsequently increase understory algal abundances due to the absence of the competitive dominant canopy species, *Macrocystis* (Reed and Foster 1984, Dayton et al 1984, Edwards 1998). However, once *Macrocystis* canopies recover, the ecosystem typically returns to an equilibrium state (Dayton et al. 1984; Edwards and Hernandez-Carmona 2005). In contrast, after a El Niño Southern Oscillation (ENSO) events, which are characterized, in part, by frequent and strong storm disturbance events during winter months, *Macrocystis* canopies typically remain absent or at low abundances over large areas of coastline (Edwards 2004, Edwards and Estes 2006). Loss of this habitat- and canopy-forming species due to ENSO conditions can persist from weeks to decades depending on the degree to which associated perturbations suppress new or dormant developing microscopic stages (Edwards 2004, Edwards and Hernandez-Carmona 2005). In addition to short-term or punctuated storm conditions, warm water can negatively impact the growth and health of individual algal species (Zimmerman and Kremer 1984). The 1997-1998 ENSO, for example, caused widespread *Macrocystis* loss across its native range in California and Baja California; the magnitude of these impacts varied greatly among latitudes and the level of wave exposure (Edwards and Estes 2006). Thus, the strength of a disturbance must be considered when examining the resilience and recovery of kelp forest ecosystems, as the ecological implications have yet to be fully understood (Connell et al. 1974, Turner and Dale 1998).

Understanding the effects of large, infrequent disturbances (LIDs) provides ecologists with the opportunity to examine an ecosystem under unique extreme circumstances (Turner and Dale 1998). A study by Edwards (2004) investigated scale-dependency in disturbance impacts in kelp forests at 90 sites, spanning from Baja California Mexico to Central California USA. Over this large geographic range, the large 1997-1998 ENSO had variable impacts on kelp forest community resilience and recovery. For example, the kelp forests were severely disturbed in Baja and Southern California, but not in central California; while recovery of these forests was rapid (occurring within six months) in southern California, but was slow (up to two years) in some locations in Baja California. Some of the differences in recovery times may have been due to physiological differences among the *Macrocystis* populations; *Macrocystis* exhibits ecotypic adaptation such that populations in cooler waters may become nutrient limited at higher nitrate levels than populations in warmer waters (Kopczak et al. 1991). Central California is characterized as having lower water temperatures, higher nutrients, and larger waves (Edwards and Estes 2006). In contrast, southern California experiences greater variation in temperature and nutrients, and thus affecting recovery time (Reed et al. 2011). How the understory algal communities were impacted and recovered is still unclear; as they are also susceptible to differing levels of disturbance (Reed and Foster 1984, Clark et al. 2004, T. McHugh pers. obs).

Historically, many subtidal kelp forest studies have focused on the effects of canopy loss on sub-canopy and understory algal layers (Reed and Foster 1984, Dayton et al. 1984, Tegner and Dayton 1987, Edwards 1998, Clark et al. 2004). However, little attention has focused on the physiological responses within the diverse group of red algae found beneath the canopy, sub-canopy, and understory algal layers. In a study investigating how shading and benthic light levels structure red algal assemblages, Clark et al. (2004) performed a series of experimental surface and sub-canopy manipulations in Stillwater Cove, Carmel Bay, California, USA over the course of two years. During this study, Clark et al. observed differences in red algae abundances and community composition within different canopy manipulation (removal) treatments. Subsequently, they grouped red algae into categories based on their response to each treatment: high, intermediate, and low light-adapted. Results suggested that total red algal abundances fluctuated seasonally, reaching maximum coverage on the benthos in the Spring, decreasing throughout the Summer, then reaching a minimum by the Winter (Clark et al. 2004). Nonetheless, the underlying process that governed this process remains unclear. Prior work suggests phenotypic plasticity among species (i.e. adaptation to different light regimes), but these studies have not addressed potential photosynthetic differences among the algae directly.

To fill the knowledge gaps in our understanding of canopy impacts on red algal assemblages, our study incorporates red algae photophysiology as a possible explanation for differences in red algae community structure following disturbances to the kelp canopies. The overarching goal of this study is to better understand how red algae respond to disturbance-induced changes in the light environment (i.e. canopy shading) using a photophysiological approach. Specifically, I addressed the following questions:

***Question 1: How do infrequent and frequent disturbances to kelp canopies impact red algal community assemblages, and does benthic cover vary among red algal species and/or between geographic locations?***

* + ***Hypothesis 1a:*** *Red algal benthic cover will be greatest in treatments with the maximum level of disturbance (Frequent-Strong) and lowest in unmanipulated treatments.*
  + ***Hypothesis 1b:*** *The impact of disturbances will differ between geographic locations.*

***Question 2: Do red algae differ in their light adaptations, and do they change seasonally?***

* + ***Hypothesis 2a:*** *Species that recruit in the treatments with the maximum level of disturbance (Frequent-Strong) will exhibit high-light adaptation characteristic.*
  + ***Hypothesis 2b:*** *Species light adaptations will fluctuate seasonally; maximum in Spring, and minimum in Winter.*

**METHODS**

System and Study Species

*System*

This study took place in two biogeographically distinct geographic locations in California that experience differences in oceanographic conditions and that have been historically targeted by researchers investigating kelp forest community composition following disturbances (e.g. Dayton et al. 1984, Reed and Foster 1984). The specific study locations are Point Loma, southern California (32.693629 N, 117.260857 W) and Carmel Bay, central California (36.541936 N, 121.952999 W); hereafter Point Loma and Carmel Bay. The two locations of study allowed us to collaborate with multiple partners (San Diego State University, UC Santa Cruz, UC Davis, Moss Landing Marine Laboratories, Monterey Bay Aquarium) to examine the impacts of prolonged and intense storm disturbance events on the California coastline.

In both Point Loma and Carmel Bay, Geographic Information System (ArcGIS) imagery of surface canopies paired with scouting dives and historic data sets facilitated site selection. Site selection criteria were based on qualitative similarities in 1) exposure to wave disturbance, 2) depth (13-15m), 3) substrate type, 4) presence of *Macrocystis* canopy cover, and 5) benthic algal assemblages*.* Sites were specifically chosen to target healthy and productive ecosystems where *Macrocystis* and understory algae occur in dense forests (North 1974, Dayton et al. 1984).

In southern California, the study sites were within the Point Loma kelp forest region, which is one of the largest (~11km) and most productive kelp forests in Southern California (Dayton et al. 1984). This system has been studied extensively by subtidal ecologists and research groups since the 1980s (e.g. Dayton et al. 1984, Dayton 1985, Tegner and Dayton 1987, Dayton et al. 1992). During this study (Fall 2015- Summer 2017), the Point Loma region experienced storm events (Figure 1a), and large temperature fluctuations (Figure 1b). The specific sites used for this study were characterized by a relatively flat sandstone bedrock substrate, and tidally driven currents (pers. obs.).During initial surveys divers observed the red alga *Acrosorium venulosum* flourishing as an epiphyte on other red algae species such as *Prionitis linearis, P. lanceolata, Rhodymenia californica* and, most predominantly, onarticulated coralline algae. Therefore, on species where epiphytic growth reached ~100%, it was recorded as ‘*A. venulosum’* (Table 1). Study sites (n=3) were separated by ~1 kilometer and occurred at a depth between 14-15m. Algal species observed by diver surveys were documented to compare species presence with those in Carmel Bay (Table 1). Lastly, in conjunction with warmer sea surface temperatures, southern California is frequently nutrient-limited (Tegner and Dayton 1987, Edwards 2004). When temperatures exceed ~17 °C nitrate concentrations drop to about 1μM, which significantly impairs *Macrocystis* survival and growth rates (Jackson 1977, Tegner and Dayton 1987, Zimmerman and Kremer 1984, Edwards 2004). During this study, Point Loma often reached surface seawater temperatures exceeding 17 °C, which certainly could have influenced algal recovery and growth (Figure 1b).

The study sites within the Carmel Bay region are within the Monterey Bay National Marine Sanctuary (MBNMS). Similar to Point Loma, Stillwater Cove within Carmel Bay is a “historic site” that has been monitored extensively by researchers pre-dating the 1980s (e.g., Reed and Foster 1984, Edwards 1998, Clark et al. 2004). Specific sites used for this study were characterized by a rugose granite bedrock substrate with sand channels running between reefs. Within the study area, study sites (n=3) were separated by ~0.8 kilometers. Within the Carmel Bay region, algal species were documented to compare species presence with those in Point Loma (Table 1). Further, central California is typically characterized by colder waters and higher nutrient levels; the system is conditioned to more frequent winter storm disturbances versus those experienced in southern California (Jackson 1977, Pennington and Chavez 2000, Edwards 2004) (Figure 1a, Figure 2a).

Figure 1: Point Loma oceanographic conditions measured at nearby Buoy Station 46232- Point Loma South, CA (191). Note oceanographic data for 2017 ends in September. (a) Daily averages of significant wave height (meters) during study 2015-2017. (b) Daily averages of SST water temperature (°C) during study 2015-2017.

Figure 2: Carmel Bay oceanographic conditions measured at nearby Buoy Station 46114 - West Monterey Bay, CA (185). Note oceanographic data for 2017 ends in September. (a) Daily averages of significant wave height (meters) during study 2015-2017. (b) Daily averages of SST water temperature (°C) during study 2015-2017. Conditions reported by the West Monterey Buoy reflect those experienced in Carmel Bay, although Monterey experiences slightly warmer water temperature due to a slightly more relaxed upwelling regime (Edwards 1998).

*Study Species*

Red algae (phylum Rhodophyta) are the most diverse group of algae with greater than 6,000 known species in marine and freshwater ecosystems (http://www.algaebase.org/). Their global distribution and diverse morphologies allow red algae to colonize many hard-substrate benthic habitats and support diverse species assemblages of small invertebrates (Foster 1985, Harrold et al., 1998, Hirst 2007). 459 species of red algae have been observed in California’s coastal waters, most of which are perennial and provide ecosystem services to small temperate reef organisms (Abbott and Hollenberg 1974). Indeed, foliose red algae create habitat for invertebrates, and indirectly benefit microcarniverous fish that prey on the invertebrates; thus, alterations to algal composition can consequently alter associated invertebrate composition and abundance (Mahoney 2015).

**Table 1: Species of algae present with moderate abundance (>10 recorded instances as primary placeholder during community surveys) in Point Loma and Carmel Bay during this study. Species presence within locations are denoted by a binary response: “X” denotes presence and an empty cell denotes the species was not observed. Species with asterisks (\*\*\*) were analyzed for this study.**

|  |  |  |
| --- | --- | --- |
| **Point Loma and Carmel Bay** | **Point Loma** | **Carmel Bay** |
| *Macrocystis pyrifera* | X | X |
| *Desmarestia ligulata* | X | X |
| *Pterygophora californica* | X | X |
| *Sargassum horneri* | X | X |
| *Cystoseira osmundacea* | X | X |
| *Laminaria farlowii* | X | X |
| *Laminaria setchelii* |  | X |
| *Eklonia arborea* | X |  |
| *Dictyota dichotoma* | X | X |
| Articulated Coralline spp. | X | X |
| Encrusting Red spp. | X | X |
| *Rhodomenia californica\*\*\** | X | X |
| *Rhodomenia pacifica* | X | X |
| *Botryocladia pseudodichotoma* | X | X |
| *Botryocladia neushelii* | X | X |
| *Callophyllis flabelluata* | X | X |
| *Gelidium spp.* | X | X |
| *Prionitis lancelota\*\*\** | X | X |
| *Prionitis linearis\*\*\** | X | X |
| *Cryptopleura ruprechtiana* | X |  |
| *Cryptopleura farlowiana\*\*\** | X | X |
| *Acrosorium venulosum\*\*\** | X |  |
| *Plocamium cartilagineum\*\*\** | X | X |
| *Laurencia pacifica* | X |  |
| *Gigartina corymbifera* | X |  |
| *Microcladia coulteri* |  | X |
| *Freyella gardeneri* |  | X |

**Experimental Design**

***Question 1****:* ***How do infrequent and frequent disturbances to kelp canopies impact red algal community assemblages, and do these impacts vary among red algal species and/or with geographic location?***

**Experimental Manipulations of Canopy Layers**

To simulate disturbances to the different kelp canopy layers, I conducted experimental clearings of the surface, subsurface, and understory canopies in three sites (= blocks) within both the Point Loma and Carmel Bay kelp forests. In Point Loma work occurred from Fall 2015 to Fall 2017, and in Carmel Bay from Spring 2016 to Fall 2017. Due to the 2015-2016 ENSO event, and logistics surrounding subtidal field surveys, I was unable to establish Carmel Bay sites until Spring 2016. Seasons are described as 1) Fall- November 2) Winter-December/January 3) Spring- May/June 4) Summer- August/September. The experimental design can be further broken into geographic locations or Locations(repeated in Point Loma and Carmel Bay), Sites within each Locations (n=3), Treatments blocked at each Site (n=4), and nine quadrats sampled per treatment (Figure 3). Four experimental treatments were established within each site to detect the impacts of storm frequency (*Frequent* or *Infrequent*) and magnitude (*Strong* or *Weak*) (Table 2). To assess frequency, I compared the treatments *Frequent-Strong* (FS) to *Infrequent-Strong* (IS), andto assess magnitude, I compared the treatment FSto *Frequent-Weak* (FW).To assess changes to the community that were driven by natural phenomena in the field, all treatments were compared to the *Control.*

Within each of the four experimental treatments, divers removed selected vegetative layers with a knife, while leaving reproductive sporophylls intact. “*Strong*” treatments were removed of canopy-forming brown algal layers such as *Macrocystis, Laminaria setchelli, Laminaria farlowii, Pterygophora californica, Dictyota spp., Sargassum spp., Cystoseira osmundacea, Desmarestia ligulata, and Eklonia arborea. “Weak”* treatments were only removed of canopy-forming *Macrocystis* algae layer*.*

**Table 2: Treatments of varying frequency and magnitude and their descriptions.**

|  |  |  |  |
| --- | --- | --- | --- |
| **Treatments** | **Abbreviation** | **Timing of clearing** | **Description** |
| *Frequent-Strong* | FS | Seasonal | Canopy-forming algae removed |
| *Infrequent-Strong* | IS | Annual | Canopy-forming algae removed |
| *Frequent-Weak* | FW | Seasonal | *Macrocystis* removed |
| *Control* | Control | n/a | n/a |

**LOCATION (N=2)**  Point Loma or Carmel Bay

**SITE (block) (N=3)**  A B C

**TREATMENT (N=4)**

FS IS FW Control

**QUADRAT (N=9)** 1 2 3 4 5 6 7 8 9

**Figure 3: Hierarchical sampling design used to measure benthic percent cover of primary placeholders and large mobile invertebrates.**

Treatments were marked with permanent bolts that were drilled into the benthos with a Chicago pneumatic drill (R900 Chicago brand®) and secured with marine-grade epoxy (Z-Spar ‘Splashzone’ A-788®). Each treatment had a radius of 7m (area=156m2), and were separated by at least 5m from the next treatment (i.e., bolts were placed 19m apart). Additionally, to ensure that divers could locate the exact location of the treatments, GPS waypoints were recorded for each treatment at each site, and bolts were marked with neon twine, PVC, and flagging tape.

To assess seasonal variation in algal benthic percent cover over time, quadrat surveys were conducted to quantify the benthic cover of primary placeholders within sites and urchin presence was recorded to quantify potential grazing pressure, using Random-Point Contacts (RPC; 16-points within 0.5m2 quadrats. Specifically, at the origin of each treatment three (N=3) meter tapes were randomly reeled-out to 7m (radius of the treatment), and three quadrats were sampled per meter tape, for a total of nine quadrats sampled per treatment.

**Statistical Analysis**

This study was conducted in two distinct biogeographical locations with different temporal starting points. Therefore, findings will be presented for each geographic location separately as they involve independent analyses. Statistical analyses for community data were done using PRIMER version 6.1.13 and PERMANOVA version 1.0.3 (PRIMER-E, Quest Research Limited©). All percent cover data were square-root transformed prior to analysis to meet requirements of normality and homoscedasticity (Sokal and Rohlf, 1995). Similarities in assemblage composition were based on Bray-Curtis similarities prior to statistical analysis. To assess changes in benthic percent cover among disturbance treatments and seasons at each location, I used separate three-way Model I randomized blocked PERMANOVAs, with the factors Season (fixed with six levels), Site=block (with three levels), and Treatment (fixed with four levels). If any factor detected statistical significance (p<0.05), permutation post hoc tests were done to identify pairwise differences. Additionally, PERMANOVA analyses testing season across site and treatments were performed as post-hoc analyses to determine differences in red algal benthic percent cover. Similarities Percentages (SIMPER) analysis were utilized to determine which species were primarily responsible for Bray-Curtis dissimilarities among treatments varying in frequency and magnitude of disturbance.

Univariate statistical analyses for individual species were done using SYSTAT version 13.1 (2017 SYSTAT Software Inc.©). Although p-values can be utilized to detect differences across each of the factors and their interactions, I utilized variance partitioning to help understand the contribution of each factor to the different responses seen each of the individual red algae species (Urquhart et al 1998, Larsen et al. 2001, Graham and Edwards 2001, Sims et al. 2006). Negative estimates of variation were set to zero (Graham and Edwards 2001).

**Photosynthesis versus Irradiance curves**

***Question 2:******Do red algae differ in light adaptations, and do they change seasonally?***

To understand how light levels at the benthos impact algal community structure, and to gain a deeper understanding of why certain species vary in density among the different treatments, I investigated the functional relationships between irradiance and rates of photosynthesis for each of the dominant red algae within each location (Table 1). Within each location, red algae were collected seasonally from within 1km of the study sites to avoid disrupting the experimental clearings, and to respect the boundaries of the Monterey Bay National Marine Sanctuary (MBNMS), and Stillwater Cove State Marine Conservation Area (SMCA) located within Carmel Bay. Live algal samples were transported to San Diego State University’s Coastal Marine Institute Laboratory (CMIL), placed into aquaria with oxygen bubblers, and were stationed within a temperature-controlled room matching the source-site conditions (10-15°C); algae were held in a Coleman 48 Quart Cooler® in total darkness for two days prior to laboratory experiments.

To assess species-specific photophysiology, I identified the most abundant red algae that recruited seasonally in Fall 2016, Spring 2017, and Summer 2017 within each location, and examined the functional relationship between photosynthesis and irradiance to assess their photosynthetic performance under different light levels. Understanding the functional relationship between photosynthesis and irradiance allowed me to corroborate treatment effects on benthic percent cover, and assess if species that recruited into the different treatments differed in photophysiology. To measure photosynthesis under varying light conditions, these samples were exposed to seven progressively increasing light levels (0, 15, 40, 120, 370, 500 700, and 1400 μmol m-2 s-1) for 10 minutes each, resulting in a total sample time of 80 minutes per individual (minimum replicates per species: n=3) (Kim et al. 2015). A minimum of three replicates of each species were individually placed in a 250 biological oxygen demand (BOD) chamber that was temperature-controlled with a water jacket, and oxygen evolution was monitored using an optical oxygen sensor (YSI ProODO®). Replicates were averaged to obtain species-level estimates of photosynthetic parameters. Because of differences between the two geographic locations (nutrient levels, phytoplankton, temperature), seawater used for analysis was collected regionally. Further, samples were also run with no algae present in the incubation flasks to examine changes in water chemistry that were not attributed to the algae under investigation.

To assess the functional relationship between photosynthesis and irradiance, I used the program Grapher (Grapher ver. 8©) to generate dose-response curves of oxygen evolution per gram of algae per hour versus irradiance, and construct photosynthesis versus irradiance (P-I) curves (Kim, J.H. person. comm.). P-I curves yielded: a) α - photosynthetic efficiency under non-saturating irradiances; b) Pmax - maximum rate of photosynthesis under saturating irradiances; c) IK - light saturation point; and d) R- respiration rate at total darkness. Further, Pmax, alpha and R reflect the photosynthetic characters used to assess differences in photoadaptations, and were used to create P-I curves within Grapher. Specifically, the following equation was used to create best-fit lines to assess temporal light adaptations in red algae species (Webb et al. 1974):

Y = Pm\*(1-exp(-alpha\*x/Pm))-respiration

**RESULTS**

**Point Loma, San Diego, Southern California**

***Question 1: How do infrequent and frequent disturbances to kelp canopies impact red algal community assemblages, and does benthic cover vary among red algal species and/or between geographic locations?***

During this study (2015-2017), the coast of California experienced oceanographic conditions characteristic of an ENSO event that not only brought large and destructive waves, but also anomalously warm ocean water. Further, urchin outbreaks or ‘barrens’ that began dominating Carmel Bay in 2014 expanded in range and were observed within the experimental treatments during final surveys in Summer 2017. By comparison, Point Loma suffered from massive kelp canopy loss and struggled to regain *Macrocystis* canopy cover across the entire bed by Summer 2017. Despite differences in oceanographic conditions that occurred in both biogeographically distinctive locations, the experimental treatments were maintained in both Point Loma and Carmel Bay for the duration of this study. In addition, red algal communities in both locations ultimately responded similarly to treatments over time in that red algal benthic percent cover did not differ among any of the treatments across season. Therefore, these results suggest that features other than light appear to be driving the organization of subtidal red algae communities.

*Preliminary Red Algal Community Surveys*

In Fall 2015, prior to experimental manipulations, no differences were detected in red algal community composition across sites, treatments, or the interaction between treatments and sites in Point Loma (Table 3). On average, *A. venulosum* occupied 22.2% more of the benthos in the FW versus FS treatment, and contributed to 38.78% of the total dissimilarity between the two treatments (see Appendix A, Table 16). Most of the dissimilarity between FS and FW treatments were driven by *A. venulosum*, *Laurencia pacifica,* filamentous red algae (turf), and juvenile red algae (Table 4). Between FS and IS treatments, most of the dissimilarity was driven by *A. venulosum*, *L. pacifica*, *Gigartina corymbifera,* and juvenile red algae.

**Table 3: Results of PERMANOVA testing differences in red algal community composition across sites and treatments in Fall 2015. P-values are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** | **% variation** |
| **Site (SI)** | 2 | 0.70814 | 0.35407 | 1.9186 | 0.074 | 10.66 |
| **Treatment (TR)** | 3 | 0.55073 | 0.18358 | 0.99476 | 0.432 | 4.37 |
| **SixTr** | 6 | 1.0115 | 0.16858 | 0.9135 | 0.602 | 0 |
| **Res** | 24 | 4.429 | 0.18454 |  |  | 84.97 |

**Table 4: Results of Similarities Percentages (SIMPER) analysis for Fall 2015 showing which species within the entire kelp forest community were primarily responsible for Bray-Curtis dissimilarity between treatments varying in frequency and magnitude of disturbance (Magnitude: Frequent-Strong v. Frequent-Weak, Frequency: Frequent-Strong v. Infrequent-Strong). Species presented have a contribution percentage >4%.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ***Frequent-Strong* vs. *Frequent-Weak***  **Avg. Dissimilarity= 63.81** | | | | | | |
| **Species** | FS Av.Abund | FW Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| ***Acrosorium venulosum*** | 0.51 | 0.38 | 24.71 | 0.92 | 38.72 | 38.72 |
| ***Laurencia pacifica*** | 0.1 | 0.08 | 8.8 | 0.65 | 13.78 | 52.5 |
| **Filamentous reds (turf)** | 0.08 | 0.08 | 6.28 | 0.69 | 9.84 | 62.34 |
| **Red juvenile** | 0.04 | 0.08 | 5.9 | 0.57 | 9.24 | 71.58 |
| ***Gigartina corymbifera*** | 0.08 | 0.04 | 5.43 | 0.59 | 8.51 | 80.09 |
| ***Prionitis linearis*** | 0 | 0.08 | 4.89 | 0.5 | 7.67 | 87.76 |
| ***Plocamium cartilagineum*** | 0.08 | 0 | 3.26 | 0.52 | 5.1 | 92.87 |
| **Frequent-Strong vs. Infrequent-Strong**  **Avg. Dissimilarity= 58.71** | | | | | | |
| **Species** | Av.Abund | Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| ***Acrosorium venulosum*** | 0.51 | 0.33 | 29.96 | 0.89 | 50.97 | 50.97 |
| ***Laurencia pacifica*** | 0.1 | 0 | 6.53 | 0.47 | 11.11 | 62.08 |
| ***Gigartina corymbifera*** | 0.08 | 0.04 | 6.36 | 0.6 | 10.82 | 72.9 |
| **Red juvenile** | 0.04 | 0.06 | 5.34 | 0.45 | 9.09 | 81.99 |
| ***Plocamium cartilagineum*** | 0.08 | 0 | 3.8 | 0.53 | 6.47 | 88.46 |

*Effects of Disturbances of Varying Frequency and Magnitude*

In Point Loma, red algae benthic percent cover did not appear to be greatly influenced by the frequency and magnitude of disturbances expressed by the four treatments (Table 5). Instead, red algal communities differed by season, and the interaction between seasons and treatment. When testing sites and treatments within each season to investigate differences in red algal community composition, it was observed that communities began to differ by site in Spring 2016 (Table 6). In addition, by Summer 2016, the interaction between sites and treatment yielded differences in red algal communities. Isolation of variance components revealed that *small-scale variability* (i.e. quadrat-to-quadrat differences) contributed greatly to red algal benthic percent cover (Table 5). Therefore, the community assemblages of red algae observed in Point Loma do not appear to be greatly influenced by experimental manipulations of the different canopy layers.

**Table 5: Results of PERMANOVA with selected variables: season, site (blocked) and treatment. Selected variables were utilized for testing differences in red algal community composition in Point Loma from Fall 2015-Summer 2017. P-values are uncorrected, and are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** | **% variation** |
| **Season (SE)** | 5 | 49620 | 9923.9 | 10.937 | **0.001** | 16.07 |
| **Site (SI)** | 2 | 7099.1 | 3549.6 | 8.3075 | **0.001** | 3.33 |
| **Treatment (TR)** | 3 | 4870 | 1623.3 | 1.4811 | 0.206 | 0.73 |
| **SExSI** | 9 | 8089.6 | 898.84 | 2.1037 | **0.001** | 2.36 |
| **SExTR** | 15 | 16565 | 1104.3 | 1.49 | **0.025** | 2.60 |
| **SIxTR** | 6 | 6435.5 | 1072.6 | 2.5103 | **0.001** | 2.75 |
| **SExSIxTR** | 27 | 19891 | 736.72 | 1.7243 | **0.001** | 6.19 |
| **Res** | 469 | 2.00 E+05 | 427.27 |  |  | 65.97 |
| **Total** | 536 | 3.19+05 |  |  |  |  |

**Table 6: Results of PERMANOVA testing site (blocked) and treatments for each season to investigate if there were differences in red algal community composition in Point Loma. Significant p-values are in bold.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Fall 2015** | | | | | |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** |
| **Site (SI)** | 2 | 0.70814 | 0.35407 | 1.9186 | 0.074 |
| **Treatment (TR)** | 3 | 0.55073 | 0.18358 | 0.99476 | 0.432 |
| **SIxTR** | 6 | 1.0115 | 0.16858 | 0.9135 | 0.602 |
| **Res** | 24 | 4.429 | 0.18454 |  |  |
| **Spring 2016** | | | | | |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** |
| **Site (SI)** | 2 | 4829.6 | 2414.8 | 5.5696 | **0.001** |
| **Treatment (TR)** | 3 | 2262.7 | 754.24 | 1.5369 | 0.17 |
| **SIxTR** | 6 | 2944.5 | 490.75 | 1.1319 | 0.315 |
| **Res** | 96 | 41623 | 433.57 |  |  |
| **Summer 2016** | | | | | |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** |
| **Site (SI)** | 1 | 1790 | 1790 | 4.8694 | **0.001** |
| **Treatment (TR)** | 3 | 4934.5 | 1644.8 | 1.0485 | 0.469 |
| **SIxTR** | 3 | 4706.4 | 1568.8 | 4.2676 | **0.001** |
| **Res** | 63 | 23159 | 367.6 |  |  |
| **Fall 2016** | | | | | |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** |
| **Site (SI)** | 2 | 3133 | 1566.5 | 3.9748 | **0.001** |
| **Treatment (TR)** | 3 | 2391 | 797.01 | 0.8373 | 0.612 |
| **SIxTR** | 6 | 5711.2 | 951.87 | 2.4152 | **0.001** |
| **Res** | 96 | 37835 | 394.11 |  |  |
| **Spring 2017** | | | | | |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** |
| **Site (SI)** | 2 | 2365.8 | 1182.9 | 2.6219 | **0.011** |
| **Treatment (TR)** | 3 | 5408.6 | 1802.9 | 1.7127 | 0.116 |
| **SIxTR** | 6 | 6316.7 | 1052.8 | 2.3335 | **0.001** |
| **Res** | 95 | 42861 | 451.17 |  |  |
| **Summer 2017** | | | | | |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** |
| **Site (SI)** | 2 | 3560.3 | 1780.2 | 3.6312 | **0.002** |
| **Treatment (TR)** | 3 | 6286.4 | 2095.5 | 1.8834 | 0.126 |
| **SIxTR** | 6 | 6676.7 | 1112.8 | 2.2699 | **0.002** |
| **Res** | 95 | 46573 | 490.24 |  |  |

Individual red algal species*, R. californica, C. farlowiana, P. linearis, P. cartilagineum, P. lanceolata*, and *A. venulosum*, exhibited differences in their overall benthic percent covers across season when integrated across sites (Figure 4). When investigated further, each species revealed variable responses in abundance across season, and within each of the treatments (Figure 5a-f). Most interestingly, within treatments, individual red algal species’ benthic covers were not greater in the FS treatment, where canopies were manipulated most pervasively, and light was most readily available. Specifically, the epiphytic and opportunistic red algae, *A. venulosum,* was observed in relatively high benthic cover (22.2% ± 0.035) relative to other red algae species before declining to 0.2% benthic cover in Summer 2017 (Figure 5f). Other species, such as *R. californica,* appeared to peak in benthic percent cover in both Summer 2016 and 2017 (Figure 5b). *P. lanceolata* and *C. farlowiana* steadily increased in benthic percent cover over time, starting at 0% in Fall 2015, and reaching ~6% by Summer 2017 (Figure 5c, 5e). Alternatively*, P. linearis* and *P. cartilagineum,* had consistently low benthic percent cover, never exceeding 1.8% benthic cover (Figure 5a, 5d). *But, in contrast to my original hypothesis, red algal benthic cover was not greatest in treatments with the maximum level of disturbance (Frequent-Strong) and lowest in unmanipulated treatments.*

**Figure 4:** **Mean (± SE) percent cover of individual red algae species totaled across site, and tested across season (n=3).**

**a**

**b**

**c**

**d**

**e**

**f**

**Figure 5: Mean (± SE) percent cover of individual red algal species across treatments and seasons (Fall 2015-Summer 2017. (a) *Plocamium cartilagineum* (b) *Rhodymenia californica* (c) *Prionitis lanceolata* (d) *Prionitis linearis* (e) *Cryptopleura farlowiana* (f) *Acrosorium venulosum* (n=3).**

The weak responses of red algae to treatments of varying disturbance level provoke new inquiries as to the processes underlying red algal benthic assemblages; our next set of tests partitioned variation among components of my statistical model to understand which factors contributed most to the overall variation for each of the targeted red algae species (Table 7). For *P. linearis*, treatment contributed to 21.05% of the overall variation in community assemblage. For *R. californica, P. lanceolata, C. farlowiana, P. cartilagineum* and *A. venulosum,* the contribution of treatment only ranged between 0 and 5.97%. Instead, factors such as season, site, and their interactions accounted for most of the variation to individual species benthic composition.

To further understand the variation observed, I used Season as a discrete variable to investigate the percent of variation due to the factors as well as the residuals (Figure 6). Here most of the variation (70-80%) in red algae community composition was due to residuals (i.e. quadrat-to-quadrat variation). With these findings,*I propose that in Point Loma, red algae community composition is varies over a spatial scale, and benthic percent cover is not greatly influenced by experimentally manipulated disturbance treatments varying in frequency and magnitude.*

**Table 7: Results of one-way ANOVAs testing season, site (blocked) and treatment as selected variables for testing differences in the contribution of variables on individual red algae species. ‘Variance % contribution’ calculations are presented to further understand the contribution of each selected variable on individual red algal species distributions and abundance within kelp forest communities. P-values are uncorrected, and are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ***Cryptopleura farlowiana*** | | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** | **variance % contribution** |
| **Treatment (TR)** | 0.066 | 3 | 0.022 | 3.12 | **0.026** | 0.55 |
| **Season (SE)** | 0.283 | 5 | 0.057 | 8.017 | 0.001 | 18.05 |
| **Site (SI)** | 0.089 | 2 | 0.044 | 6.28 | **0.002** | 7.59 |
| **SI x TR** | 0.172 | 6 | 0.029 | 4.068 | **0.001** | 18.05 |
| **SE x SI** | 0.129 | 10 | 0.013 | 1.826 | 0.054 | 7.38 |
| **SE x TR** | 0.297 | 15 | 0.02 | 2.807 | **0.001** | 4.10 |
| **SI x SE x TR** | 0.481 | 30 | 0.016 | 2.269 | **0.001** | **44.29** |
| **Error** | 3.306 | 468 | 0.007 |  |  |  |
|  |  |  |  |  |  |  |
| ***Rhodymenia californica*** | | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** | **variance % contribution** |
| **Treatment (TR)** | 0.073 | 3 | 0.024 | 2.438 | 0.064 | 0.00 |
| **Season (SE)** | 0.554 | 5 | 0.111 | 11.062 | **0.001** | **35.93** |
| **Site (SI)** | 0.157 | 2 | 0.078 | 7.831 | **0.001** | 14.72 |
| **SI x TR** | 0.098 | 6 | 0.016 | 1.624 | 0.139 | 5.19 |
| **SE x SI** | 0.282 | 10 | 0.028 | 2.819 | **0.002** | 23.38 |
| **SE x TR** | 0.389 | 15 | 0.026 | 2.588 | **0.001** | 0.00 |
| **SI x SE x TR** | 0.43 | 30 | 0.014 | 1.433 | 0.067 | 20.78 |
| **Error** | 4.695 | 469 | 0.01 |  |  |  |
| ***Plocamium cartilagineum*** | | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** | **variance % contribution** |
| **Treatment (TR)** | 0.016 | 3 | 0.005 | 1.425 | 0.235 | 5.97 |
| **Season (SE)** | 0.005 | 5 | 0.001 | 0.284 | 0.922 | 0.00 |
| **Site (SI)** | 0.039 | 2 | 0.02 | 5.138 | **0.006** | **71.64** |
| **SI x TR** | 0.025 | 6 | 0.004 | 1.106 | 0.358 | 0.00 |
| **SE x SI** | 0.035 | 10 | 0.003 | 0.917 | 0.517 | 0.00 |
| **SE x TR** | 0.062 | 15 | 0.004 | 1.086 | 0.367 | 22.39 |
| **SI x SE x TR** | 0.092 | 30 | 0.003 | 0.804 | 0.762 | 0.00 |
| **Error** | 1.783 | 469 | 0.004 |  |  |  |
| ***Prionitis linearis*** | | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** | **variance % contribution** |
| **Treatment (TR)** | 0.01 | 3 | 0.003 | 0.963 | 0.41 | 21.05 |
| **Season (SE)** | 0.006 | 5 | 0.001 | 0.311 | 0.906 | 0.00 |
| **Site (SI)** | 0.049 | 2 | 0.025 | 6.775 | 0.001 | 0.00 |
| **SI x TR** | 0.014 | 6 | 0.002 | 0.625 | 0.711 | 0.00 |
| **SE x SI** | 0.029 | 10 | 0.003 | 0.795 | 0.634 | 0.00 |
| **SE x TR** | 0.046 | 15 | 0.003 | 0.845 | 0.627 | **78.95** |
| **SI x SE x TR** | 0.074 | 30 | 0.002 | 0.678 | 0.903 | 0.00 |
| **Error** | 1.723 | 476 | 0.004 |  |  |  |
| ***Prionitis lanceolata*** | | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** | **variance % contribution** |
| **Treatment (TR)** | 0.001 | 3 | 0 | 0.037 | 0.991 | 0.00 |
| **Season (SE)** | 0.288 | 5 | 0.058 | 9.555 | **0.001** | 46.49 |
| **Site (SI)** | 0.037 | 2 | 0.018 | 3.056 | **0.048** | 5.26 |
| **SI x TR** | 0.035 | 6 | 0.006 | 0.961 | 0.451 | 0.00 |
| **SE x SI** | 0.054 | 10 | 0.005 | 0.886 | 0.546 | 0.00 |
| **SE x TR** | 0.151 | 15 | 0.01 | 1.669 | 0.054 | **48.25** |
| **SI x SE x TR** | 0.148 | 30 | 0.005 | 0.814 | 0.748 | 0.00 |
| **Error** | 2.832 | 469 | 0.006 |  |  |  |
| ***Acrosorium venulosum*** | | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** | **variance % contribution** |
| **Treatment (TR)** | 0.33 | 3 | 0.11 | 6.966 | **0.001** | 3.95 |
| **Season (SE)** | 3.748 | 5 | 0.75 | 47.489 | **0.001** | **62.65** |
| **Site (SI)** | 0.554 | 2 | 0.277 | 17.539 | **0.001** | 11.55 |
| **SI x TR** | 0.256 | 6 | 0.043 | 2.698 | **0.014** | 4.78 |
| **SE x SI** | 1.141 | 10 | 0.042 | 7.227 | **0.001** | 6.90 |
| **SE x TR** | 0.648 | 15 | 0.043 | 2.738 | **0.001** | 4.87 |
| **SI x SE x TR** | 0.617 | 30 | 0.021 | 1.303 | 0.134 | 5.31 |
| **Error** | 7.402 | 469 | 0.016 |  |  |  |

**Figure 6:Using season as a discrete variable, I investigated the percent variance estimates for site (block), treatment, SI x TR and Residuals (small-scale variability) in Point Loma.**

*Red Algae Photophysiology*

***Question 2: Do red algae differ in light adaptations, and do they change seasonally?***

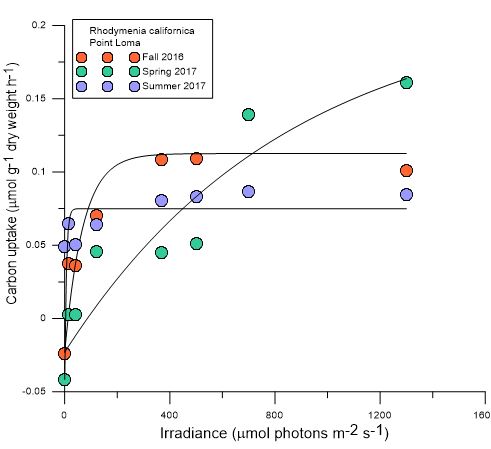
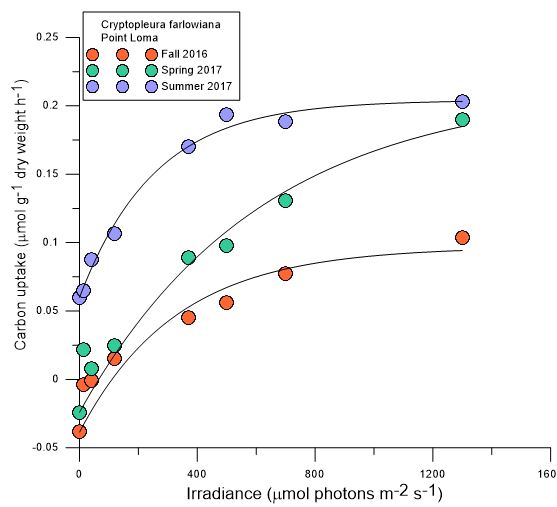
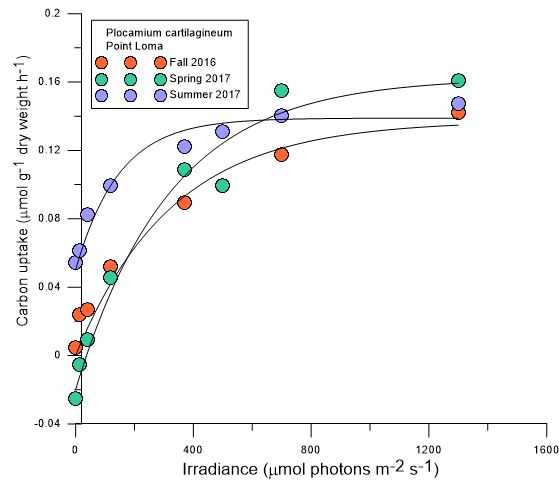
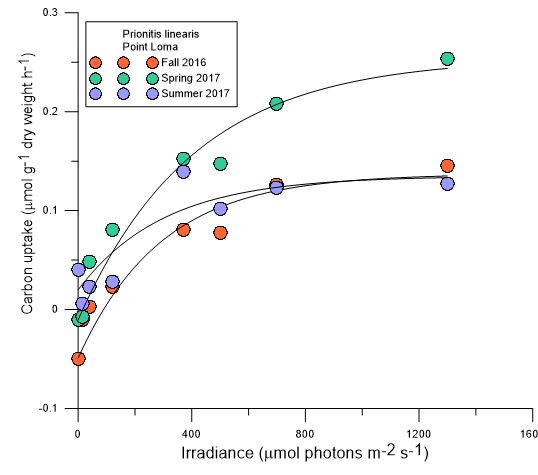
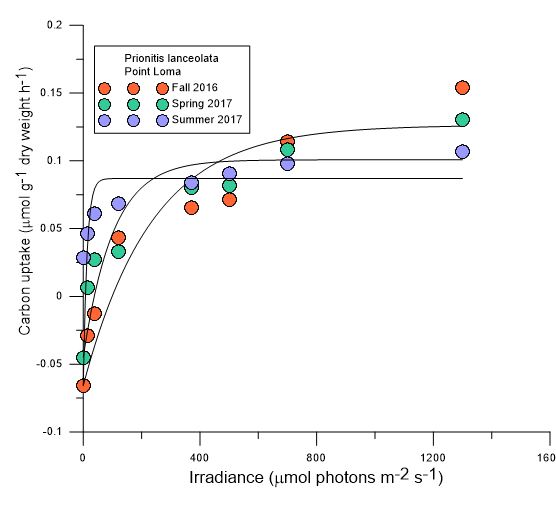
My investigation of red algae photophysiology yielded two major points regarding their relationship with light across season, and comparatively among species. First, when individual species’ photophysiological responses were tested across season, no differences were detected in Pmax (maximum photosynthesis reached) for any species except *P. cartilagineum* (see Appendix D, Table 21). Second, when individual species’ Pmax were compared within each season, only one of three seasons revealed differences among species (Table 8). The results presented again suggest that red algae do not exhibit differences in light adaptations that appear strong enough to drive their benthic community assemblages. These results do not negate light as an influence on red algae species, but rather that light adaptations do not appear to be strong enough to characterize red algae as having “high-light” or “low-light” adaptations within the Point Loma kelp forest as suggested by Clark et al. (2004).

I identified five species that were present in all three seasons: Fall 2016, Spring 2017, Summer 2017 (Figure 7 a-e). In Fall 2016, *R. californica, C. farlowiana, P. linearis, P. cartilagineum,* differed in Pmax (Table 8). Alternatively, species-specific Pmax did not differ in Spring 2017 or Summer 2017. Further, no seasonal differences were detected in photophysiology (Pmax, alpha, respiration) for *C. farlowiana, R. californica,* or *P. lanceolata. P. cartilagineum* experienced differences in Pmax across season, however, other photophysiological parameters such as alpha and respiration did not follow similar trends. Similarly, *P. linearis* yielded differences in respiration across season, however, Pmax and alpha yielded no differences (see Appendix D, Table 21).

At the species level, three red algae individuals reached the greatest Pmax in Spring 2017: *C. farlowiana*, *R. californica*, and *P. linearis* (Appendix D, Table 21). Alternatively, the greatest Pmax reached for *P. cartilagineum* and *P. lanceolata* was in Fall 2016. Among all species observed, the lowest Pmax was reached by *C. farlowiana* in Fall 2016, and the greatest was *P. linearis* in Spring 2017. Interestingly, all species appeared to reach Pmax at or below an irradiance of 400 µmol photons m-2 s-1.

**Table 8: Results of one-way ANOVA testing differences in the Pmax across the five dominant species (*P. lanceolata, P. linearis, C. farlowiana, R. californica*, and *P. cartilagineum)* in Fall 2016, Spring and Summer 2017.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Fall 2016** | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** |
| **SPECIES** | 0.013 | 4 | 0.003 | 3.822 | **0.039** |
| **Error** | 0.008 | 10 | 0.001 |  |  |
| **Spring 2017** | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** |
| **SPECIES** | 0.032 | 4 | 0.008 | 3.164 | 0.064 |
| **Error** | 0.025 | 10 | 0.002 |  |  |
| **Summer 2017** | | | | | |
| **Source** | **Type III SS** | **df** | **MS** | **F-Ratio** | **p-Value** |
| **SPECIES** | 0.015 | 4 | 0.004 | 0.87 | 0.518 |
| **Error** | 0.04 | 9 | 0.004 |  |  |

**

**e**

**a**

**b**

**c**

**d**

**Figure 7 (a-e): Photosynthesis v Irradiance curves measuring the relationship between carbon uptake and irradiance for individual red algae species, across Fall 2016, Spring 2016, and Summer 2017 in Point Loma. (a) *Prionitis lanceolata* (b) *Prionitis linearis* (c) *Plocamium cartilagineum* (d) *Cryptopleura farlowiana* (e) *Rhodymenia californica***

**Carmel Bay, Monterey Peninsula, California**

***Question 1: How do infrequent and frequent disturbances to kelp canopies impact red algal community assemblages, and does benthic cover vary among red algal species and/or between geographic locations?***

*Preliminary Red Algal Community Surveys*

In Spring 2016, prior to experimental manipulation, no differences were detected in red algae community composition across sites, treatments, or between sites and treatments (Table 9). Most of the dissimilarity among FS and FW treatments were driven by *P. linearis*, *P. cartilagineum,* juvenile red algae*,* and *R. californica*  (Table 10). Within FS and IS treatments, most of the dissimilarity was driven by *P. linearis*,juvenile red algae*,* *P. cartilagineum*, and *Microcladia coulteri*.

**Table 9: Results of PERMANOVA testing differences in red algal community composition across selected sites and treatments in Spring 2016. P-values are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p- value** |
| **Site** | 2 | 1252.6 | 626.32 | 1.7425 | 0.093 |
| **Treatment** | 3 | 1276.1 | 425.36 | 1.1834 | 0.337 |
| **SIxTR** | 6 | 1323.3 | 220.55 | 0.61361 | 0.906 |
| **Res** | 96 | 34506 | 359.43 |  |  |

**Table 10: Results of Similarities Percentages (SIMPER) analysis for Spring 2016 showing which species within the entire kelp forest community were primarily responsible for Bray-Curtis dissimilarity between treatments varying in frequency and magnitude of disturbance (Magnitude: Frequent-Strong v. Frequent-Weak, Frequency: Frequent-Strong v. Infrequent-Strong). Species presented have a contribution percentage >4%.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ***Frequent-Strong* vs. *Frequent-Weak***  **Avg. Dissimilarity= 89.42** | | | | | | |
| **Species** | **FS Av.Abund** | **FW Av.Abund** | **Av.Diss** | **Diss/SD** | **Contrib%** | **Cum.%** |
| ***Prionitis linearis*** | 0.14 | 0.08 | 27.78 | 0.8 | 31.07 | 31.07 |
| ***Plocamium cartilagineum*** | 0.08 | 0.08 | 16.7 | 0.69 | 18.67 | 49.74 |
| **Juvenile reds** | 0.08 | 0.03 | 13.45 | 0.55 | 15.04 | 64.78 |
| ***Rhodomenia californica*** | 0.07 | 0.03 | 8.24 | 0.59 | 9.22 | 74 |
| ***Microcladia coulteri*** | 0.04 | 0.02 | 5.15 | 0.49 | 5.77 | 79.76 |
| ***Callophyllis flabelluata*** | 0.01 | 0.05 | 4.82 | 0.46 | 5.39 | 85.16 |
| ***Cryptopleura farlowiana*** | 0.02 | 0.01 | 4.35 | 0.3 | 4.87 | 90.02 |
| ***Frequent-Strong* vs. *Infrequent-Strong***  **Avg. Dissimilarity= 91.07** | | | | | | |
| **Species** | **FS Av.Abund** | **IS Av.Abund** | **Av.Diss** | **Diss/SD** | **Contrib%** | **Cum.%** |
| ***Prionitis linearis*** | 0.14 | 0.05 | 25.13 | 0.76 | 27.59 | 27.59 |
| **Juvenile reds** | 0.08 | 0.07 | 19.63 | 0.66 | 21.55 | 49.15 |
| ***Plocamium cartilagineum*** | 0.08 | 0.04 | 13.62 | 0.6 | 14.95 | 64.1 |
| ***Microcladia coulteri*** | 0.04 | 0.05 | 9.41 | 0.63 | 10.34 | 74.44 |
| ***Rhodomenia californica*** | 0.07 | 0.03 | 8.95 | 0.55 | 9.82 | 84.26 |
| ***Cryptopleura farlowiana*** | 0.02 | 0.02 | 3.99 | 0.42 | 4.38 | 88.64 |

*Effects of Disturbances of Varying Frequency and Magnitude*

In Carmel Bay, red algae community composition did not appear to be greatly influenced by the frequency or magnitude of disturbances as estimated by the four treatments (Table 11). Instead, red algal benthic percent cover differed by season, site (block), seasons and site, and site and treatment. This suggests spatial and temporal fluctuations in red algae community composition, with the differences among treatments in one season not being consistent in other seasons.

When testing sites and treatments to assess differences in red algal community composition within each season no differences were detected between treatments from Spring 2016-Summer 2017 (Table 12). In addition, site and treatment only differed in Summer 2016 and Spring 2017. Communities began to differ by site in Summer 2016, but in Fall 2016, no differences in community composition were detected in any of the selected variables. However, by Winter 2017, differences were detected between sites, and remained significant for the duration of this study. More specifically, variance components revealed differences in the contribution of each factor on red algae community composition, as they were mostly due to residuals or small-scale variation (Table 11). Therefore, much as in Point Loma, the lack of response by red algae communities to the experimental treatments in Carmel Bay suggested small-scale variability or ‘patchiness’ was more important to red algal community composition than species’ light-adaption characters (e.g. Clark et al. 2004, Mahoney 2015).

**Table 11: Results of PERMANOVA with selected variables: season, site (blocked) and treatment. Selected variables were utilized for testing differences in red algal community composition in Carmel Bay from Fall 2015-Summer 2017. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** | **% variation** |
| **Season (SE)** | 5 | 13367 | 2673.4 | 2.0015 | **0.015** | 3.44 |
| **Site** | 2 | 12492 | 6246 | 22.695 | **0.001** | 7.67 |
| **Treatment** | 3 | 4432.5 | 1477.5 | 1.8132 | 0.129 | 1.13 |
| **SExSI** | 10 | 13358 | 1335.8 | 4.8538 | **0.001** | 8.17 |
| **SExTR** | 15 | 4161.9 | 277.46 | 0.89173 | 0.666 | 0.00 |
| **SIxTR** | 6 | 4889.4 | 814.9 | 2.961 | **0.001** | 2.77 |
| **SExSIxTR** | 30 | 9.34E+03 | 311.17 | 1.1306 | 0.152 | 1.11 |
| **Res** | 572 | 1.57E+05 | 275.21 |  |  | 75.71 |

**Table 12: Results of post-hoc PERMANOVA testing season, and using site (blocked) and treatment as selected variables for investigating differences in red algal community composition in Carmel Bay. Significant p-values are in bold.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Spring 2016** | | | | | |
| **Source** | df | SS | MS | Pseudo-F | p-value |
| **Site (SI)** | 2 | 1252.6 | 626.32 | 1.7425 | 0.087 |
| **Treatment (TR)** | 3 | 1276.1 | 425.36 | 1.9286 | 0.099 |
| **SIxTR** | 6 | 1323.3 | 220.55 | 0.61361 | 0.902 |
| **Res** | 96 | 34506 | 359.43 |  |  |
| **Summer 2016** | | | | | |
| **Source** | df | SS | MS | Pseudo-F | p-value |
| **Site (SI)** | 2 | 10537 | 5268.4 | 30.407 | **0.001** |
| **Treatment (TR)** | 3 | 2014.4 | 671.46 | 1.8307 | 0.235 |
| **SIxTR** | 6 | 2201 | 366.84 | 2.1173 | **0.011** |
| **Res** | 95 | 16460 | 173.26 |  |  |
| **Fall 2016** | | | | | |
| **Source** | df | SS | MS | Pseudo-F | p-value |
| **Site** | 2 | 1252.6 | 626.32 | 1.7425 | 0.104 |
| **Treatment** | 3 | 1276.1 | 425.36 | 1.9286 | 0.108 |
| **SIxTR** | 6 | 1323.3 | 220.55 | 0.61361 | 0.905 |
| **Res** | 96 | 34506 | 359.43 |  |  |
| **Winter 2016** | | | | | |
| **Source** | df | SS | MS | Pseudo-F | p-value |
| **Site (SI)** | 2 | 3616.2 | 1808.1 | 6.3812 | **0.001** |
| **Treatment (TR)** | 3 | 1210.3 | 403.43 | 1.3019 | 0.362 |
| **SIxTR** | 6 | 1859.6 | 309.93 | 1.0938 | 0.389 |
| **Res** | 93 | 26351 | 283.35 |  |  |
| **Spring 2017** | | | | | |
| **Source** | df | SS | MS | Pseudo-F | p-value |
| **Site (SI)** | 2 | 6812.1 | 3406 | 14.441 | **0.001** |
| **Treatment (TR)** | 3 | 1498.6 | 499.53 | 0.52541 | 0.88 |
| **SIxTR** | 6 | 5709.3 | 951.55 | 4.0342 | **0.001** |
| **Res** | 97 | 22879 | 235.87 |  |  |
| **Summer 2017** | | | | | |
| **Source** | df | SS | MS | Pseudo-F | p-value |
| **Site (SI)** | 2 | 2369.9 | 1184.9 | 4.9544 | **0.002** |
| **Treatment (TR)** | 3 | 1329 | 443 | 1.4557 | 0.214 |
| **SIxTR** | 6 | 1826 | 304.34 | 1.2725 | 0.185 |
| **Res** | 95 | 22721 | 239.17 |  |  |

Individual red algal species*, R. californica, C. farlowiana, P. linearis,* and *P. cartilagineum,* yielded differences in their overall benthic percent cover across season when totaled across site (Figure 8). Further, each species revealed variable responses in abundance across season, and within each treatment (Figure 9a-d). Most interestingly, within treatments, total individual red algae species benthic cover was not greater in the FS treatment where canopies were manipulated most pervasively, and light was most readily available. Specifically, *P. cartilagineum,* reached maximum in benthic cover in Summer 2016 within the FS treatments (Figure 9a). However, by Fall 2016, benthic cover within the FS treatment plummeted to 3%, likewise in other treatments. *P. linearis* also maintained greatest benthic percent cover within FS treatments during Spring 2016, Summer 2016, and Fall 2016 before declining to 0% cover in Winter 2016 (Figure 9b). For the remainder of the study, *P. linearis* populations never exceeded 1% benthic cover. *R. californica* greatly fluctuated in abundance across treatments, ranging between 1-4% benthic cover, before reaching 0% across all treatments in Summer 2017 (Figure 10c). *C. farlowiana* was observed in very low abundances (<1% percent cover) across all seasons, and was not present in the FS treatment until Winter 2016 (Figure 10d).

**Figure 8: Mean (± SE) percent cover of individual red algae species across season, and averaged across treatments (n=3).**

**Figure 9: Mean (± SE) percent cover of individual red algae species. across treatment and season (Spring 2016-Summer 2017). (a) *Plocamium cartilagineum* (b) *Rhodymenia californica* (c) *Cryptopleura farlowiana* (d) *Prionitis linearis.***

Similar to Point Loma, no single species increased substantially in the altered high-light environment provided by the FS treatment; all species maintained variable abundances across season and within treatments. Subsequently, I utilized variance components analyses to detect which factors yielded the highest contribution of variation for each of the targeted red algae species (Table 13). For all species observed, treatment did not greatly contribute to individual species community composition. Specifically, the contribution of treatment to variation in assemblages of *C. farlowiana, R. californica,* *P. cartilagineum,* and *P. linearis* only ranged between 0% and 9.46%. Instead, factors such as season, site, and their interactions accounted for most of the variation to individual species composition observed.

To further understand the variation in red algal community composition, I used season as a discrete variable to investigate the percent of variation due to the factors as well as the residuals (Figure 10). Most of the variation was due to residuals, as it accounted for ~50-90% of the variation contributing to red algae community composition. With these findings,*I propose that in Carmel Bay, red algae community composition is spatially variable, and benthic percent cover is not greatly influenced by experimentally manipulated disturbance treatments varying in frequency and magnitude.*

**Table 13: Results of one-way ANOVA testing species, and using season, site (blocked) and treatment as selected variables for testing differences in the contribution of variables on individual red algae species. ‘Variance % contribution’ calculations are presented to further understand the contribution of each selected variable on individual red algal species distributions and abundance within kelp forest communities. P-values are uncorrected, and are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ***Cryptopleura farlowiana*** | | | | | | |
| **Source** | Type III SS | df | Mean Squares | F-Ratio | p-Value | % variation |
| **Season (SE)** | 0.004 | 5 | 0.001 | 2.643 | 0.022 | 0.00 |
| **Site (SI)** | 0.003 | 2 | 0.002 | 4.96 | 0.007 | 21.05 |
| **Treatment (TR)** | 0.001 | 3 | 0 | 0.793 | 0.498 | 0.00 |
| **SI x TR** | 0.004 | 6 | 0.001 | 2.048 | 0.058 | 31.58 |
| **SE x SI** | 0.007 | 10 | 0.001 | 2.248 | 0.014 | **47.37** |
| **SE x TR** | 0.003 | 15 | 0 | 0.574 | 0.896 | 0.00 |
| **SI x SE x TR** | 0.006 | 30 | 0 | 0.598 | 0.957 | 0.00 |
| **Error** | 0.189 | 572 | 0 |  |  |  |
| ***Rhodymenia californica*** | | | | | | |
| **Source** | Type III SS | df | Mean Squares | F-Ratio | p-Value | % variation |
| **Season (SE)** | 0.028 | 5 | 0.006 | 2.371 | 0.038 | 3.64 |
| **Site (SI)** | 0.13 | 2 | 0.065 | 27.196 | 0 | **76.36** |
| **Treatment (TR)** | 0.009 | 3 | 0.003 | 1.204 | 0.307 | 3.64 |
| **SI x TR** | 0.011 | 6 | 0.002 | 0.752 | 0.608 | 0.00 |
| **SE x SI** | 0.051 | 10 | 0.005 | 2.127 | 0.021 | 16.36 |
| **SE x TR** | 0.021 | 15 | 0.001 | 0.577 | 0.893 | 0.00 |
| **SI x SE x TR** | 0.04 | 30 | 0.001 | 0.559 | 0.973 | 0.00 |
| **Error** | 1.371 | 572 | 0.002 |  |  |  |
| ***Plocamium cartilagineum*** | | | | | | |
| **Source** | Type III SS | df | Mean Squares | F-Ratio | p-Value | % variation |
| **Season (SE)** | 0.349 | 5 | 0.07 | 8.365 | 0 | 2.46 |
| **Site (SI)** | 0.781 | 2 | 0.391 | 46.862 | 0 | **46.44** |
| **Treatment (TR)** | 0.196 | 3 | 0.065 | 7.848 | 0 | 9.46 |
| **SI x TR** | 0.257 | 6 | 0.043 | 5.141 | 0 | 12.73 |
| **SE x SI** | 0.33 | 10 | 0.033 | 3.961 | 0 | 13.64 |
| **SE x TR** | 0.199 | 15 | 0.013 | 1.591 | 0.071 | 0.00 |
| **SI x SE x TR** | 0.436 | 30 | 0.015 | 1.741 | 0.009 | 15.28 |
| **Error** | 4.769 | 572 | 0.008 |  |  |  |
| ***Prionitis linearis*** | | | | | | |
| **Source** | Type III SS | df | Mean Squares | F-Ratio | p-Value | % variation |
| **Season (SE)** | 0.226 | 5 | 0.045 | 12.305 | 0 | 10.70 |
| **Site (SI)** | 0.111 | 2 | 0.055 | 15.112 | 0 | 18.18 |
| **Treatment (TR)** | 0.054 | 3 | 0.018 | 4.933 | 0.002 | 7.49 |
| **SI x TR** | 0.027 | 6 | 0.005 | 1.239 | 0.285 | 1.07 |
| **SE x SI** | 0.346 | 10 | 0.035 | 9.428 | 0 | **49.73** |
| **SE x TR** | 0.059 | 15 | 0.004 | 1.074 | 0.378 | 0.00 |
| **SI x SE x TR** | 0.171 | 30 | 0.006 | 1.552 | 0.032 | 12.83 |
| **Error** | 2.098 | 572 | 0.004 |  |  |  |

**Figure 10: Using season as a discrete variable, I investigated the % variance estimates for site (block), treatment, SI x TR and Residuals (small-scale variability) in Carmel Bay.**

*Red Algae Photophysiology*

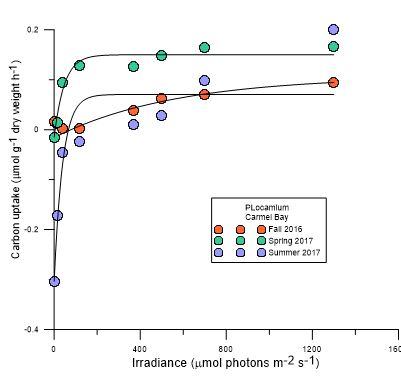
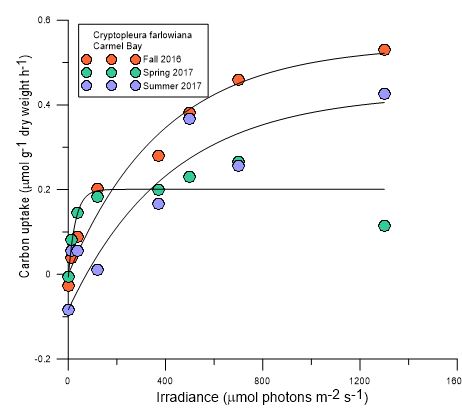
***Question 2: Do red algae differ in light adaptations, and do they change seasonally?***

In Carmel Bay, examining red algae photophysiology yielded two major points regarding their relationship with light across season, and comparatively among species. First, when individual species’ photophysiological responses were tested across time, no differences were detected in Pmax across season for *R. californica, P. linearis,* *C. farlowiana,* or *P. cartilagineum* (Figure 11a-d; see Appendix D, Table 22). Second, when individual species’ Pmax was compared within each season, no differences were detected. These findings signify that red algae in Carmel Bay do not exhibit differences in light adaptations that appear strong enough to drive their benthic community assemblages. Again, these results do not conclude that light does not influence red algae species, but rather that light adaptations do not appear to be strong enough to characterize red algae as having “high-light” or “low-light” adaptations within the Carmel Bay kelp forest.

During this study I identified four species that were present for all three seasons: Fall 2016, Spring 2017, Summer 2017.Species-specific photosynthetic characters (Pmax, alpha, and respiration) did not differ across season for *R. californica, P. linearis,* and *P. cartilagineum*. *C. farlowiana* experienced differences in alpha across season, however, other photophysiological parameters such as Pmax and respiration did not follow similar trends (Table 21). Between *C. farlowiana, R. californica, P. linearis, and P. cartilagineum*, no differences were detected among species in Fall 2016, Spring 2017, or Summer 2017(see Appendix D, Table 22). Two red algae individuals reached the greatest Pmax in Fall 2016: *C. farlowiana* and *P. linearis*. Alternatively, the greatest Pmax reached for *P. cartilagineum*  and *R. californica* was in Fall 2016 (Figure 11b, c). Among all species observed, the lowest Pmax was reached by *P. linearis* in Summer 2017 (Figure 11d), and the greatest was *C. farlowiana* in Fall 2016 (Figure 11a). Further, *C. farlowiana* reached the second greatest Pmax value in Summer 2017.

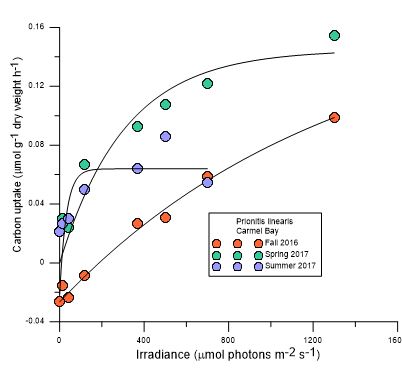
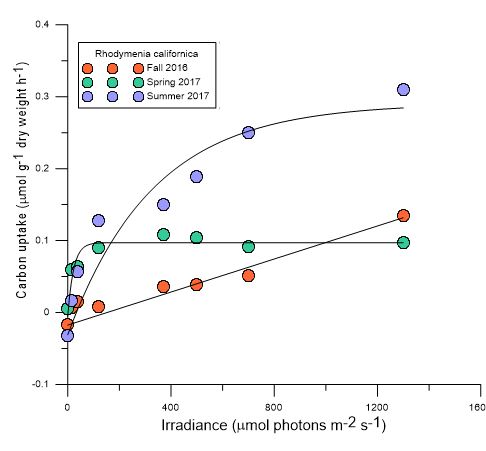
**Table 14: Results of one-way ANOVAs, with species as the factor and season as the selected variable. This table presents Pmax across species in Fall 2016, Spring or Summer 2017.**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Fall 2016** | | | | | |
| **Source** | **Type III SS** | **df** | **Mean Squares** | **F-Ratio** | **p-Value** |
| **SPECIES** | 0.405 | 3 | 0.135 | 3.075 | 0.091 |
| **Error** | 0.351 | 8 | 0.044 |  |  |
| **Spring 2017** | | | | | |
| **Source** | **Type III SS** | **df** | **Mean Squares** | **F-Ratio** | **p-Value** |
| **SPECIES** | 0.031 | 3 | 0.01 | 3.924 | 0.062 |
| **Error** | 0.018 | 7 | 0.003 |  |  |
| **Summer 2017** | | | | | |
| **Source** | **Type III SS** | **df** | **Mean Squares** | **F-Ratio** | **p-Value** |
| **SPECIES** | 0.352 | 3 | 0.117 | 3.493 | 0.07 |
| **Error** | 0.269 | 8 | 0.034 |  |  |

****

**b**

**a**

****

**d**

**c**

**Figure 11 (a-d): Photosynthesis v Irradiance curves measuring the relationship between carbon uptake and irradiance for individual red algae species, across Fall 2016, Spring 2016, and Summer 2017: (a) *Cryptopleura farlowiana* (b) *Plocamium cartilagineum* (c) *Rhodymenia californica* (d) *Prionitis linearis***

**DISCUSSION**

Increases in storm events can result in the loss of canopy-forming species, which consequently alters benthic light and hydrodynamic conditions, and impacts kelp forest community structure (Reed and Foster 1984, Dayton et al. 1984, Dayton 1985). Previous studies investigating disturbance events in kelp forests have found that consistent removal of canopy-forming species yield a positive response in sub-canopy and understory species (Reed and Foster 1984, Dayton et al. 1984, Dayton 1985, Edwards 1998). Although these studies have detected strong links between benthic irradiance and algal community composition, these studies have been limited to 1) the responses of macroalgae within the canopy, sub-canopy, and understory layers, and 2) maintaining treatments to avoid any canopy growth (e.g. Reed and Foster 1984, Dayton et al. 1984, Edwards 1998, Clark et al. 2004). Therefore, my study aimed to reduce gaps in knowledge by investigating, specifically, the responses of red algal communities to disturbances of varying frequency and magnitude, and if their community assemblages were driven by light adaptations. Specifically, the main finding of this study is that red algal benthic cover was not altered under different canopy manipulations, and that photophysiology was highly variable among species or within a species across season, as has been hypothesized in previous studied (e.g. Reed and Foster 1984, Dayton et al. 1984, Clark et al. 2004).

In one seminal study in Carmel Bay, Clark et al. (2004) assigned light-adaptability characteristics to red algae based on changes to their assemblages following experimental canopy manipulations. These post-hoc groupings were based on changes in red algae abundances in treatments that varied in their level of canopy-loss, and were not directly measured via photophysiological investigations. Although the relative percent cover of a few species was observed in high abundances within no-canopy treatments, most species differed only slightly following the canopy manipulations (Clark et al. 2004). The responses of red algae communities to our kelp canopy manipulations were consistent between Point Loma and Carmel Bay in that no species flourished within the FS treatments, or displayed high-light adaptations. Expectations that experimental clearings would facilitate the proliferation of high light-adapted species and increased red algal abundance were not supported in our study. This suggests that other life history characteristics (e.g. reproduction, spore dispersal, grazing pressure) may play a larger role in red algae communities than previously understood. In our study, the variability among species in response to treatments of differing disturbance levels across season challenges our understanding of the relationship between light and understory algal community organization seen in temperate kelp forest ecosystems (Reed and Foster 1984). Isolation of variance components showed that *small-scale variability* (i.e. quadrat-to-quadrat differences) contributed greatly to red algal benthic percent cover, considering red algal percent cover did not vary between treatments or seasons. Instead, variation was observed at a larger spatial scale rather than a species scale.

While some studies have utilized canopy manipulations to elicit responses from opportunistic species (e.g. *Desmarestia ligulata;* Edwards 1998), red algal species did not follow these patterns in our study. In fact, photophysiological experiments revealed no differences in light adapted characteristics among species or across season. This substantiates the results found in Clark et al. (2004) which stated, “One of the most surprising results of this study was the weak response of red algae as a whole to the kelp clearings” (pg. 19). My study explored light adaptations as a possible explanation for red algal community assemblages, considering an a *priori* expectation that high light species would flourish within the FS treatments that seasonally eliminated canopy, sub-canopy, and understory layers (Clark et al. 2004). Instead, my study found patchiness in red algae communities across season, site, and treatment, and that treatments that differed in level of disturbance did not impact red algal benthic percent cover. In terrestrial systems, understory species are more readily able to gather light, usually due to gaps within the canopy. However, within marine ecosystems, and most notably kelp forests, gathering light at the benthos is genuinely complicated due to light attenuation by suspended particulates within the water column and the absorption of light by wavelength; photons with longer wavelengths (i.e. red) are absorbed more readily than those with shorter wavelengths (i.e. blue). In the ocean, light is scattered and scarce, making the effects of canopy shading not as predictable.

Central California, typically experiences colder water temperatures, higher nutrient concentrations, and intense disturbance events (relative to southern California) which provide good conditions for reproduction and photosynthesis among subtidal primary producers. Despite these oceanographic conditions, red algae percent cover was greater in Point Loma than it was in Carmel Bay. For example, six red algae species targeted in Point Loma, *(R. californica, P.* *cartilagineum, C. farlowiana, P. linearis, P. lanceolata*, and *A. venulosum*) collectively fluctuated between 7.1% to 25% benthic cover. In Carmel Bay, *R. californica, P. cartilagineum, C. farlowiana,* and *P. linearis* fluctuated between 3%-12.9% benthic cover.

As demonstrated in previous studies, and supported by this one, the understory kelp *L.* *farlowii* appeared to be more resilient to such perturbations than *Macrocystis* and *P. californica (*Dayton et al., 1984*)*. This can be the result of its prostrate morphology, as it was presentacross every treatment and every seasonal sampling period during this study. Further, even in FS treatments that cleared *L. farlowii* seasonally, this species reestablished benthic cover. Following expectations of understory recovery (Dayton et al. 1984, Reed and Foster 1984) and opportunism following disturbance events (Edwards 1998), *L. farlowii* abundance was greatest in FW treatments where just *Macrocystis* canopies were cleared. The abundance of understory *L. farlowii* within the two treatments can be interpreted as Point Loma experiencing a natural FW disturbance event that seasonally removed or even thinned *Macrocystis* canopy layers, and contributed to the proliferation of *L. farlowii.* However, regardless of the treatment or natural oceanographic processes, by Summer 2017, *L. farlowii* benthic percent cover was analogous among treatments. This indicates that *L. farlowii* presence within the Point Loma kelp forest is persistent, and is important as a shading canopy layer.

Although not the focus of this study, understanding the effects of *L. farlowii* is especially relevant as this species could be experiencing an increase in abundance where it has been previously observed as “rare” due to changes in oceanographic regimes, competitors, or grazers. This study along with observations by long-term data collection programs in central California (PISCO) have reported increased observations of *L. farlowii* in Monterey Bay and Carmel Bay than previous years (Gaylord, C. and Miller K.A. 2014 pers. comm., T. McHugh pers. observ). This could have potential impacts for algal communities in locations where its abundance was previously rare, like central California. Likewise, interspecific competition with understory high-light adapted species such as *D. ligulata* could ensue further complicating kelp forest community organization.

This study did not monitor the growth of red algae across seasons, however, in Point Loma and Carmel Bay, divers observed visibly larger red algae species within the FS treatments (T. McHugh pers. observ.). This is important to note because although red algae benthic percent cover was not greatly altered by treatment level, the increased benthic irradiances could have positively influenced the growth of red algae. In addition, natural disturbance events occurring off the California coast (2014 “marine heat wave” event (Bond et al. 2015), 2014-2016 ENSO (Cai et al. 2014), Sea Star Wasting Syndrome (Hewson et al. 2014), record-high wave heights; (Table 3) were observed during this study. Investigating the responses of kelp forests to multiple stressors are vital for understanding how the coast of California will be influenced in the future.

Future studies involving red algae communities should investigate life history characteristics as a possible reason for the patchiness observed in Point Loma and Carmel Bay red algal communities. Specifically, *P. cartilagineum* physically fragments its thallus to reproduce, and with non-motile flagella, its dispersal is dependent on currents to reproduce (Kain 1987), which could facilitate a small dispersal range.In our study, variation among sites contributed greatly to differences in *P. cartilagineum* benthic percent cover in both Point Loma (71.6%) and Carmel Bay (46.44%). Therefore, future studies should consider small-scale studies to investigate how red algae reproduction may influence community composition. Further, dispersal can be attributed to drifting specimens that are fertile, within the euphotic zone, and able to release spores while unattached to the benthos (Cole and Sheath 1990). Considering red algae can release spores upon detachment, future studies should consider the currents present in the specific location of study. For example, the west wind drift route that spans between the Falkland Islands and New Zealand has been proposed as a possible method for red algae species dispersal, due to the similarities in algal community composition on sub Antarctic islands (Hommersand 1986). Thus, red algae community structure is a complex mechanism that has the potential to be dictated by a variety of abiotic influences.

**CONCLUSIONS**

Counter to expectations, red algae did not demonstrate significant responses in benthic percent cover to changes light availability via disturbances. Additionally, red algae individuals did not display species-specific differences in light adaptations or across season. Therefore, I suggest that red algae community organization is not driven by individual species photosynthetic performance. Rather, the underlying mechanisms dictating red algal community assemblages are complex, as oceanographic conditions are dynamic and annually fluctuate in wave conditions, temperature, and nutrients. The analogous responses of red algae within two biogeographically distinctive locations in California provide insight on how temperate reefs in California may respond to storm propagated disturbances in the future. Lastly, reinstated patchiness allows future researchers to hone-in more explicitly at species ecologies under various oceanographic conditions as a potential reason for red algal organization observed in kelp forest ecosystems.

To conclude, the weak responses expressed by red algae to experimental manipulation, paired with their highly variable photophysiological responses across season, yield a new line of inquiry: If light adaptations do not drive red algae community organization, then what does?

**REFERENCES**

Bender, E. A., Case, T. J., & Gilpin, M. E. (1984). Perturbation experiments in community ecology: theory and practice. *Ecology*, *65*(1), 1-13.

Bischoff, B. & Wiencke, C. 1993. Temperature requirements for growth and survival of macroalgae from Disko-Island (Greenland). *Helgol. Wiss. Meeresunters.* **47**:167 – 91.

Bjerknes, Jakob. "Atmospheric teleconnections from the equatorial pacific 1."*Monthly Weather Review* 97.3 (1969): 163-172.

Bond, N. A., Cronin, M. F., Freeland, H., & Mantua, N. (2015). Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters*, *42*(9), 3414-3420.

Brown, M.B., M.S. Edwards and K.Y. Kim (2014). Effects of climate change on the physiology of giant kelp, *Macrocystis pyrifera*, and grazing by purple urchin, *Strongylocentrotus purpuratus*. Algae 29: 203-215.

Byrnes, Jarrett E., et al. 2011 "Climate‐driven increases in storm frequency simplify kelp forest food webs." *Global Change Biology* 17.8: 2513-2524.

Cai, W., Borlace, S., Lengaigne, M., Van Rensch, P., Collins, M., Vecchi, G., ... & England, M. H. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature climate change*, *4*(2), 111-116.

Chavez, F. P., et al. "Biological and chemical consequences of the 1997–1998 El Niño in central California waters." *Progress in Oceanography* 54.1 (2002): 205-232.

Clark, George E., et al. "Assessing the vulnerability of coastal communities to extreme storms: the case of Revere, MA., USA." *Mitigation and adaptation strategies for global change* 3.1 (1998): 59-82.

Cole, K. M., & Sheath, R. G. (Eds.). (1990). *Biology of the red algae*. Cambridge University Press.

Connell, J. H. (1974). Ecology: field experiments in marine ecology. *Experimental marine biology*, 21-54.

Dayton, P. K., Currie, V., Gerrodette, T., Keller, B. D., Rosenthal, R., & Tresca, D. V. (1984). Patch dynamics and stability of some California kelp communities. *Ecological monographs*, *54*(3), 253-289.

Dayton, P. K. (1985). Ecology of kelp communities. *Annual review of ecology and systematics*, *16*(1), 215-245.

Dayton, P. K., Tegner, M. J., Parnell, P. E., & Edwards, P. B. (1992). Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs*, *62*(3), 421-445.

Ebeling, A. W., Laur, D. R., & Rowley, R. J. (1985). Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Marine Biology*, *84*(3), 287-294.

Edwards, M. S., & Estes, J. A. (2006). Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective. *Marine Ecology Progress Series*, *320*, 79-87.

Edwards, M. S. (1998). Effects of long-term kelp canopy exclusion on the abundance of the annual alga Desmarestia ligulata (Light F). *Journal of Experimental Marine Biology and Ecology*, *228*(2), 309-326.

Edwards, M. S. (2000). THE ROLE OF ALTERNATE LIFE‐HISTORY STAGES OF A MARINE MACROALGA: A SEED BANK ANALOGUE?. *Ecology*, *81*(9), 2404-2415.

Edwards, M.S. (2004). Estimating scale dependency in disturbance impacts: El Niños and giant kelp forests in the Northeast Pacific. Oecologia 138: 436-447.

Edwards, MS and SD Connell (2012). “Competition” In: Seaweed Ecophysiology and Ecology. Pgs 135-156. Edited by C. Wiencke and K. Bischof. Published by Springer.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modelling, and impacts. Science 289:2068–2074.

Eggeling, W. J. (1947). Observations on the ecology of the Budongo rain forest, Uganda. *The Journal of Ecology*, 20-87.

Freshwater, D. W., et al. 1994. A gene phylogeny of the red algae (Rhodophyta) based on plastid rbcL. Proc. Natl. Acad. Sci. USA Vol. 91: 7281-7285.

Groshotz, E. 2002. Ecological and evolutionary consequences of coastal invasions. Trends in Ecology and Evolution 17:22–27.

Hewson, I., Button, J. B., Gudenkauf, B. M., Miner, B., Newton, A. L., Gaydos, J. K., & Fradkin, S. (2014). Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences*, *111*(48), 17278-17283.

Hommersand, M. H. (1986). The biogeography of the South African marine red algae: a model. *Botanica marina*, *29*(3), 257-270.

IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M.

Jackson, G. A. (1977). Nutrients and production of giant kelp, Macrocystis pyrifera, off southern California. *Limnology and Oceanography*, *22*(6), 979-995.

Kain, J. M. (1987). Seasonal growth and photoinhibition in Plocamium cartilagineum (Rhodophyta) off the Isle of Man. *Phycologia*, *26*(1), 88-99.

Kim, JH, E.J. Kang, K. Kim, H.J. Jeong, L. Kitack, M.S. Edwards, M.G. Park, BG. Lee, and K.Y. Kim (2015). Evaluation of carbon flux in vegetative bay based on ecosystem production and CO2 exchange driven by coastal autotrophs. Algae 30: 121-137.

Latif, Mojib, and Timothy P. Barnett (1996). "Decadal climate variability over the North Pacific and North America: Dynamics and predictability." *Journal of Climate*9.10 : 2407-2423.

Lubchenco, J., & Gaines, S. D. (1981). A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics*, *12*(1), 405-437.

Mahoney, Brenna. (2014). Life in a patchy world: species-habitat relationships link macroalgal communities to higher trophic levels in temperate rocky reefs. UC Santa Cruz: Ecology and Evolutionary Biology. Retrieved from: <http://escholarship.org/uc/item/4538220c>

McKay, H.H. 1933. *The life history of Pterygophora californica Ruprecht*. University of California Press,

Meehl, G. A., Teng, H., & Arblaster, J. M. (2014). Climate model simulations of the observed early-2000s hiatus of global warming. *Nature Climate Change*, *4*(10), 898-902.

Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:257–289.

NOAA 2015: http://www.cpc.ncep.noaa.gov/products/analysis\_monitoring/lanina/enso\_evolution-status-fcsts-web.pdf

North, W. J., & Pearse, J. S. (1970). Sea urchin population explosion in southern California coastal waters. *Science*, *167*(3915), 209..

Paine, R. T. (1966). Food web complexity and species diversity. *The American Naturalist*, *100*(910), 65-75.

Pennington, T.J., and F.P. Chavez. 2000. Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll and primary production at station H3/M1 over 1989–1996 in Monterey Bay, California." *Deep Sea Research Part II: Topical Studies in Oceanography* 47.5:947-973.

Ragan, M. A., et al. 1994. A molecular phylogeny of the marine red algae (Rhodophyta) based on the nuclear small-subunit rRNA gene. Proc. Natl. Acad. Sci. USA Vol. 91: 7276-7280.

Reed, D. C., & Foster, M. S. (1984). The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. *Ecology*, *65*(3), 937-948.

Roemmich, D., and J. McGowan. (1995). Climatic warming and the decline of zooplankton in the California current. Science 267:1324–1326.

Seymour, R. J., Tegner, M. J., Dayton, P. K., & Parnell, P. E. (1989). Storm wave induced mortality of giant kelp, Macrocystis pyrifera, in southern California. *Estuarine, Coastal and Shelf Science*, *28*(3), 277-292.

Schiel, D. R., & Foster, M. S. (2015). *The biology and ecology of giant kelp forests*. Univ of California Press.

Sousa, W. P. (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, *60*(6), 1225-1239.

Tegner, M. J., & Dayton, P. K. (1987). El Nino effects on southern California kelp forest communities. *Advances in Ecological research*, *17*, 243-279.

Turner, M. G., & Dale, V. H. (1998). Comparing large, infrequent disturbances: what have we learned?. *Ecosystems*, *1*(6), 493-496.

Webb, W.L., Newton, M., Starr, D.: Carbon dioxide exchange of Alnus rubra: A mathematical model. – Oecologia 17: 281-291, 1974

Zimmerman, R. C., & Kremer, J. N. (1984). Episodic nutrient supply to a kelp forest ecosystem in Southern California. *Journal of Marine Research*, *42*(3), 591-604.

APPENDIX A

POINT LOMA KELP FOREST COMMUNITY

Baseline surveys, including all kelp forest species, were conducted prior to experimental clearings within each treatment plot to ensure that proposed study site and treatment locations had similar community assemblages. Overall, species abundances within the kelp forestcommunitygreatly fluctuated across seasons and treatments, further supporting previous literature focusing on the seasonal variability and resilience of kelp forest ecosystems to perturbations (Dayton et al 1984; Table 15). Here, I first investigated if kelp forestbenthic percent cover(defined as any sessile primary placeholders) changed within the treatments and across season. Kelp forestcommunity compositionin Point Loma varied significantly among seasons, sites, treatments and their interactions (Table 2). In addition, variance components revealed differences in the contribution of each factor on kelp forest community composition. Residuals, or small-scale variation, contributed to 31.81% of overall differences in community composition, whereas season and treatment accounted for 13.83% and 7.02% respectively.

Community composition did not differ in Fall 2015 prior to experimental manipulation of treatments, but was significantly different between the FS and FW treatments from Spring 2016 to Summer 2017 (Table 16). Although the differences observed between FS and FW are apparent within the kelp forestcommunity, it is important to consider the seasonal experimental manipulation of canopy layers to maintain treatment effects and elicit responses by the understory red algae community. Nonetheless, most of the dissimilarities observed between the FS and FW treatments were driven by articulated and encrusting coralline algae, the opportunistic red alga *Acrosorium venulosum,* and the understory brown alga *Laminaria farlowii* (Table 17). Community composition between the FS and IS treatments was significantly different from Summer 2016 to Summer 2017, as species that most greatly contributed to differences were epiphytic detritus, *A. venulosum*, encrusting coralline algae, and articulated coralline algae.

**Table 15: Results of PERMANOVA with season (Fall 2015- Summer 2017), site (North, Central, South) and treatment (Frequent-Strong, Frequent-Weak, Infrequent-Strong, Control) as selected variables for testing how these factors influences entire Point Loma kelp forest community composition. P-values are uncorrected, and are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Source | df | SS | MS | Pseudo-F | P(perm) | % variation |
| Season (SE) | 5 | 2.06E+05 | 41265 | 17.375 | **0.001** | 13.83 |
| Site (SI) | 2 | 78893 | 39447 | 16.609 | **0.001** | 10.45 |
| Treatment (TR) | 3 | 45993 | 15331 | 6.4553 | **0.001** | 7.02 |
| SExSI | 9 | 95819 | 10647 | 4.4828 | **0.001** | 10.69 |
| SExTR | 15 | 8.33E+04 | 5553.1 | 2.3382 | **0.001** | 7.91 |
| SIxTR | 6 | 5.37E+04 | 8950.1 | 3.7685 | **0.001** | 8.80 |
| SExSIxTR | 27 | 1.08E+05 | 4009.1 | 1.6881 | **0.001** | 9.50 |
| Res | 469 | 1.11E+06 | 2375 |  |  | 31.81 |

**Table 16. Results of PERMANOVA post-hoc pair-wise test with treatment (FS-*Frequent-Strong,* FW-*Frequent-Weak,* IS-*Infrequent-Strong, Control*) as a factor and season (Fall 2015-Summer 2017) as a selected variable for testing statistical differences in responses to treatments across season for the entire kelp forest community in Point Loma. P-values are uncorrected, and are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Treatment Interactions** | **Fall 2015** | **Spring 2016** | **Summer 2016** | **Fall 2016** | **Spring 2017** | **Summer 2017** |
| **FS, FW** | 0.207 | **0.046** | **0.001** | **0.003** | **0.001** | **0.001** |
| **FS, CONTROL** | 0.197 | **0.009** | **0.001** | 0.098 | **0.001** | **0.001** |
| **FS, IS** | 0.569 | 0.079 | **0.002** | **0.001** | **0.001** | **0.001** |
| **FW, CONTROL** | 0.094 | 0.248 | **0.001** | 0.064 | 0.513 | 0.513 |
| **FW, IS** | 0.3 | **0.002** | **0.01** | **0.001** | **0.001** | **0.001** |
| **CONTROL, IS** | 0.409 | 0.086 | **0.002** | 0.152 | **0.002** | **0.002** |

**Table 17. Results of Similarities Percentages (SIMPER) Analysis showing which species within the entire kelp forest community were primarily responsible for Bray-Curtis Dissimilarity between treatments varying in frequency and magnitude of disturbance (Magnitude: Frequent-Strong v. Frequent-Weak, Frequency: Frequent-Strong v. Infrequent-Strong).**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ***Frequent-Strong* and *Frequent-Weak***  **Avg. dissimilarity= 82.54%** | | | | | | |
| **Species** | FS Av.Abund | FW Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| **Articulated coralline** | 0.16 | 0.25 | 6.16 | 1.1 | 7.47 | 7.47 |
| **Encrusting coralline** | 0.12 | 0.23 | 5.9 | 1.04 | 7.15 | 14.62 |
| ***Acrosorium venulosum*** | 0.18 | 0.1 | 5.36 | 0.8 | 6.49 | 21.11 |
| ***Laminaria farlowii*** | 0.09 | 0.19 | 5.26 | 0.87 | 6.37 | 27.48 |
| **Encrusting Red** | 0.07 | 0.21 | 5.13 | 0.96 | 6.22 | 33.7 |
| **Epiphytic detritus** | 0.17 | 0.07 | 4.92 | 0.7 | 5.95 | 39.65 |
| **Sand** | 0.12 | 0.13 | 4.38 | 0.82 | 5.3 | 44.96 |
| ***Rhodomenia californica*** | 0.14 | 0.08 | 4.03 | 0.8 | 4.89 | 49.84 |
| ***Frequent-Strong* and *Infrequent-Strong***  **Average dissimilarity= 83.16** | | | | | | |
| **Species** | FS Av.Abund | IS Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
| **Epiphytic detritus** | 0.17 | 0.23 | 7.25 | 0.93 | 8.72 | 8.72 |
| ***Acrosorium venulosum*** | 0.18 | 0.13 | 5.94 | 0.81 | 7.14 | 15.86 |
| **Encrusting coralline** | 0.12 | 0.21 | 5.8 | 0.96 | 6.98 | 22.84 |
| **Articulated coralline** | 0.16 | 0.13 | 4.99 | 0.92 | 6.01 | 28.85 |
| ***Rhodymenia californica*** | 0.14 | 0.11 | 4.56 | 0.84 | 5.49 | 34.33 |
| **encrusting red** | 0.07 | 0.15 | 4.1 | 0.83 | 4.93 | 39.26 |
| **Sand** | 0.12 | 0.09 | 4.03 | 0.76 | 4.84 | 44.11 |
| ***Laminaria farlowii*** | 0.09 | 0.09 | 3.56 | 0.66 | 4.28 | 48.38 |

The brown alga *Laminaria farlowii* maintained presence in all treatments across season, reaching greatest percent cover in Spring 2017 within the Frequent-Weak treatment and Control (Figure 3). Further, the magnitude of disturbances, (FS v. FW), appeared to have an influence on the *L. farlowii* populations. On average, *L. farlowii* occupied 10% more of the benthos in the FW versus FS treatment, and contributed to 6.37% of the total dissimilarity between the two treatments (Table 5). This is not surprising considering understory species positively respond to the removal of a canopy-forming species such as *Macrocystis* (Reed and Foster 1984, Dayton et al 1984), and treatments were designed to capture these responses if they existed. Although differences in the magnitude of disturbances appeared to elicit a positive response in *L. farlowii* populations, by the end of the study in Summer 2017, percent cover observed across all treatments was similar, ranging from 5.1-8.4% cover (Figure 4). Interestingly, FW and Controltreatments followed similar trends in Year 2 (Fall 2016-Summer 2017), drawing our attention to the natural level of disturbance occurring in Point Loma during this sampling period. Specifically, post-hoc analyses reported for the FW and Control treatments in Spring 2016, Fall 2016, and Spring 2016 (p>0.05) all indicate potential homogenization of the two treatments, as Point Loma experienced Winter and Spring storm disturbances that resulted in similar impacts to the FW treatment by removing *Macrocystis* canopies and maintaining understory *L. farlowii* kelp species (Figure 1a, Figure 4). Ultimately, and over the course of this two-year study, experimental manipulation of kelp canopy layers did not appear to greatly influence *L. farlowii* populations; instead, *L. farlowii* appears to be a resilient and fundamental species present within the Point Loma kelp forest.

**Figure 4: Mean (± SE) percent cover of understory *Laminaria farlowii* across treatment and season (Fall 2015-Summer 2017).**

APPENDIX B

CARMEL BAY KELP FOREST COMMUNITY

Corroborating the results in Point Loma, species abundances within the Carmel Bay kelp forestcommunitygreatly fluctuated across seasons and treatments, further supporting previous literature focusing on the seasonal variability and resilience of kelp forest ecosystems to perturbations (e.g. Reed and Foster 1984, Edwards 1998, Clark et al. 2004; Table 18). Kelp forestcommunity compositionvaried significantly among seasons, sites, treatments (p=0.001) and their interactions. Furthermore, variance components revealed differences in the contribution of each factor on kelp forest community composition. Residuals or small-scale variation contributed to 46.58% of overall differences in community composition, whereas season and treatment accounted for 10.59% and 5.12%, respectively.

In Spring 2016, prior to experimental manipulation, kelp forest community composition did not vary among any of the treatments (Table 19). Specifically, apart from Fall 2016, kelp forest community composition was significantly different between the FS and FW treatments from Summer 2016 to Summer 2017 (all p<0.05). Across seasons most of the dissimilarities observed between FS and FW treatments were driven by articulated and encrusting coralline algae, sand, encrusting red algae, and *P. cartilagineum* (Table 15). Community composition between the FS and IS treatments was significantly different only in Summer 2016, Winter 2016, and Spring 2017 (Table 19). Species that contributed the most to differences between FS and IS treatments were primarily due to articulated and encrusting coralline sand, encrusting red algae, the sub-canopy forming species *Pterygophora californica* (4.91%) and *P. cartilagineum* (4.79%) (Table 20).

**Table 18: Results of PERMANOVA with season, site and treatment as selected variables for testing how these factors influences entire kelp forest community composition from Fall 2015-Summer 2017. P-values are uncorrected, and are considered significant if p<0.05. Significant p-values are in bold.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Source** | **df** | **SS** | **MS** | **Pseudo-F** | **p-value** | **% Variation** |
| **Season (SE)** | 5 | 2.00E+05 | 39975 | 16.67 | 0.001 | 10.59 |
| **Site (SI)** | 2 | 72487 | 36243 | 14.339 | 0.001 | 12.05 |
| **Treatment (TR)** | 3 | 39736 | 13245 | 5.7542 | 0.001 | 5.12 |
| **SExSI\*\*** | 9 | 92887 | 10321 | 4.4569 | 0.001 | 10.72 |
| **SExTR** | 15 | 82425 | 5495 | 2.2946 | 0.001 | 0.00 |
| **SIxTR** | 6 | 50278 | 8379.7 | 3.3153 | 0.001 | 8.81 |
| **SExSIxTR** | 27 | 1.07E+05 | 3946 | 1.704 | 0.001 | 6.12 |
| **Res** | 237 | 5.49E+05 | 2315.7 |  |  | 46.58 |

**Table 19: Results of PERMANOVA post-hoc pair-wise test with treatment as a factor and season as a selected variable for testing differences in responses to treatments across season for the entire kelp forest community in Carmel Bay. P-values are uncorrected, and are considered significant if p<0.05 (in bold).**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Treatment Interactions** | **Spring 2016** | **Summer 2016** | **Fall 2016** | **Winter 2016** | **Spring 2017** | **Summer 2017** |
| **FS, FW** | 0.167 | **0.003** | 0.19 | **0.015** | **0.024** | **0.01** |
| **FS, CONTROL** | 0.532 | **0.023** | 0.531 | 0.282 | **0.017** | **0.001** |
| **FS, IS** | 0.531 | **0.001** | 0.518 | **0.005** | **0.001** | 0.08 |
| **FW, CONTROL** | 0.107 | **0.045** | 0.097 | 0.346 | 0.216 | **0.036** |
| **FW, IS** | 0.558 | 0.537 | 0.574 | 0.581 | **0.029** | 0.154 |
| **CONTROL, IS** | 0.479 | 0.677 | 0.466 | 0.114 | **0.034** | **0.047** |

**Table 20: Results of Similarities Percentages (SIMPER) analysis showing which species within the entire kelp forest community were primarily responsible for Bray-Curtis dissimilarity between treatments varying in frequency and magnitude of disturbance (Magnitude: FS v. FW, Frequency: FS v. IS). Species presented have a contribution percentage >4%**.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| ***Frequent-Strong*** vs. ***Frequent-Weak*** | | | | | | |
| **Species** | **FS Av.Abund** | **FW Av.Abund** | **Av.Diss** | **Diss/SD** | **Contrib%** | **Cum.%** |
| **Articulated coralline** | 0.25 | 0.34 | 7.11 | 1.17 | 9.55 | 9.55 |
| **Encrusting coralline** | 0.29 | 0.36 | 6.24 | 1.16 | 8.38 | 17.93 |
| **Sand** | 0.17 | 0.13 | 5.2 | 0.86 | 6.99 | 24.92 |
| **Encrusting Red** | 0.15 | 0.16 | 4.79 | 0.99 | 6.44 | 31.36 |
| ***Plocamium cartilagineum*** | 0.14 | 0.08 | 4.09 | 0.75 | 5.5 | 36.86 |
| ***Diopatra ornata*** | 0.11 | 0.07 | 3.52 | 0.63 | 4.73 | 41.59 |
| ***Pterygophora californica*** | 0.06 | 0.13 | 3.42 | 0.72 | 4.59 | 46.18 |
| **Frequent-Strong vs. Infrequent-Strong** | | | | | | |
| **Species** | **FS Av.Abund** | **IS Av.Abund** | **Av.Diss** | **Diss/SD** | **Contrib%** | **Cum.%** |
| **Articulated coralline** | 0.25 | 0.25 | 6.53 | 1.1 | 8.41 | 8.41 |
| **Encrusting coralline** | 0.29 | 0.28 | 6.32 | 1.18 | 8.14 | 16.55 |
| **Sand** | 0.17 | 0.15 | 5.62 | 0.84 | 7.24 | 23.79 |
| **Encrusting red** | 0.15 | 0.13 | 4.48 | 0.95 | 5.77 | 29.56 |
| ***Pterygophora californica*** | 0.06 | 0.14 | 3.81 | 0.74 | 4.91 | 34.47 |
| ***Plocamium cartilagineum*** | 0.14 | 0.05 | 3.72 | 0.69 | 4.79 | 39.26 |
| **Tunicate spp.** | 0.09 | 0.1 | 3.5 | 0.75 | 4.5 | 43.76 |
| ***Diopatra ornata*** | 0.11 | 0.05 | 3.29 | 0.6 | 4.24 | 48 |
| **Epiphytic detritus** | 0.08 | 0.1 | 3.27 | 0.67 | 4.21 | 52.21 |
| **Bare Rock** | 0.06 | 0.1 | 3.23 | 0.6 | 4.17 | 56.38 |

APPENDIX C

URCHINS IN CARMEL BAY

**Urchin Barren Formation in Carmel Bay**

In Point Loma, urchins were primarily observed within cracks in the benthic substrate and rarely seen unprotected within the treatments. Further, they were observed passively feeding on kelp detritus as it drifted by their protected dwelling. However, over the course of this study, many locations within central California experienced a loss of kelp to urchin grazing (spp. *Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus*) subsequently resulting in urchin barren formation (pers. obs.). However, urchin barrens were not observed within the established Carmel Bay sites until the final sampling period in Summer 2017. From Spring 2016-2017 urchin presence within quadrats was relatively consistent, reaching a maximum of 25 urchins in the Central site (Figure 3). Yet, by Summer 2017, the number of urchins present across all sites and treatments reached a total of 211. Most notably, in the central site, between Spring 2017 and Summer 2017 sampling periods, urchin presence increased by 54%.

**Figure 3: Total number of urchins present within Carmel Bay, CA (all sites and treatments) from Spring 2016 to Summer 2017.**

APPENDIX D

PHOTOPHYSIOLOGY MEASUREMENTS

**Table 21: Mean (±SE) photophysiology measurements (Pmax, alpha and respiration) for individual red algae species in Point Loma. Algae photophysiology was measured across three seasons: Fall 2016, Spring 2016, and Summer 2017.**

|  |  |  |  |
| --- | --- | --- | --- |
| *Cryptopleura farlowiana* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.13466 (± 0.021) | 0.00044 (± 0) | -0.3852(± 0.016) |
| **Spring 2017** | 0.1965 (± 0.025) | 0.00073(± 0) | -0.03391 (± 0.018) |
| **Summer 2017** | 0.14892(± 0.012) | 0.00112(± 0.001) | 0.06005(± 0.042) |
| **Did photophysiological parameters (Pmax, alpha, R) vary across season?** | NO  p=0.153 F=2.610 df=2 | NO  p=0.634, F=0.491, df=2 | NO  p=0.079, F=3.994, df=2 |
| *Plocamium cartilagineum* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.20024 (± 0.024) | 0.00049 (± 0.001) | 0.00461(± 0.014) |
| **Spring 2017** | 0.1902(± 0.028) | 0.00089 (± 0.001) | -0.02505(± 0.019) |
| **Summer 2017** | 0.08742(± 0.027) | 0.00057 (± 0.001) | 0.05441(± 0.026) |
| **Did photophysiological vary across season?** | **YES**  **p=0.043, F=5.551, df=2** | NO  p=0.527, F=0.713, df=2 | NO  p=0.81, F=3.920, df=2 |
| *Rhodymenia californica* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.13743 (± 0.005) | 0.0015 (± 0.001) | -0.02378(± 0.008) |
| **Spring 2017** | 0.25355(± 0.022) | 0.00155(± 0.001) | -0.03115(± 0.039) |
| **Summer 2017** | 0.18466(± 0.072) | 0.00144(± 0.001) | -0.02594 (± 0.013) |
| **Did photophysiological vary across season?** | NO  p=0.248, F=1.774, df=2 | NO  p=0.997, F=0.003, df=2 | NO  p=0.976, F=0.024, df=2 |
| *Prionitis lanceolata* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.19531(± 0.017) | 0.00122(± 0.001) | -0.06575(± 0.001) |
| **Spring 2017** | 0.14478 (± 0.017) | 0.00219(± 0.001) | -0.04498(± 0.016) |
| **Summer 2017** | 0.14672 (± 0.013) | 0.00162 (± 0.001) | -0.0233(± 0.002) |
| **Did photophysiological vary across season?** | NO  p=0.141, F=2.981, df=2 | NO  p=0.762, F=0.286. df=2 | NO  p=0.112, F=3.503, df=2 |
| *Prionitis linearis* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.18848 (± 0.007) | 0.00064 (± 0.001) | -0.04957(± 0.002) |
| **Spring 2017** | 0.27158(± 0.044) | 0.0008(± 0.001) | -0.01045(± 0.010) |
| **Summer 2017** | 0.15923(± 0.020) | 0.00059(± 0.001) | 0.04052(± 0.012) |
| **Did photophysiological vary across season?** | NO  p=0.071, F=4.24, df=2 | NO  p=0.852, F=0.164, df=2 | **YES**  **p=0.001, F=26.218, df=2** |

**Table 22: Mean (±SE) photophysiology measurements (Pmax, alpha and respiration) for individual red algae species in Carmel Bay. Algae photophysiology was measured across three seasons: Fall 2016, Spring 2016, and Summer 2017*.***

|  |  |  |  |
| --- | --- | --- | --- |
| *Cryptopleura farlowiana* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.571 (± 0.226) | 0.002 (± 0.001) | -0.026(± 0.014) |
| **Spring 2017** | 0.234 (± 0.034) | 0.011(± 0.003) | -0.034 (± 0.027) |
| **Summer 2017** | 0.512(± 0.191) | 0.001(± 0.001) | -0.083(± 0.047) |
| **Did species vary across season?** | NO  p=0.392 F=1.098 df=2, 6 | **YES**  **p=0.030,** **F=6.606, df=2, 6** | NO  p=0.453, F=0.906, df=2, 6 |
| *Plocamium cartilagineum* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.109 (± 0.056) | 0.002 (± 0.001) | -0.052(± 0.028) |
| **Spring 2017** | 0.177(± 0.031) | 0.006 (± 0.003) | -0.015(± 0.004) |
| **Summer 2017** | 0.205(± 0.007) | 0.001 (± 0.001) | 0.011(± 0.017) |
| **Did species vary across season?** | NO  p=0.252, F=1.749, df=2, 6 | NO  p=0.297, F=1.498, df=2, 6 | NO  p=0.144, F=2.725, df=2, 6 |
| *Rhodymenia californica* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.154 (± 0.030) | 0.001 (± 0.0) | -0.025(± 0.015) |
| **Spring 2017** | 0.104 (± 0.021) | 0.005 (± 0.002) | -0.006(± 0.005) |
| **Summer 2017** | 0.290(± 0.091) | 0.005(± 0.004) | -0.038(± 0.016) |
| **Did species vary across season?** | NO  p=0.132, F=2.887, df=2, 6 | NO  p=0.436, F=0.955, df=2, 6 | NO  p=0.293, F=1.515, df=2, 6 |
| *Prionitis linearis* | | | |
| **Season** | **Pmax** | **Alpha** | **Respiration** |
| **Fall 2016** | 0.196 (± 0.056) | 0.000 (± 0.00001) | -0.047(± 0.019) |
| **Spring 2017** | 0.115(± 0.039) | 0.001(± 0.00001) | 0.003(± 0.00001) |
| **Summer 2017** | 0.037(± 0.006) | 0.001(± 0.00001) | -0.002 (± 0.00001) |
| **Did species vary across season?** | NO  p=0.092, F=4.004, df=2, 5 | NO  p=0.669, F=0.436, df=2, 5 | NO  p=0.071, F=4.684, df=2, 5 |