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Title: Phytoplankton Shading of Marine Benthic Macrophytes: Implications for Intertidal Community Structure

Abstract Approved:

Bruce Menge
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Previous observations of light levels and phytoplankton abundances along the Oregon coast demonstrated that phytoplankton attenuated light sufficiently to potentially limit the growth of intertidal macrophytes and therefore structure local intertidal communities. Inspired by this observation, in spring 2004, I initiated a study to quantify the direct and indirect benthic community response to different light regimes. Frames supporting plastic mesh were installed to shade macroalgae in the *Hedophyllum* zone. With unshaded treatments, the shade treatment manipulated the light levels available to benthic algal species at two sites differing in historic pelagic productivity. Treatments included shaded, unshaded, and manipulation control plots that were 0.25 m^2 in area. The experiment began in mid June and ran through the end of August, 2004. The direct response variables were the growth rate and abundance accumulation of the perennial intertidal kelp *Hedophyllum sessile.* The indirect responses measured were the changes in abundance of understory red algae. Results indicated that shade decreased growth rates of *Hedophyllum* and that the extent of growth rate reduction varied between sites. The response of total cover of understory algae was not strongly different between treatments and the response of individual algal groups differed between treatments and between sites. At Fogarty Creek, an area of historically high macroalgal abundance and comparatively low phytoplankton abundance, the primary response to increased shade was an increase in foliose red algae. At Strawberry Hill, an area of lower macroalgal abundance, the primary response was an increase in dominance of coralline algae. The response of algal diversity to different canopy treatments also differed between sites. Diversity of understory algae was highest beneath the artificial shades at Fogarty Creek whereas at Strawberry Hill, the diversity was the highest beneath intact canopy. The difference in responses of the understory assemblage at the two sites was interpreted to signify potential differences in the ecological role of the canopy. At Fogarty Creek, the canopy appears to reduce algal abundance and diversity, presumably through competitive inhibition, whereas at Strawberry Hill the canopy appears to facilitate increased algal abundance and diversity, presumably through habitat amelioration. While underscoring the need to include parameters of environmental stress when modeling changes in total production, these results are consistent with estuarine studies that demonstrate that as nutrient loading increases, the community shifts from a mixed autotroph assemblage to one dominated by phytoplankton. Thus in open

coast systems where annual benthic production can exceed the pelagic production by a factor of 5-10, increased nutrients may also shift these systems towards greater dominance by phytoplankton and reduced macrophytes. As perennial macrophytes such as kelp and sea grasses are also extraordinarily important habitat modifiers and provide nursery habitat for several species of fish and invertebrates, large-scale reduction of macrophytes could also lead to profound modifications of coastal ecosystem dynamics.

Phytoplankton Shading of Marine Benthic Macrophytes:
Implications for Intertidal Community Structure

by
Maria T. Kavanaugh

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APPROVED:

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Maria T. Kavanaugh, Author

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Several people were crucial to the successful completion of this study. The extra hands and balancing rationale of Lea Goodrich were essential in all parts of this study. I could not have done nearly the amount of work nor enjoyed nearly as much without her. Jessica Flitcroft also provided tremendous help in the field and lab, and sorted biomass samples without complaint. Little did she know that her composed biology TA would lead such a hectic research schedule (likely, she had a glimpse). Morgan Packard and Susan Holmes also lent their time in sorting biomass samples and assisting with studies into the photo- physiology of *Hedophyllum* that would have made the master's thesis too lengthy if included. Morgan Packard, Matt Robart, Amber Steed, Karen Lashenke, Clara Funk, and Joe Tyburczy all helped with the dreaded dismantling of the shades and collecting of biomass samples. Morgan Packard, Clara Funk, and Jessica Flitcroft were all extraordinarily generous with their time, lending extra field support.

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CONTRIBUTION OF AUTHORS

The impetus of this study was based on findings of Dr. Menge and Dr. Karina Nielsen and some of their work is included in the thesis. They are co-authors on Chapters 2 and 3.

Lea Goodrich was essential to the installation and maintenance of both the field and lab experiments and is a co-author on Chapter 2.

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CHAPTER 1

General Introduction

Models of global warming and increased anthropogenic alteration of biogeochemical cycles generally predict increased phytoplankton primary production (PP) in the coastal ocean (Rabouille, 2001, Vitousek et al., 1997). Models of oceanographic regime shift (e.g. ENSO) also focus on changes in planktonic-based production (Philander, 1989) and the resultant changes in "bottom-up" effects are likely to be of great importance to marine ecosystems (e.g., Bustamante et al 1995; Menge et al. 1997, 2003, 2004). With higher phytoplankton concentrations, for example, growth and survival of planktotrophic larvae and filter-feeding invertebrates are likely to increase, with a host of potential ecological indirect effects likely as a consequence.

While current bottom-up models address changes in aquatic systems due to increases in the abundance of the phytoplankton (McQueen et al., 1989) or benthic macrophytes (Morgan et al., 2003), little is known regarding the interaction between the two autotrophic groups. For example, the consequences of phytoplankton shading on benthic communities especially those dominated by macroalgae, is poorly known (Birkeland, 1997; Borum and Sand Jensen, 1996; Valiela et al., 1997).

Phytoplankton Shading

Evidence from estuarine studies suggests that nutrient loading can result in shifts from a mixed autotroph assemblage to one dominated by phytoplankton. Valiela and colleagues (1992, 1997) determined the proportion of total community production derived from sea grasses, macroalgae, and phytoplankton in estuaries with different nutrient loading and retention times. According to their model (Fig. 1.1), as nutrient loading and water residence time increases, seagrasses give way successively to macroalgae then to phytoplankton. Because phytoplankton growth rates far exceed those of both macroalgae and sea grasses in high nutrient conditions (Pedersen and Borum, 1996) their accumulated biomass in the water column is predicted to shade out the benthic autotrophs (Costa, 1988; Valiela et al. 1992, 1997).

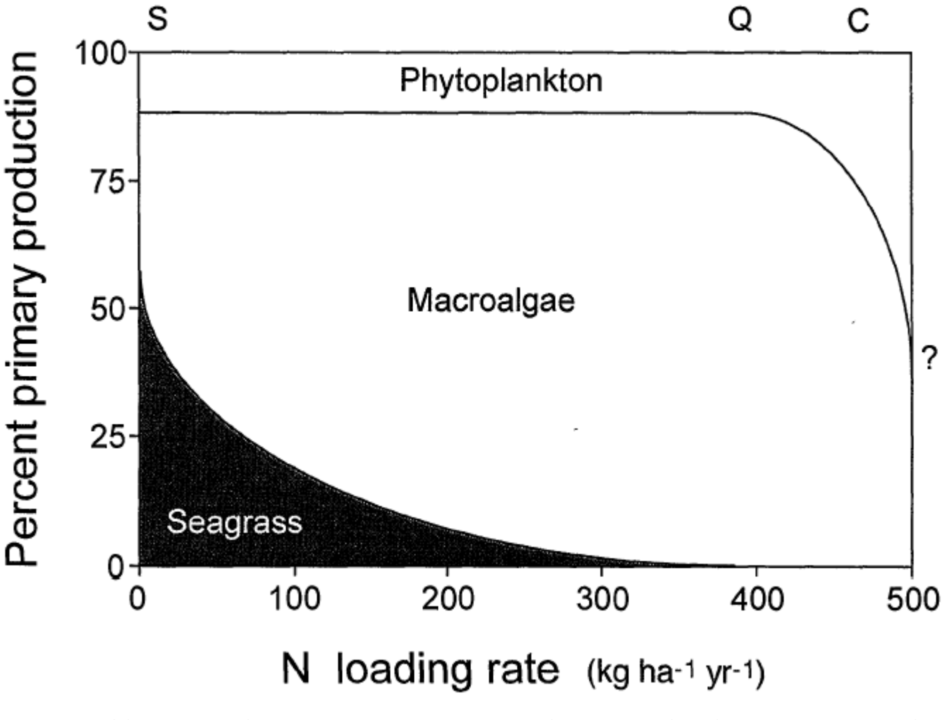


Fig 1.1 Model of increase in phytoplankton dominance with increased nutrient loading (From Valiela et al, 1997).

The large-scale effects of climate change on changing the periodicity and intensity of natural nutrient input into coastal systems and the resultant change in total community production is poorly understood. The effects of increased nutrient input on open coast systems have been largely ignored (Borum and Sand-Jensen, 1996; Bokn et al. 2003; but see Nielsen 2001, 2003, Nielsen & Navarrete 2004, Bracken and Nielsen 2004, Bustamante et al. 1995). Because of the physical complexity of the coastal environment, modeling efforts that looked at changes in both pelagic and benthic production have also been limited to enclosed or semi-enclosed systems and the resultant eutrophication that occurs after anthropogenic nutrient loading (Borum and Sand-Jensen, 1996). An earlier view was that the water residence times required for phytoplankton accumulation were too short in the high energy open-coast systems (Valiela et al., 1997). Now it is recognized that areas of *naturally* high productivity, specifically areas of high seasonal upwelling, often have regular occurrences of hypoxia (Grey et al., 2002), the most readily measurable effect of eutrophication.

A shift in dominance from benthic macrophytes to phytoplankton will have profound ecological and biogeochemical effects in coastal systems. Open coast systems can often support benthic primary production of over 1000 g C m^{-1} y^{-1} which represents a major proportion of the total annual primary productivity in shallow coastal regions (Borum and Sand-Jensen, 1996; Mann, 1972) Benthic macroalgae have important roles as ecosystem engineers (sensu Jones, 1994) modifying sedimentation (Irving and Connell, 2003), temperature, and flow (Bruno and Bertness, 2001). Benthic macrophytes also provide nursery habitat for commercially important fish (Mann, 1972; Jackson, 2001) and invertebrates.

Background: Potential for Shading in the Rocky Intertidal

While intertidal ecologists have looked at the concentration of phytoplankton as a mechanism that may be responsible for shaping benthic communities due to increased food availability (Menge et al., 1994) and upwelling/larval transport associations (Menge et al., 1997, 2003, 2005), ecologists have largely ignored light-limitation as a mechanism that could influence community structure. Three criteria must be met in order for phytoplankton shading to be a factor in shaping intertidal communities:

1. Nutrient influx must be sufficiently high to support dense phytoplankton loads,
2. Phytoplankton must be retained close to shore for shading to occur for ecologically relevant periods of time,
3. Growth of intertidal macrophytes must be sufficiently limited by the light available during phytoplankton blooms.

The Oregon coast, dominated by seasonal upwelling and relaxation, supports high productivity throughout the spring and summer. Studies show the magnitude and duration of near shore phytoplankton blooms coupled with distinct differences in intertidal communities differ between regions along the Oregon coast (Menge et al., 1994, 1997a, b, 2004). Relative to Cape Perpetua shores, Cape Foulweather shores are typified by greater abundance of intertidal macrophytes and lower abundances of sessile invertebrates. While experimental evidence suggests that nutrient limitation can influence macroalgal abundance and diversity in mid to high zone pools along the Oregon coast (Nielsen 2001, 2003; Bracken & Nielsen 2004), the underlying mechanisms behind these mesoscale differences remain unclear. While mesoscale variation in algal assemblages along Chilean rocky shores are apparently driven by variation in nutrient loading from upwelling (Nielsen & Navarrete 2004), nutrient influxes via upwelling in Oregeon do not appear to be limiting at either region (Menge et al., 1997).

The central Oregon coast is typified by intermittent seasonal upwelling (Menge et al. 2004). During upwelling, nutrient-rich water is brought to the surface and made available for phytoplankton. The upwelling circulation pattern, however, generally pushes new production offshore away from shallow benthic communities. Eddy circulation and relaxation events, however, can return both larvae and phytoplankton to the very near shore region (Halpin et al., 2004).

Water samples taken in the surf zone suggest that Cape Perpetua is a region of localized retention of phytoplankton (Menge et al. 1997a, Grantham et al. 2004). During 2001-2003, the spring-summer mean chlorophyll levels in the surf zone were approximately 50- 60 micrograms l^{-1} at Cape Perpetua vs. less than 20 μg/l at Cape Foulweather. PAR (photosynthetically active radiation) sensor data suggest that these inter-cape differences in phytoplankton abundance can affect the amount of light reaching intertidal macroalgae during high-tide immersion (Nielsen et al. in prep.). During a period of high production in the summer of 2002 the average attenuation coefficients, or the amount of light ‘lost’ per unit depth, were 2 times greater at Cape Perpetua than at Cape Foulweather (Fig. 1.2, Nielsen et al., in prep.). With an attenuation coefficient of 3, approximately 99 percent of light is absorbed in the first meter of water.

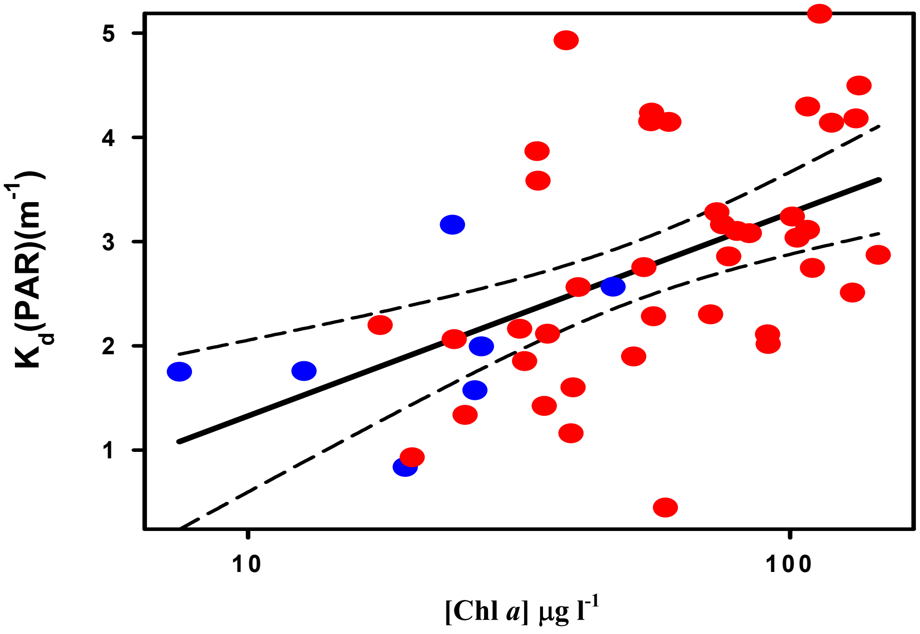


Figure 1.2. Chlorophyll concentration and Light Attenuation during a period of Moderate Production along the Oregon coast, July 2002 (K. J. Nielsen, in prep.). The red dots denote Strawberry Hill, the blue, Fogarty Creek. $R^2 = 0.39$, $p<0.0001$.

Thus, bio-optical properties can potentially affect benthic communities in shallow open coast systems. The goal of this study was to evaluate how light attenuation by phytoplankton impacts the physiology and ecologyl of benthic primary producers and benthic communities. Because the effect of different light regimes on growth and abundance may vary between sites, by canopy layer, or by species, we designed and executed an experiment that investigates effects of varying light regimes on the intertidal kelp, *Hedophyllum sessile*, and on the understory assemblage at Fogarty Creek and Strawberry Hill, two sites along the central Oregon coast.

In Chapter 2, I present an experiment in which we manipulated the light available to the kelp with the use of artificial shades. The degree of shading was derived from modeled total light availability based on 2002 measured attenuation coefficients. The goal of this study was to determine if the light experienced during a period of moderate production in summer 2002 could be limiting to the intertidal kelp.

To test for site-level differences in growth rates under controlled light levels, we carried out a "common-garden" type experiment in flow-through laboratory tanks at Hatfield Marine Science Center in Newport, Oregon. This experiment was conducted twice, first with ambient nutrient levels and then with manipulated nutrient levels designed to mimic coastal upwelling conditions.

In Chapter 3, I shifted focus to changes in the understory species, their diversity and abundances. The goal of this study was two-fold. First, we wanted to understand the indirect effects of phytoplankton shading on the understory assemblage of a kelp community. We also wanted to understand the relative role of the canopy at the two field sites where environmental stress levels, specifically temperature during emersion and scour due to sand, are different.

Finally, in the last chapter, I present some general conclusions regarding the fluctuating bio-optical environment. I briefly review the salient theory regarding competition and facilitation in marine environments and include notions of how ecological theory may be used to predict patterns of macroalgal abundance and diversity. Low zone algae, especially understory species, may be subject to light limitation during immersion (Kavanaugh et al., this study) and varying degrees of stress (desiccation and photoinhibition) during emersion. Therefore, I present a general model that includes differential physiology and an environmental stress gradient into an ecological model of phytoplankton/kelp/understory assemblage interactions. This model can then be used to test patterns of macrophyte abundance and diversity in areas of high/low phytoplankton abundance over a larger spatial scale.

CHAPTER 2

EXPLORING POTENTIAL COMPETITIVE EFFECTS OF PHYTOPLANKTON: DOES SHADING AFFECT INTERTIDAL KELP GROWTH?

ABSTRACT

Previous observations along the Oregon coast demonstrated that phytoplankton accumulation led to high standing stocks in the surf zone along the Oregon coast. The high standing stock of phytoplankton, as proxied by chlorophyll-a levels, was associated with severe attenuation of the light available to the benthos. Inspired by this observation, in spring 2004 I initiated a study to quantify the benthic community response to different light regimes, specifically that which would occur during high pelagic production. Frames supporting plastic mesh were installed to shade macroalgae in the low intertidal zone to manipulate the light levels available to benthic algal species at two sites with historical and persistent differences in average pelagic productivity. Treatments included shaded and unshaded plots that were 0.25 m^2 in area. The experiment began in mid June and ran through the end of August. The response variable was growth rate and relative change in percent cover of the intertidal kelp *Hedophyllum sessile*. Results indicated that shade decreased growth rates of *Hedophyllum* and that the extent of growth rate reduction varied between sites. Shading also resulted in decreases in accumulation of biomass, as measured by changes in percent cover. These results were consistent with estuarine studies that demonstrate that as nutrient loading increases, the community may shift from a mixed autotroph assemblage to one dominated by phytoplankton. Thus in open coast systems where annual benthic production can exceed the pelagic production by a factor of 5-10, increased nutrients also seem likely to shift these systems towards greater

dominance by phytoplankton and reduced macrophytes. As perennial macrophytes such as kelp and sea grasses are also important habitat modifiers and provide nursery habitat for several species of fish, large-scale reduction of macrophytes could lead to profound modifications of coastal ecosystem dynamics.

Introduction

Models of global warming and increased anthropogenic alteration of biogeochemical cycles generally predict increased phytoplankton primary production in the coastal ocean (Rabouille, 2001). Models of oceanographic regime shift (e.g. ENSO) also focus on changes in planktonic-based production (Philander, 1989) and the resultant alteration of "bottom-up" effects are of great importance to marine ecosystems (e.g., Bustamante and Branch, 1995; Menge et al. 1997, 2003, 2004). With higher phytoplankton concentrations, for example, growth and survival of planktotrophic larvae and filter-feeding invertebrates seem likely to increase, with a host of potential ecological changes likely as a consequence. However, one potential consequence of such phytoplankton blooms, the effects of shading on benthic communities, especially those dominated by macroalgae, is poorly known.

Benthic macrophyte assemblages are critical to biogeochemical cycles and ecological interactions. Open coast systems can often support benthic primary production of over 1000 g C m^{-1} y^{-1} (Borum and Sand-Jensen, 1996). The production is high because annual primary production of perennial kelps and sea grasses is five (Borum and Sand-Jensen, 1996) to ten times (Mann, 1972) greater than that of phytoplankton. Kelps have important roles as ecosystem engineers and provide nursery habitat for commercially important fish (Mann, 1972). Therefore, a shift in dominance from benthic macrophytes to phytoplankton will have not only have profound ecological effects but may likely reduce total community production.

A discovery of light limitation for intertidal macrophytes would be surprising, as light would not be expected to be limiting in intertidal environments (Dring, 1987).

While the term limiting can imply vertical or biogeographic range extents, here it is meant in a physiological sense, i.e. leading to suboptimal growth. PAR (photosynthetically active radiation) sensor and surf zone chlorophyll-a data show that differences in phytoplankton abundance affect the amount of light reaching intertidal macroalgae during high-tide immersion along the Oregon coast (Nielsen et al. in prep). During a period of moderate to high production in the summer of 2002 the average attenuation coefficients, or the amount of light 'lost' per unit depth, were approximately 2 times greater in an intertidal region of Cape Perpetua than that of Cape Foulweather (Nielsen et al., in prep). The potential, therefore, exists for bio-optical properties to affect the benthic community in shallow open coast systems

During spring and summer 2004, we tested the hypothesis that the growth rate of intertidal kelp, *Hedophyllum sessile*, could be limited by the amount of light previously measured (Nielsen in prep) during periods of moderate phytoplankton production along the Oregon coast. We used a combination of modeling, experimental manipulation, *in situ* and laboratory measurements of growth and abundance of *Hedophyllum*, under different light regimes at two sites of historically different planktonic production. In order to account for differences in local physical characteristics, we also measured differences in plot slope, rugosity, water flow and differences in temperature and sediment accumulation between sites. Upwelling indices are modeled over 3-degree latitude bins-a scale too coarse to allow site-level resolution. They are reported here for the period during which the study was conducted as a reference only.

Methods

Site Selection

The field experiment was conducted at two sites on the central Oregon coast, Fogarty Creek (44.84 N, 124.05 W) and Strawberry Hill (44.24 N, 124.11 W). These sites have similar patterns of upwelling and macro-nutrient concentrations yet historically different levels of phytoplankton (measured as chlorophyll-a) (Menge et al., 1997). The sites are also characterized by differences in relative abundances of sessile invertebrates and macrophytes. Fogarty Creek has high relative abundances of macroalgae and low relative abundances of sessile filter feeders such as barnacles and mussels. The reverse is true for Strawberry Hill (Menge et al., 1994).

Previous studies have demonstrated that the two sites differ in several physical parameters. Temperatures tend to be slightly higher at Strawberry Hill (Halpin et al., 2002) and qualitatively at least, sand deposition seems to be greater at Strawberry Hill than at Boiler Bay, a site adjacent to Fogarty Creek (Trowbridge 1992, Menge et al., 1997). Field observations taken during 15+ years of intensive field studies indicate that little sand deposition occurs at Fogarty Creek as well (Menge et al. 2005, B. A. Menge, pers. obs.). Importantly, the continental shelf is much wider at Strawberry Hill (Fig. 1.1), potentially facilitating greater larval and or phytoplankton retention (Menge et al. 1997).

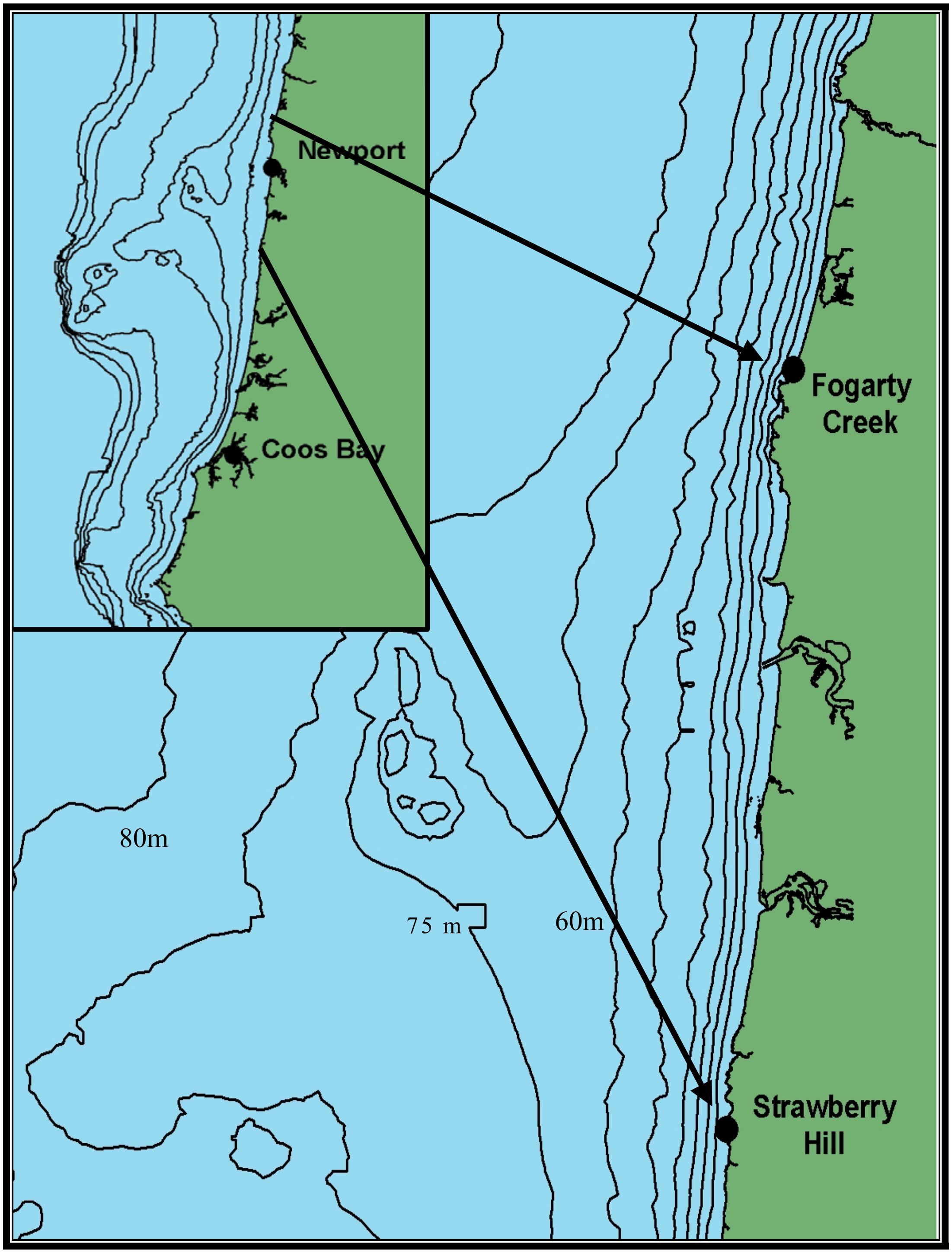


Figure 2.1: Map of Oregon coast showing field sites, Strawberry Hill and Fogarty Creek. The linear distance between sites is approximately 65 km. Note increased shelf width at Strawberry Hill.

Experimental design

To manipulate light input to macrophytes, shades covering 50 x 50 cm plots were installed in the lower intertidal. The use of shaded plots in field experimentation has been demonstrated in low and high intertidal habitats (Bertness et al. 1999, Burnaford, 2004; Harley 2003). Shades were designed by attaching vexar mesh to a stainless steel frame with both cable ties and washers and locking nuts. Stainless steel all-thread supports were inserted approximately 15 cm into holes drilled into the bedrock, and cemented into the holes with Z-spar. The shading mesh was elevated approximately 20 centimeters over the rock surface. The goal of the design was to not only to block an ecologically relevant percentage of the light but to provide a structure that would stand up to the waves and allow ample water flow.

The experimental light regime was intended to mimic that experienced by organisms during summer 2002, based on PAR (photosynthetically active radiation) sensor and chlorophyll-a data collected by Nielsen et al. (in prep.). I estimated the percentage of total light that would be blocked by water attenuation coefficients between 1.7 and 3, the coefficients derived for Fogarty Creek and Strawberry Hill respectively, during a three-week period in late summer 2002 (Nielsen et al., in prep). Attenuation coefficients were derived using data taken by PAR sensors that were placed in the low zone and in the near-terrestrial zone at each site. Attenuation coefficients (K_d) were calculated using the following equation:

$$I_x = I_o e^{-K_d z}$$

where I_o is the surface irradiance derived from the terrestrial PAR sensor, I_x is the irradiance at depth and derived from the PAR sensor in the low intertidal, and z is the depth of the water column derived from an existing tidal model (Tides and Currents, Or Nobeltec Corp , 1999).

The model has two important assumptions. First, it assumes that the growth rate of an autotroph can be linked to its net primary productivity (Eppley, 1981), which includes daily losses due to respiration and photoprotection. The model used a time period when emersion periods were longest and low tides occurred through the late morning through the middle of the day (early July, 2002). The daylight component used a typical cloudless day as a baseline. By using full sunlight and modeling over a period where low tides are longest and occur during mid-day, the effects of varying water bio-optical qualities would be minimized; therefore the model is somewhat conservative. Thus when considering total light available to intertidal organisms across changes in bio-optical properties, any measured effect could be considered relatively robust.

Second, the model assumes that the rate of photosynthesis during emersion compared to immersion is negligible due to carbon limitation and photoprotection/photoinhibition. *Hedophyllum*, like other macrophytes, likely continue to photosynthesize at some rate during emersion. Previous experiments demonstrate for even high intertidal algae photosynthesis during emersion is an order of magnitude less than immersion (Williams and Dethier, 2005) accounting for much more variation than differences between sites. The differential response between emersion and immersion in that study was interpreted as carbon limitation. A high light low carbon scenario would likely induce a photo-protection response (Demmig-Adams and Adams, 1992) and effectively decrease net photosynthesis.

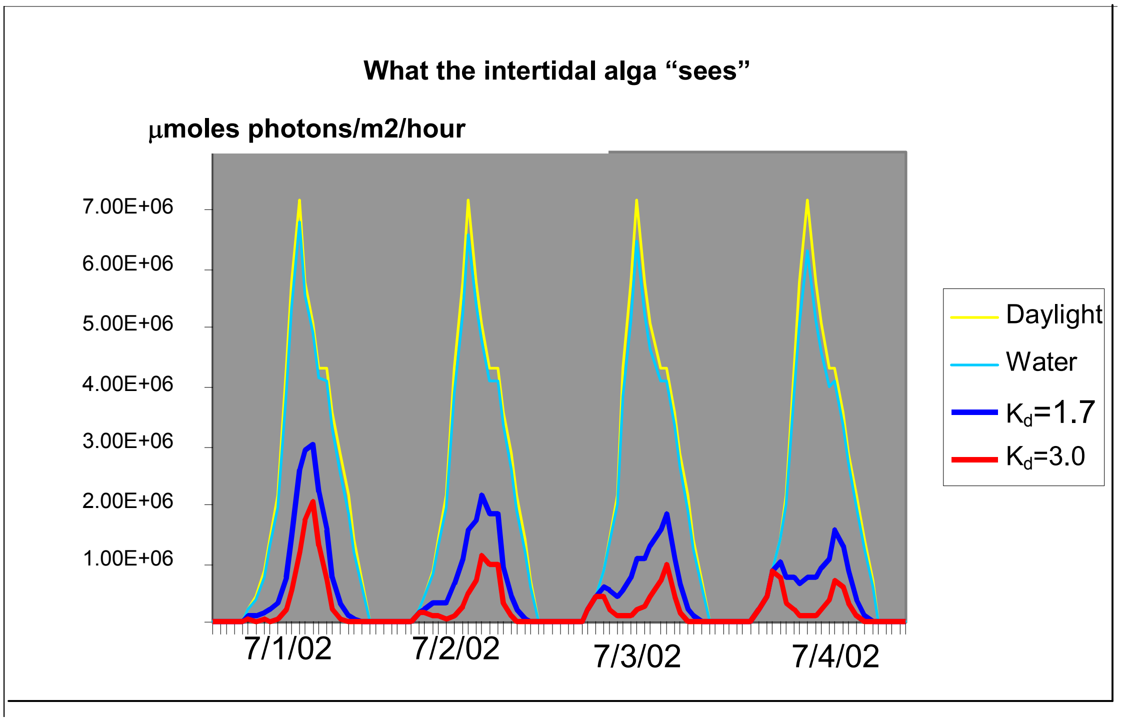


Figure 2.2: Modeled Intertidal Light Environment for Different Attenuation Coefficients for four days (96 hours) in early July, 2002. Taking a conservative approach by using a two week tidal period in July of 2002 when the periods of emersion were longest during daylight hours (low tides) and using an integrated tidal and daylight model, the amount of light available to a hypothetical plot at 1.0 feet above MLLW was calculated. Comparing the attenuation coefficients of 1.7 and 3.0, the calculated mean coefficients for Fogarty Creek and Strawberry Hill respectively (K. J. Nielsen, in prep.) to that of pure seawater and integrating over the two week period, only 39 and 28 percent of the light remains at the respective sites.

The bio-optical model was then used to calculate the amount of total light available to intertidal organisms at 1.0 feet (0.31 m) above Mean Lower Low Water (MLLW), which is the approximate elevation of the *Hedophyllum* zone (Kavanaugh et al., unpublished data). Using the conservative estimates of integrated tidal height (and therefore water depth), the attenuation coefficients, a 16 hour day length, and full sunlight, I derived the proportion of light available to organisms compared to that available under clear water conditions (Figure 2.2). Only 28-39 percent of the light is available to low zone organisms along the Oregon coast for the modeled conditions. This range was then used to determine the total shading for experimental units.

I used a portable light meter to quantify the level of shading in the plots. Dependent upon slope and aspect of individual plots, vexar shades blocked between 60 and 75 percent of ambient light at the center of the plot. PAR values were determined using a hand held quantum meter (Apogee inc, Model QSX-01)(see Appendix for PAR data). To minimize potential alteration of flow by the mesh, shades were not extended down the sides of the supports. The experiment was monitored biweekly, during which the few torn shades were repaired and fouling organisms were removed. Thus, the relative percentage of light blocked remained fairly constant through the duration of the experiment and mimicked the shading caused by the phytoplankton production experienced in 2002.

Kelp growth- Field Experiment

We chose to focus on the intertidal kelp, *Hedophyllum sessile* Setchell (hereafter called *Hedophyllum*) for the growth measurements. *Hedophyllum* is a competitive dominant (Dayton 1975) and like other macroalgae, likely seasonally responds with increased growth during periods of upwelling (B. Menge unpublished data). *Hedophyllum* has two morphologies, a smooth type and an irregularly bullate or ruffled type. Along exposed shores, the smooth type dominates; it was on this morph on which we based the growth measurements.

To measure growth rates, a hole was punched 5 centimeters from the base (to avoid damaging the meristem) during each visit (Larkum, 1986; Mann and Kirkman, 1981). *Hedophyllum* has intercalary meristematic tissue that is concentrated near the stipe or base of blades. Growth was calculated as the mean difference between the previous hole and the new hole.

The experimental set up consisted of haphazardly setting up plots centered over *Hedophyllum* plants through the center of the *Hedophyllum* zone at each site. The zones at each site differed in their vertical extent, but differences in elevations of plots between treatments and between sites were kept to a minimum (see Appendix). All plots faced approximately west.

Replicates consisted of an artificially shaded plot in which *Hedophyllum* blades were trimmed to 15 cm to avoid abrasion effects of the mesh on the kelp blades (+shade, + trim) and a non-shaded control (-shade, +trim) in which plots were marked and *Hedophyllum* was trimmed to 15 cm. An unmanipulated reference plot (-shade, –trim) was added as a procedural control for trimming and to quantify the background fluctuations in understory abundance. As growth measurements would likely be confounded by abrasion effects, a + shade –trim plot was not included in the experimental design. During each tide series from approximately mid May to the end of August 2005, we measured *Hedophyllum* growth. During each visit, blades in the trimmed plots were re-trimmed to 15 cm.

Kelp Growth- Common Garden Laboratory Experiment

To determine population growth rates under controlled conditions, we initiated a lab experiment in August 2004. Growth rates were measured across three different light levels and under two successive nutrient treatments, ambient and replete.

Hedophyllum thalli were collected from both sites and placed in laboratory tanks to measure growth in controlled laboratory mesocosms. Tanks were held in a temperature-controlled room with flow-through seawater. Solenoid valves were installed on input and output pipes and programmed to synchronize with the tidal regime. Sodium metal halide lamps (400W) were suspended above each of six tanks or blocks. PAR values were determined using a hand held quantum meter (Apogee inc, Model QSX-01). Treatments were randomly placed within blocks (individual tanks) and were irradiated with 100% of full light (7.56-11.12 PAR quanta /m ^{2} /day) 30% of full light (1.94-3.24 PAR quanta /m ^{2} /day) and 0% of full light treatments (0.05 PAR quanta /m ^{2} /day). While these light levels constitute approximately 1/3-1/2 of actual spring light (PAR=24-30 quanta /m ^{2} /day, R. Letelier pers.comm.), the absolute range of what is experienced by low intertidal communities in central Oregon are currently being investigated (Nielsen, *in prep*.) Covers made of nursery fabric and black plastic were constructed for the respective 30% and 0% treatments; 100% treatments had no cover. All light and tide cycles were programmed to mimic the long days (14-15 hours) and morning tides of late spring. Ambient temperature was kept at approximately 12^{o}C. Fresh blades were collected from the field prior to each test. *Hedophyllum* thalli were trimmed to similar size, hole-punched at five centimeters from base, and ten thalli, five from each site, were placed randomly at uniformly-spaced locations in each tank. Blades were secured with

PVC clamps which were lashed to the bottom of the tanks using stainless steel wire. A total of six replicates were used. Blades were allowed to acclimate for one week to mesocosm light levels and ambient nutrient conditions (4-10 μmolar nitrate) prior to treatment.

Two successive nutrient tests were conducted to determine the relative growth rates of *Hedophyllum* under different light and nutrient levels. The first test was conducted in ambient nutrient levels ranging from approximately 4- 10 μmolar nitrate and ran for approximately 3 weeks (August 18- September 8, 2004). The second mesocosm experiment tested *Hedophyllum* growth rates under nutrient-replete conditions and ran from September 21 to September 30, 2004. For the high nutrient experiment, a 0.4 molar nutrient solution (15:1 sodium nitrate-sodium phosphate) was dripped into tanks. Reservoir concentration, drip rate, tank volume, and turnover rate were calculated in order to keep the concentration of nitrate ions between 35-50 micromolar. This concentration is similar to that occurring during upwelling conditions along the Oregon coast. Due to increased incidence of necrosis (possibly due to increased bacterial infection), this treatment was suspended approximately 10 days post nutrient addition.

Physical measurements.

Site and plot level variability can contribute to differences in growth via differences in nutrient availability or water flow, sedimentation effects, and temperature effects. Macronutrients such as nitrate and phosphate are brought to the photic zone predominantly by seasonal upwelling in this system. Data regarding upwelling strength and periodicity using the Bakun Index (Bakun 1986) were downloaded from NOAA's Pacific Fisheries Environmental Laboratory (http://pfel.noaa.gov). We used chlorophyll-a, obtained from measurements in bottle samples taken from shore (Menge et al. 1997) as our estimate of phytoplankton concentration.

To quantify water flow in the plots, we used dental chalk flow blocks (Yund et al. 1991, Menge et al. 1996). Dental chalk (primarily consisting of calcium carbonate) has relatively constant dissolution rates under constant temperatures. The chalk blocks were deployed in the center of shaded and unshaded treatments at both sites four times during the season. Dry weight loss during the deployment was the measure of relative flow.

To quantify sand content of water flowing over the plots, we installed mesh-enclosed sponges, "Dobies®," at each experimental block at both sites. Dobies were collected and replaced at regular intervals throughout the duration of the experiment. The sponges were thoroughly rinsed over a 53 μm sieve. While some dissolved and tiny particulate matter escaped during the sieving process, larger organic particulates and sand were retained in the sieve. Samples were dried at 67°C for two days, weighed, combusted at 400°C in a muffle furnace, and reweighed to estimate the sand and organic content of each sample

Additional physical measurements included site temperature, plot slope and plot rugosity. *In situ* temperature was recorded with Hobo Stowaway underwater temperature loggers. Plot slope was calculated using a visual estimate scale (1= flat, 2= 30 degrees, 3 = 60 degrees, 4= vertical). Scale estimates were later verified with an inclinometer to +/- 3 degrees. A rugosity index was calculated using the ratio of topographic surface area to planar area, i.e. the surface length including all features compared to a straight line held above the plot. All plots faced approximately west.

Statistical Analysis

All statistical analyses were performed using JMP V.4 and SAS V.8.1 software. We used repeated measures analysis of variance to determine the relative magnitude and persistence of the effects of shading and site on the growth rate of *Hedophyllum sessile* through the duration of the experiment. For most analyses, the more conservative multivariate approach was used. Univariate statistics are also reported when the results differed from multivariate. If Mauchley's criterion of sphericity was satisfied (Prob $X^2>0.05$), unadjusted values were reported; otherwise the Huynh-Feldt (1976) adjustment for epsilon was employed. In order to test for the effect of shading on abundance accumulation, analysis of variance was used to determine differences in percent cover of *Hedophyllum* before treatment and six weeks afterward.

In order to test for potential site-level and between treatment effects in physical characteristics, we used two-way ANOVA to test for differences in plot slope, plot rugosity, and mean flow sediment, organic matter, water column chlorophyll-a concentrations, mean water and air temperatures, mean daily maxima and mean daily temperature range. Stepwise multiple linear regression was used to determine the relative effect size of several potential measured explanatory variables on the longitudinal grand mean (N= 30) of *Hedophyllum* growth rates: treatment, site, rugosity, slope, sediment accumulation, organic matter accumulation, mean percent cover of sand (visually estimated), relative herbivore abundance and relative *Katharina tunicata* abundance (number/plot), the black chiton which is known to associate with *Hedophyllum* (Burnaford, 2004).

In the mesocosm experiments, we used analysis of variance to test the effects of light treatment and site on *Hedophyllum* growth rate for both the ambient and replete nutrient tests. As light levels varied between tanks, simple linear and log-linear regression were also used to determine if there was any difference in the relative effect of increased light on *Hedophyllum* growth due to site origin

Results

Chlorophyll-a

Chlorophyll-a (hereafter chl-a) concentrations were much lower in 2004 than in the previous three years (Fig. 2.3). From 2001-2003, chl-a concentrations in the surf zone had summer peaks in July and August, reaching maxima between 55-110 micromoles chl *a* l^{-1} at Strawberry Hill and less than 20 micromoles chl-a l-1 at Fogarty Creek. In 2004, concentrations were much less than previous years and site-level differences were weakly reversed (Fig. 2.3).

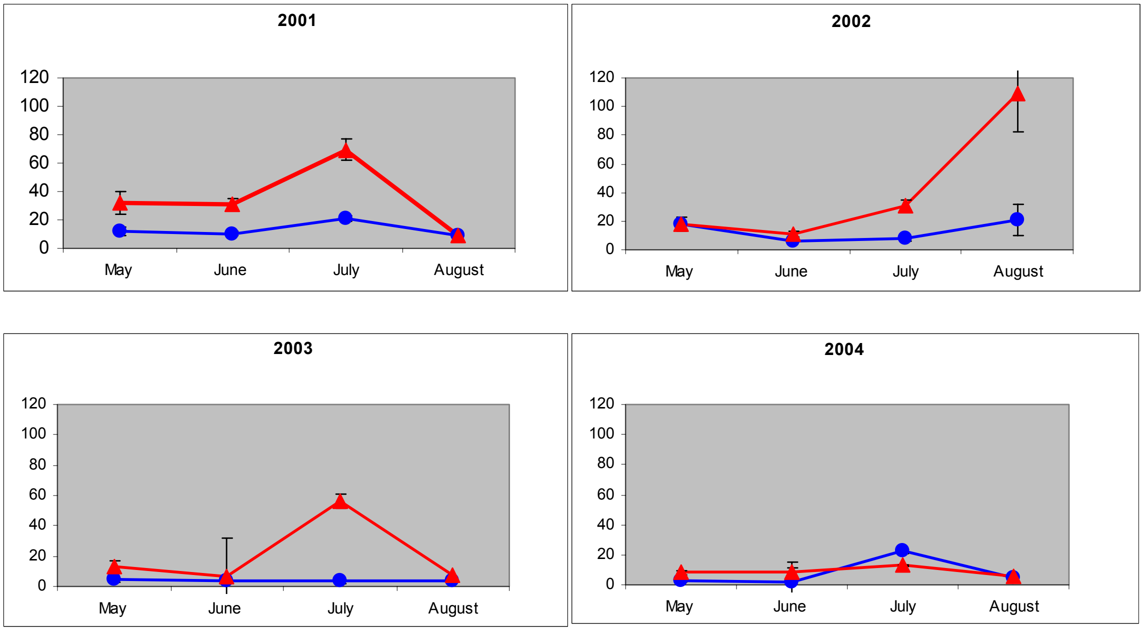


Figure 2.3. Mean Summer Surf Zone Chlorophyll Concentration (+/- SEM) at Fogarty Creek and Strawberry Hill Oregon.

Sand

Sand occurrence was several times higher at Strawberry Hill than at Fogarty Creek (Fig. 2.4, Table 2.1, $p<0.01$). Particulate organic matter did not differ between the two sites (Table 2.1).

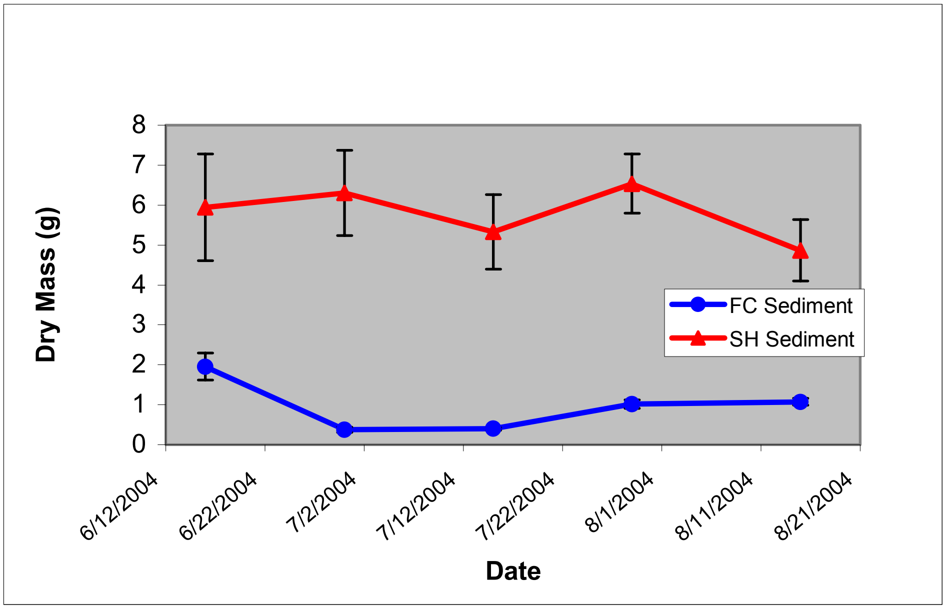


Figure 2.4. Differences in Sand Accumulation in dobies at Fogarty Creek and Strawberry Hill during Summer 2004.

Percent sand in plots

Repeated measures analysis of percent sand in experimental plots revealed a pattern similar to that occurring in collectors. There was more sand in plots at Strawberry Hill than at Fogarty Creek (5- 6% compared to negligible, $p<0.05$) and there was no treatment or treatment by site interaction.

Water Flow

Flow rates did not differ between sites (Fig. 2.5) but there was a greater overall erosion rate of the chalk blocks beneath the shades), especially at Fogarty Creek (Table 2.1, "flow")

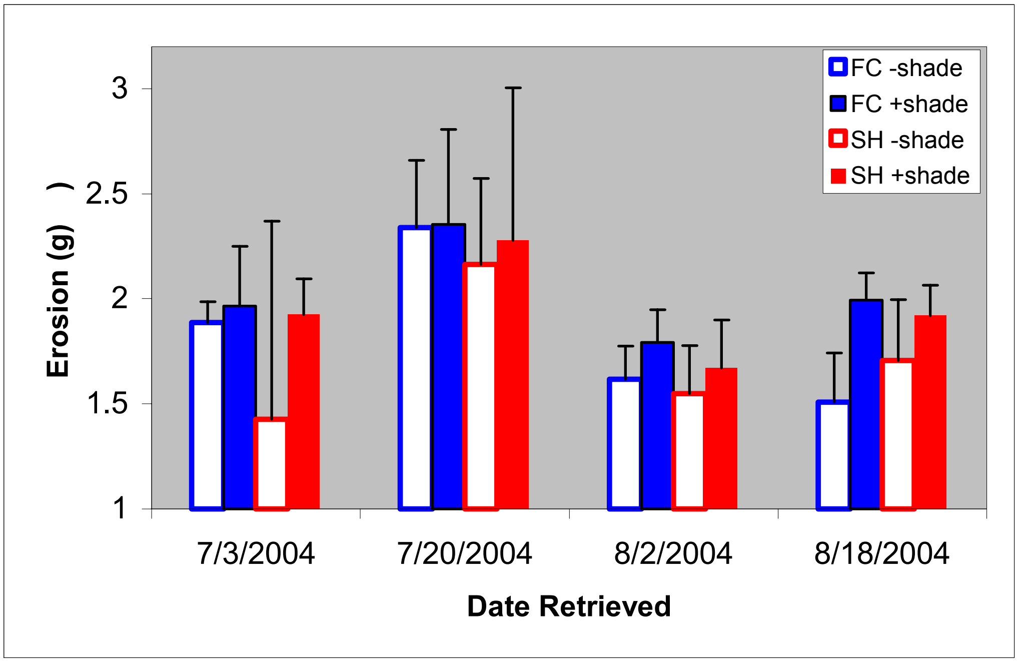


Figure 2.5. Mean Water Flow (+/- 95 CI) of Control and Shaded Plots at Fogarty Creek and Strawberry Hill. Flow was measured in untrimmed plots only to avoid thallus scour of the chalk blocks.

Temperature

Mean water temperature, mean daily maximum, and mean temperature range did not differ between the two sites. Mean air temperature was nearly 1.2 degrees higher at Strawberry Hill than at Fogarty Creek, however (Table 2.1, 13.4>12.24, $p<0.01$) resulting in the overall mean daily temperature being 0.24 degrees warmer at Strawberry Hill (11.33>11.09, $p<0.05$).

Plot Slope and Rugosity

Rugosity and slope were not different between treatments within or across sites. Strawberry Hill plots were approximately 13 degrees steeper than those at Fogarty Creek ($p<0.05$).

TABLE 2.1: DIFFERENCES IN LOCAL PHYSICAL MEASUREMENTS BETWEEN SITES AND TREATMENTS. Growth rate is shown for reference. Values shown in bold are significant at $p<0.05$ level. Nd= no data

	Fogarty Creek			Strawberry Hill		
	- shade + trim	+shade + trim	shade -trim	- shade + trim	+shade + trim	shade -trim
Growth rate (cm/day)	**0.31**	**0.23**	**0.37**	0.38	**0.22**	0.40
Rugosity	1.21	1.17	1.27	1.21	1.27	1.36
Slope (degrees)	13.50	13.00	12.50	24.00	28.00	28.50
Flow (g lost /day)	**1.83**	**2.04**	nd	1.76	1.93	nd

TABLE 2.2: DIFFERENCES IN TREATMENT-LEVEL PHYSICAL MEASUREMENTS.

Growth rate is shown for reference. Values shown in bold are significant at $p<0.05$ level. Nd= no data

	- shade + trim	+shade + trim	-shade -trim
Growth rate (cm/day)	0.35	**0.22**	0.38
Rugosity	1.21	1.22	1.32
Slope (degrees)	18.75	20.50	20.50
Flow (g lost /day)	**1.79**	**2.00**	nd

TABLE 2.3: DIFFERENCES IN SITE-LEVEL PHYSICAL PARAMETERS.

Growth rate is shown for reference. Values shown in bold are significantly different from each other at $p<0.05$ level. Mean values represent 5 replicates at 5 sample times post-press. Italicized parameters denote longitudinal only means. Rugostity is the mean surface length to plane length ratio. Slope is represented as the mean slope index back calculated into a degree value. Flow is represented by the mean change in mass of *in situ* chalk blocks due to erosion. Sand is represented by the mean mass of sand deposited in Dobie collectors.

	Fogarty Creek	Strawberry Hill
Rugosity (30)	1.22	1.28
Slope (30)	**13**	**26.8**
Flow (20)	1.93	1.85
Sand (10)	**0.96**	**5.86**
Organic Matter (10)	0.073	0.075
Chl a- water column (27)	13.72 (7)	10.65 (20)
Temperature (June 1-July 30)		
Daily AVG - emersed (40)	**12.24**	**13.4**
Daily AVG- immersed (60)	10.91	11.14
Daily AVG (60)	**11.09**	**11.33**
Daily Maximum (60)	13.48	13.76
Daily Range (60)	3.69	3.66

Upwelling

Mean upwelling generally increased through the month of July and then gradually decreased (Fig. 2.8). Due to the coarse spatial resolution of the wind-derived indices, upwelling differences between sites could not be resolved, nor could temporal correlation between growth rates and rate of influx of nutrients via upwelling, since serial correlation could not be detected with such a short data series (t=7). Qualitatively, however, the mean growth rate of *Hedophyllum* at both sites appeared to be related to the mean upwelling index for the majority of this study (Fig. 2.6).

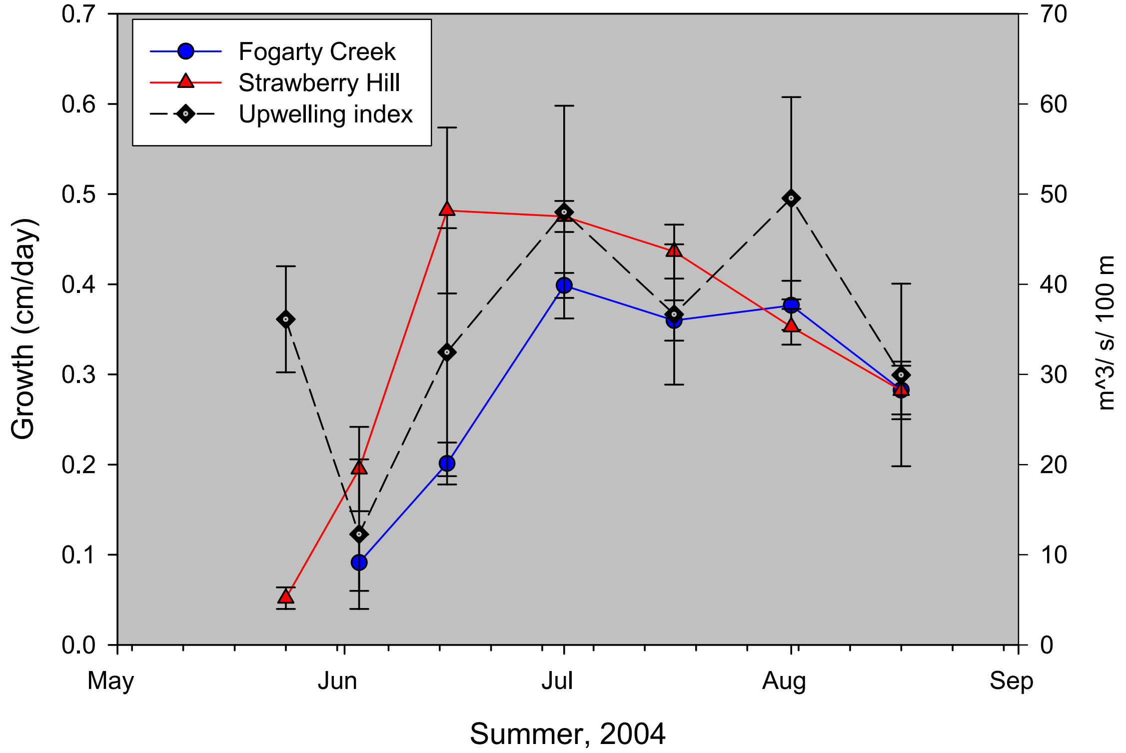


Figure 2.6. Temporal Trend of *Hedophyllum* Growth and Upwelling.
Error bars denote SEM. Growth rates from Fogarty Creek and Strawberry Hill are shown separately and represent non-shaded individuals. Further information on growth rates are shown in next section.

Effect of Shading

The rate of *Hedophyllum* growth was less in the + shade treatment than in either of the control plots (-shade and manipulation control) (Fig. 2.7, Table 2.4). Growth of *Hedophyllum* was context-dependent (Table 2.4: site x shade interaction, p=0.03) with the shade effect being stronger at Strawberry Hill than at Fogarty Creek (Fig. 2.7). The strength of the shading effect also varied through time (time x shade within subject interaction, p<0.01) with the greatest effect being in mid and late July 2004. The site effect, however, was time independent. There was no significant difference in *Hedophyllum* growth rate between the two control treatments (–shade, and manipulation control) (p=0.13; Table 2.5).

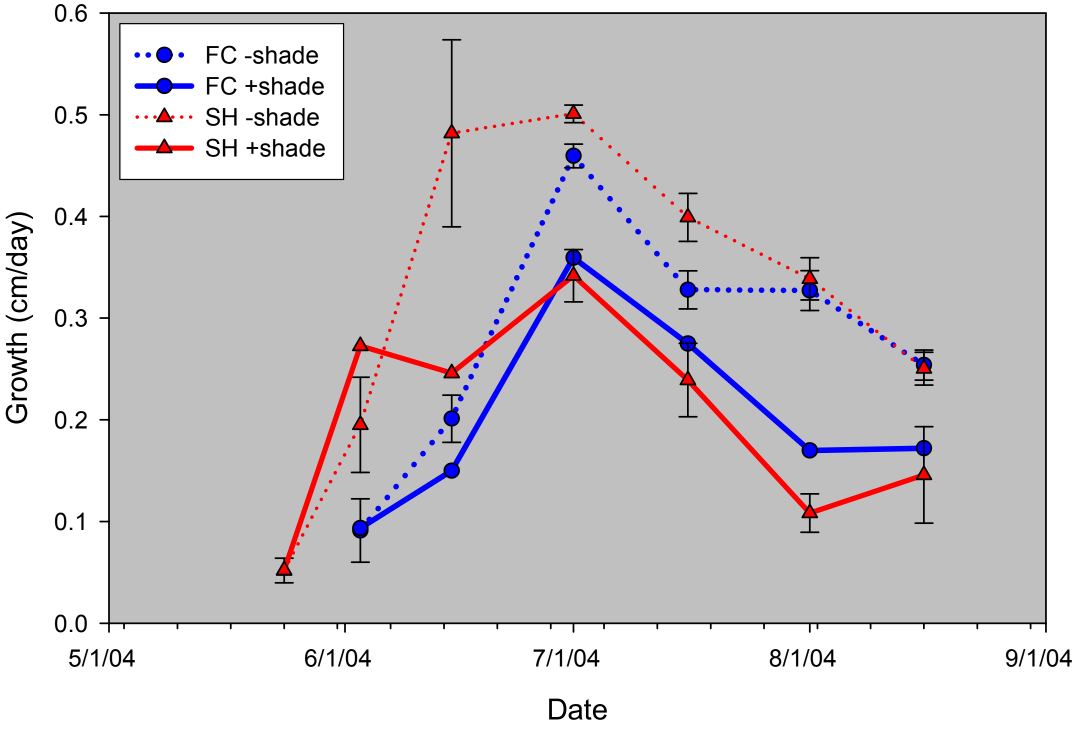


Figure 2.7. Effect of shading on *Hedophyllum sessile* growth, May – August 2004. Growth rates (+/- SEM) are shown for *Hedophyllum sessile* in two treatments: Shaded (+shade, +trim) Control (-shade, +trim).The arrow denotes period when shades were successfully installed. As no statistically significant difference was found between shade control and manipulation control, the latter is omitted for clarity.

TABLE 2.4: EFFECT OF EXPERIMENTAL SHADE FACTOR AND SITE ON *Hedophyllum sessile* GROWTH (cm/day).

Values bolded denote difference at p<0.05 level.

Between Subjects

Source of variation	MS	Exact F	DF	Prob>F
Shade	4.137	103.417	1	**<.0001**
Site	0.011	0.280	1	0.6015
Site*Shade	0.212	5.301	1	**0.0299**
Error	.04		25	

Within Subjects Multivariate

Source of Variation	MS	Exact F	DF	Prob>F
Time	1.924	14.751	3	**<.0001**
Time*Shade	0.916	7.021	3	**0.0016**
Time*Site	0.290	2.226	3	0.1123
Time*Site*Shade	0.058	0.448	3	0.7208
Error	0.13		23	

TABLE 2.5: EFFECT OF CONTROL TREATMENTS AND SITE ON *Hedophyllum sessile* GROWTH.

Treatments include Control (-artificial shade, +trim), and Intact/Trim Control (-artificial shade, -trim). Values bolded denote difference at $p<0.05$ level.

Between Subjects

Source of Variation	MS	Exact F	DF	Prob>F
Site	0.243	3.890	1	0.0661
Treatment	0.161	2.578	1	0.1279
Error	0.062			

Within Subjects-Multivariate

Source of Variation	MS	Exact F	DF	Prob>F
Time	4.822	22.505	3	**<.0001**
Time*Site	0.610	2.846	3	0.0756
Time*Treatment	3.743	17.466	3	**<.0001**
Error	0.214		14	

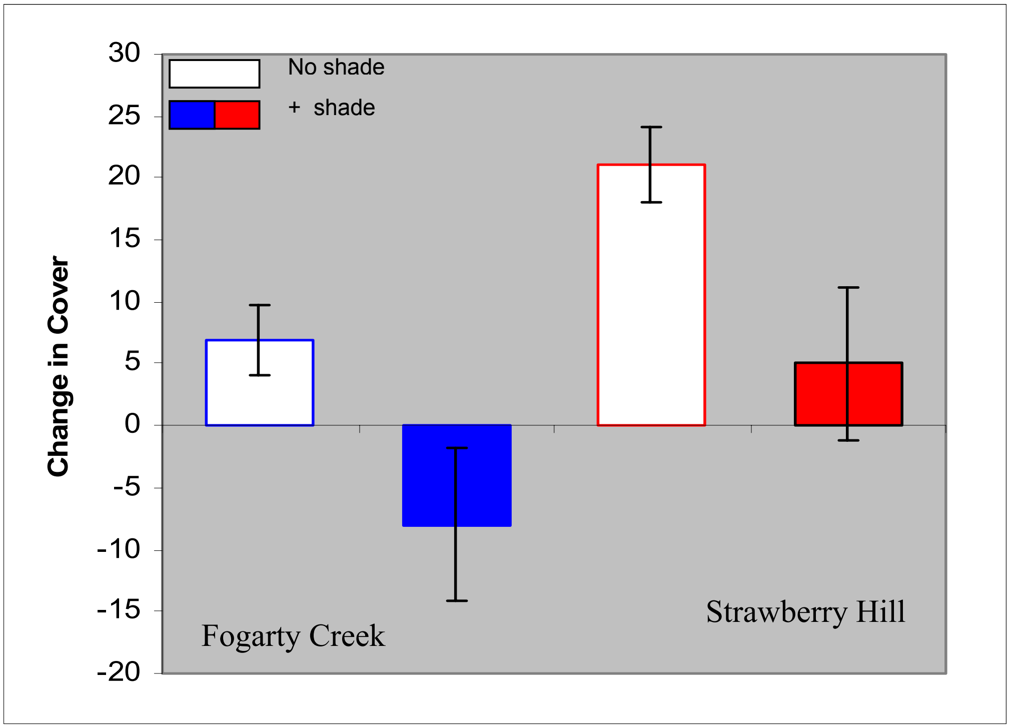


Figure 2.8. Differences in changes in percent cover of *Hedophyllum sessile* in plots with and without shading. For this analysis the - shade control and manipulation control plots were pooled. (N (+shade)= 5; N (control)= 10 per site.

The effects of shading on change of percent cover of *Hedophyllum* were similar to those on growth. Within sites, unshaded plots increased in cover more than shaded (Fig. 2.8, $p<0.05$) and the greatest increase in cover corresponded with the highest growth rates, in unshaded plots at Strawberry Hill.

Step-wise Multiple Linear Regression of Overall Means

Using longitudinal grand means (N =30), three explanatory variables (shading, trimming, and site) remained after forward and backward stepwise regression (Table 2.4). Variables eliminated included: slope rugosity, mean organic matter, mean percent cover of sand, and mean density of *Katharina tunicata.*

A 60-75 percent reduction in downward irradiance led to a mean decrease in growth rate of approximately 25 percent overall (Table 2.6, mean growth rate= 0.300 cm/day; mean shade effect –0.078 cm/day, $p < 0.001$) and accounted for over 72 percent of the variance in growth of *Hedophyllum* (Table 2.6, $R^2 = 0.72$ reduced model, shade only;). Trimming, after accounting for the shade effect, still had a negative effect on mean growth rate, although its magnitude was approximately 1/3 that of shading (Table 2.6, trim effect = -0.027, $p<0.01$). Finally, there was an overall effect of site, with Fogarty Creek exhibiting overall growth rates of approximately 0.06 cm day less than Strawberry Hill after accounting for shading and trimming (Table 2.6, $p<0.01$). These additional variables, however, contributed only an additional 10 percent of variance explained to the model (full model: $R^2 =0.82$; reduced model: $R^2 =0.72$).

TABLE 2.6. "BEST FIT" MODEL FROM STEPWISE REGRESSION of ALL OBSERVED EXPLANATORY VARIABLES on *Hedophyllum* GROWTH RATE.

Model R^2= 0.82, p<0.0001; parameters below. Reduced Model: shade effect only, R^2=0.72, p<0.001. Effect estimates bolded , p<0.05. See text for initial list of explanatory variables.

Parameter	Estimate	SE	t Ratio	Prob>|t|
Intercept	0.300	0.0148	20.31	<.0001
Sand (in plots)	-0.002	0.0016	-1.53	0.1401
Shade effect {Shaded-Control&Trim Control}	**-0.078**	0.0078	-10.02	**<.0001**
Trim effect{Control-Trim Control}	**-0.027**	0.0095	-2.84	**0.009**
Herbivores	0.001	0.0002	1.76	0.0915
Fogarty Creek	**-0.061**	0.0202	-3.04	**0.0056**

Kelp growth-Common garden experiment

In the laboratory experiment, growth rate of *Hedophyllum* differed between trials, treatments and populations (Fig. 2.9). During the first trial, under ambient nutrient levels, *Hedophyllum* growth was higher in light treatments compared to dark treatments but only in blades from Strawberry Hill (Fig. 2.9A). Under replete nutrient conditions (Fig. 2.9B), growth was greater than in ambient nutrient conditions, but the blades from the two sites differed in their responses to the different levels of light. For Fogarty Creek *Hedophyllum*, blades in 30% light grew the greatest compared to others from FC in different light treatments (100% =30%>0%, $p<0.05$). Growth of blades from Fogarty Creek in 30% light was also greater than in blades from Strawberry Hill under 30% light. For Strawberry Hill *Hedophyllum*, blades grew more under 100% light than both 30% and 0% light (100%> 30%= 0%, $p<0.05$). Blades from Strawberry Hill in 100% light also grew faster than blades from Fogarty Creek in 100% light ($p<0.01$).

Since measured light levels in the six tanks varied considerably, growth was also measured as a response to continuous levels of light as measured by an insitu light meter. Growth of *Hedophyllum* from Strawberry Hill was positively linearly correlated with increasing light levels ($R^2=0.66$, $p<0.05$) whereas growth of blades from Fogarty Creek was asymptotic (Fig. 2.10). *Hedophyllum* from Fogarty Creek seemed to have maximal growth rates at a daily influx of approximately 3 PAR quanta/m ^{2}/day and then reduced growth rates with higher light levels.

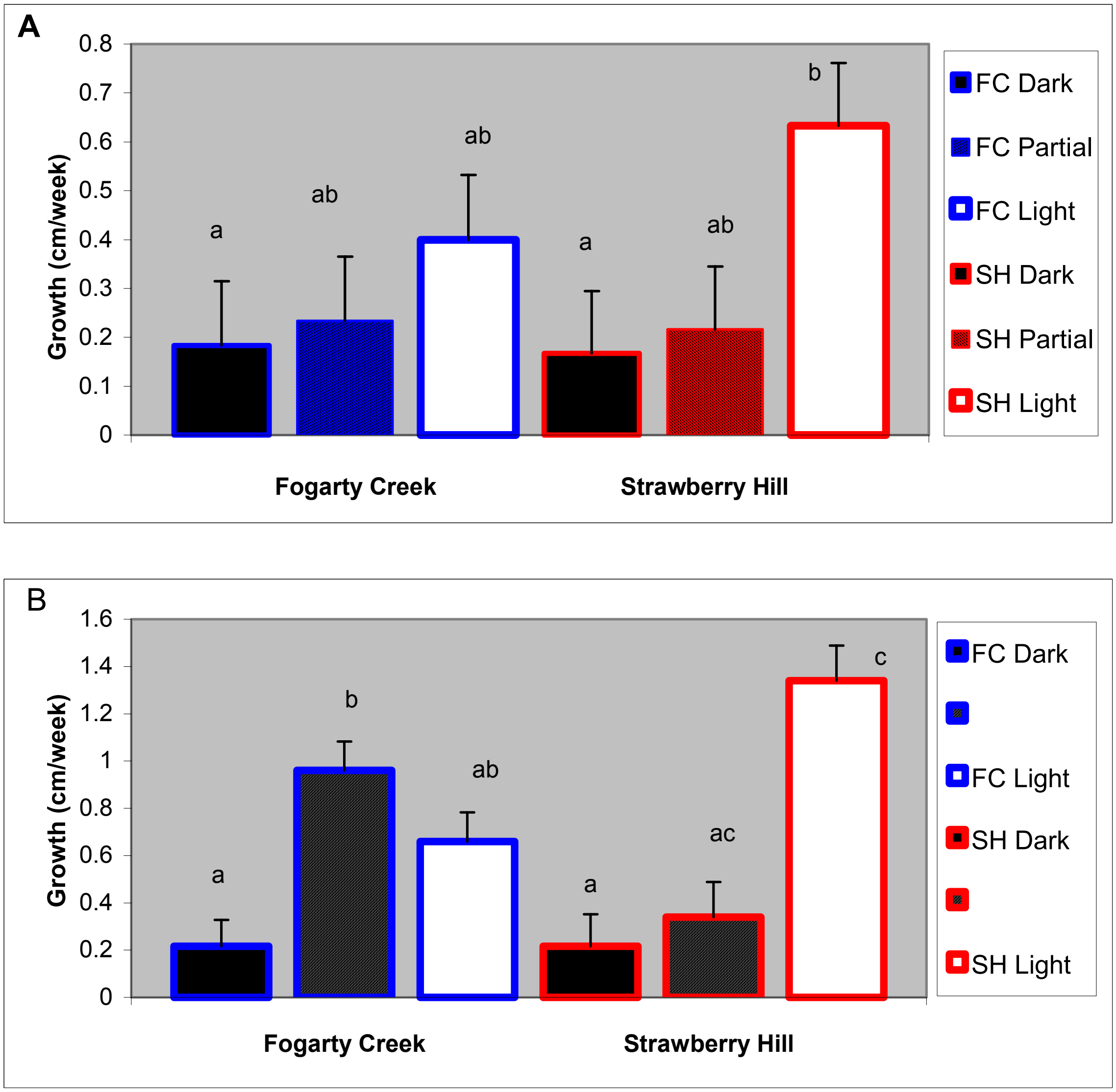


Figure 2.9. Mean growth rates (+/- SEM) under different light levels for blades of *Hedophyllum sessile* from Strawberry Hill and Fogarty Creek reared in common garden mesocosms with ambient (A) and (B) nutrient influx that mimic upwelling levels along the central Oregon coast. Means with distinct letters differ at p<0.05 level.

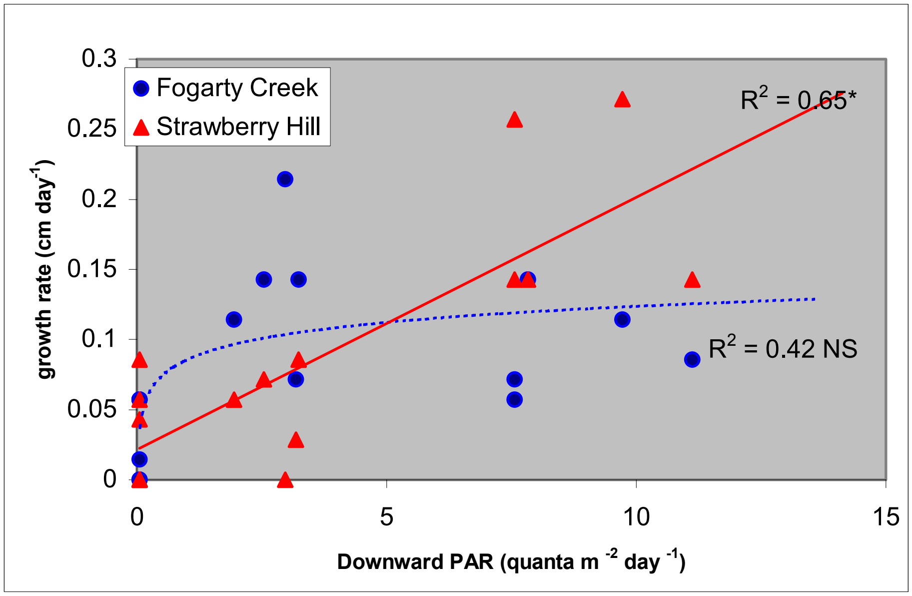


Figure 2.10. Effect of Light on Growth of *Hedophyllum sessile* in Common Garden Mesocosm. Correlation coefficients are calculated for each site separately. For Fogarty Creek a log-linear model was used; for Strawberry Hill a linear model was used. *= $p<0.05$, NS= not statistically significant.

Discussion

In our study, a moderate decrease in light resulted in decreased growth rates of the intertidal kelp, *Hedophyllum sessile,* in both field and laboratory conditions. Phytoplankton abundance was atypically low and similar between sites during summer 2004; so the experiments were not confounded by differing phytoplankton shading effects. Thus, the artificial shades suitably mimicked the light environment historically (2001-2003) experienced by macrophytes in the Cape Perpetua region. In the field, shading resulted in more than a 25 percent reduction in growth rates, and the effect was different in magnitude between sites.

At Strawberry Hill, the low intertidal zone has relatively high abundances of sessile filter feeding invertebrates and low abundances of macroalgae, while at Fogarty Creek, the low intertidal zone has low levels of invertebrates and high abundances of macroalgae. Given the low abundance of macrophytes at Strawberry Hill, the higher growth rate of *Hedophyllum* at this site is opposite to what would be expected. However results of the laboratory experiments indicate that there may be different light phenotypes at the two sites. The growth rates of the Strawberry Hill thalli in the laboratory were linearly related to light levels ($R^2 = 0.65$, $p<0.05$) and experienced no growth declines at higher light levels (PAR= 10-15 quanta m^{-2} day^{-1}), possibly indicating a sun-adapted population. The Fogarty Creek thalli, however, had a maximal growth rate at a relatively low PAR (2.5 –3 quanta m^{-2} day^{-1}) and growth appeared to decrease with increased light levels. During periods of low phytoplankton production, as that which occurred in 2004, the Strawberry Hill population would thus be expected to have greater growth rates in the absence of artificial shading and this was what was observed. Sun-adapted populations would also be expected to respond to decreased light levels with faster growth than would shade-adapted populations (Herbert and Waaland 1987, Gerard, 1987), which again is supported by the results of the field experiment. Further experimentation is necessary, however, to determine whether the site-level differences are apparent during the spring and early summer, as well as in the late summer when the lab experiments were conducted.

Prior research indicates that nutrient availability, water flow (Hurd, 2000), and temperature (Gerard and Dubois, 1988; Tegner 1997) can change the effects of light on growth rates. However, in 2004 ambient nutrients were similar at the two sites (F. Chan, pers. comm.) and were kept constant in laboratory conditions. Further, water flow did not differ between sites. Temperatures were slightly higher at Strawberry Hill, but overall the data support our interpretation that the observed effect was due to light limitation and not to changes in nutrients, water flow or temperature.

Over time, 60-75 percent reduction in downward irradiance led to mean decrease in growth rate of approximately 25 percent overall, and accounted for over 72 percent of the variance in growth of *Hedophyllum*. This is substantial, especially considering that the absolute percentage of light blocked would likely be much less when considering different solar angles and the reflection of light from neighboring blades outside of the plot. As historical levels of shading during moderate phytoplankton production were much higher than that which produced a significant shading effect, the likelihood is great that phytoplankton concentration in the plankton plays an important role in structuring benthic macrophyte communities along the Oregon coast.

Although it might be expected that the alga would respond to shade by shifting energy toward proteins for pigment production, we saw no recovery of growth rates suggesting the effects of shade were persistent. The persistence of the shading effect is important in understanding the resiliency of the system to changes in light regimes and we suggest should be further explored in experiments that consider both algal physiology and the effects of herbivory in shaping apparent patterns in productivity and emergent patterns in community ecology.

Modeling the relative impact of light history/acclimation and spatio-temporal extent of phytoplankton retention over different nutrient regimes is crucial to understanding the large scale effects of phytoplankton abundance on kelp physiology and therefore the effect on benthic production. The relative differences in retention can be proxied by combining information of light attenuation, chlorophyll-a, and temperature changes over time. The potential for sun/shade-adapted populations can be further determined by reciprocal transplants or by modeling the ambient light history experienced at the two sites. During our experiment, PAR sensors were installed at both sites in the low zone and on the bluff above each bench to determine real time ambient light levels; both PAR sensors at Strawberry Hill unfortunately failed, so light data are unavailable and this question remains for future investigation. Ultimately, longer term monitoring at a larger spatial scale will be necessary to determine the extent of coupling between upwelling, nearshore phytoplankton production and intertidal kelp dynamics.

The results of this study suggest that light limitation might be important even in intertidal environments where plants are periodically exposed to full sunlight and where the deepest level of immersion is only about 3 meters. The effects of shading were persistent, and occurred at light levels likely higher than that which occurred during historic moderate production. Furthermore, they revealed potential site level differences in kelp populations and their ability to cope with different light regimes. These results underscore the necessity for further research into the dynamics of pelagic and benthic productivity in shallow water system, particularly in the context of the underwater light environment and how it is affected by pelagic productivity.

CHAPTER 3

EXPLORING CONSEQUENCES OF PHYTOPLANKTON SHADING ON KELP COMMUNITIES: DIFFERENTIAL EFFECTS OF LIGHT AND STRESS ON UNDERSTORY COMMUNITIES

ABSTRACT

In marine benthic habitats, canopy species can change the physical environment of the understory community through light modification, thallus scour, change in sediment patterns, limitation of recruitment of algal sporules and sessile invertebrates and stress amelioration for some mobile species. To determine the relative changes in algal canopy abundance and understory assemblages that result from different levels of light and stress, we studied the algal community beneath and around the intertidal canopy-forming kelp, *Hedophyllum sessile*, at two sites of differing environmental stress and historic phytoplankton productivity on the central Oregon coast. The treatments included a shaded plot in which the canopy was trimmed (+shade, +trim), an "open" canopy plot (-shade, +trim), and an intact canopy manipulation control (-shade, -trim). Though the response of total cover of understory algae was not different between treatments, responses of individual algal groups differed between treatments and between sites. At Fogarty Creek, an area of historically high macroalgal abundance in the low zone and comparatively low phytoplankton abundance, the primary response to increased shade was an increase in foliose red algae. At Strawberry Hill, an area of low macroalgal abundance in the low zone and comparatively high phytoplankton abundance, the dominant groups beneath the shades were articulated and crustose corallines. The response of algal diversity to different canopy treatments also differed between sites. Diversity of understory algae was highest beneath the artificial shades at Fogarty Creek

whereas at Strawberry Hill, the diversity was the highest beneath intact canopy. Physical variables measured indicated greater environmental stress at Strawberry Hill. At Fogarty Creek, the canopy appears to reduce algal abundance and diversity, presumably through competitive inhibition, whereas at Strawberry Hill the canopy appears to facilitate increased algal abundance and diversity, presumably through habitat amelioration. These results underscore the need to include models of environmental stress gradients when considering the relative role of the canopy and its effects on the understory community.

Introduction

Increases in nutrient loading in the environment have been shown to drastically affect community structure. Direct effects include increases in short-term productivity, decreases in diversity and resilience (Vitousek et al., 1997; Tilman, 1996) in terrestrial systems and algal blooms (e.g. Valiela et al., 1997; Sand Jensen and Borum, 1991) in aquatic and marine environments. Indirect effects, however, to understory species and to higher trophic groups either via bottom up effects or changes in physical structure are more difficult to discern.

Canopy-forming kelps are important habitat modifiers in both intertidal and shallow subtidal marine ecosystems (Dayton, 1975; Reed and Foster, 1984; Dayton, 1985). Canopy species can change the physical environment of the understory community in several ways. These changes include light modification (Reed and Foster, 1984), thallus scour (Hawkins, 1983), change in sediment patterns (Kennelly and Underwood, 1993; Melville and Connell, 2001) and limitation of recruitment of algal sporules and sessile invertebrates (Hawkins, 1983; Leonard, 1999). Generally, the role of canopy-forming kelps is that of an "ecosystem engineer" (e.g., Jones et al., 1994). That is, they play a critical role in shaping community structure by affecting local abundances and distributions of other organisms in the community. Therefore changes in the abundance of the dominant canopy species by environmental perturbations such as phytoplankton accumulation may have profound effects on both community structure and total community production.

Previously, the ecological role of kelp canopies have been documented both through experimentation and through observing the changes in species assemblage when the canopy species have been removed due to extreme disturbances such as storms or pollution (e.g. Dayton 1975; Dayton and Tegner, 1984; Dayton, 1985; Benedetti-Cecchi, 2001; Connell, 2003). However, kelps are also subject to change from more subtle perturbations such as changes in nutrients or light. The focus in this chapter will be on the responses of understory algal species to manipulation of shading by the canopy species *Hedophyllum sessile,* which in turn could be dependent on shading by dense concentrations of phytoplankton.

General model

The experimental observations were conducted in the context of an experiment investigating the effect of the intertidal light environment, its modification by phytoplankton accumulation, and the resultant changes in growth of the intertidal kelp, *Hedophyllum sessile* (Chapter 2). If light limitation indeed affects a dominant canopy species such as *Hedophyllum sessile*, do we observe indirect effects on the algal understory? Previous experiments have demonstrated that shading decreased the growth rate and abundance of *Hedophyllum sessile*, a competitive dominant in Oregon rocky intertidal communities (Chapter 2). The removal or decrease in canopy species by perturbations such as storms generally results in positive changes in both biomass and species richness of the understory (Pearse and Hines, 1979; Kendrick et al., 2003). However, in contrast to kelp removal by storms, if the disturbance was due to shading by phytoplankton, the factor responsible for reducing kelp may persist in the absence of the canopy. Thus, we might expect that phytoplankton shading will have a direct negative effect on understory species by continuing to limit light in the absence of the canopy species (Figure 3.1, Scenario 1). Alternatively, an understory dominated by semi-shade tolerant red algae may respond positively to the phytoplankton shading as a result of reduced competition from the competitively dominant canopy species (Fig. 3.1, Scenario 2).

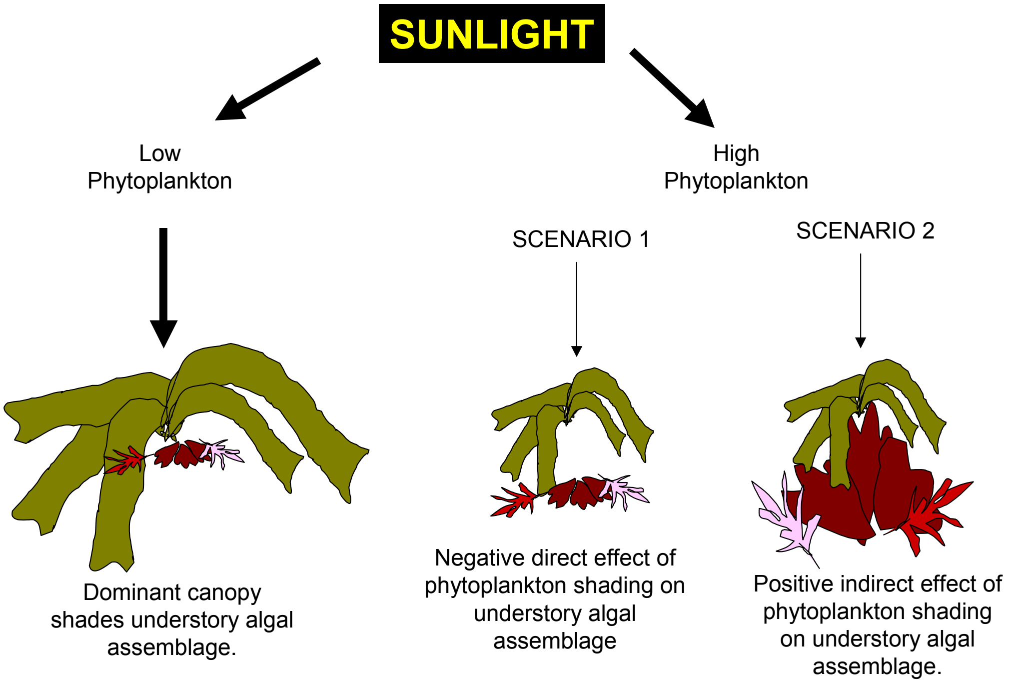


Figure 3.1. Model of potential effects of phytoplankton loading on algal understory assemblage. This model assumes predominantly negative effects of the canopy on the understory assemblage via light attenuation.

Artificial shades designed to mimic light levels experienced by intertidal algal assemblages when water column productivity is persistently high were installed at two sites along the Oregon coast, Fogarty Creek and Strawberry Hill. Previous studies have demonstrated that the two sites differ in several physical parameters that may lead to differing environmental stress. Temperatures tend to be slightly higher at Strawberry Hill (Halpin et al., 2002; Chapter 2) and sand deposition is greater at Strawberry Hill and other sites at Cape Perpetua than at Fogarty Creek and other sites at Cape Foulweather (Trowbridge, 1992; Menge et al, 1997; Chapter 2).

MATERIALS and METHODS

Site Selection

The field experiment was conducted at two sites on the central Oregon coast, Fogarty Creek (44.84 N, 124.05 W) and Strawberry Hill (44.24 N, 124.11 W). These sites have similar patterns of upwelling and macronutrient concentrations yet have persistently different levels of phytoplankton (quantified as chlorophyll-a) in the water column (Menge et al., 1997). The sites are also characterized by differences in relative abundances of sessile invertebrates and macrophytes. Fogarty Creek has high relative abundances of macroalgae and low relative abundances of sessile filter feeders such as barnacles and mussels. The reverse is true for Strawberry Hill (Menge et al., 1994).

Experimental design

Shades were installed in the lower intertidal to manipulate the light available to the macroalgal community. The feasibility of shading plots in rocky intertidal field experimentation has been demonstrated in low and high intertidal habitats (Burnaford, 2004; Bruno and Bertness, 2001; Harley 2003). Shades were designed by attaching vexar mesh to a stainless frame with both cable ties and washers and locking nuts. Stainless steel all-thread supports were inserted approximately 15 cm into holes drilled into the bedrock, and cemented into the holes with Z-spar. The shading mesh was elevated approximately 20 centimeters over the rock surface. The goal of the design was to not only to block an ecologically relevant percentage of the light but to provide a structure that would stand up to the waves and allow ample water flow.

Treatments.

Hedophyllum is a competitive dominant in the low zone of exposed rocky shores along the Oregon coast. The experimental set up consisted of setting up 0.25 m^2 plots through the center of the *Hedophyllum* zone at each site and measuring the changes in the understory assemblage. Treatment assignment within each replicate of three plots was random. Each of 5 replicates included three treatments: a shaded plot in which the canopy was trimmed to 15 cm to eliminate abrasion effects while retaining the plant in situ (+shade, +trim), a non-shaded control in which canopy blades were likewise trimmed (-shade, +trim), and an untrimmed control (-shade, -trim) to assess natural fluctuations in the understory.

During each tide series from approximately mid May to the end of August 2005, we measured abundances of understory algae in each plot. Percent cover of algal species was categorized into cover classes (0, 1, 5, 15, 25, 50 75, 85, 95, 99, 100) using visual estimation (Dethier et al., 1993).

Statistical Analysis.

The responses of groups to the manipulations were assessed at different taxonomic resolution to compare the effects of shading on the understory assemblage as a whole and between functional groups. All statistical analyses were performed using JMP V.4 and SAS V.8.1 software. Repeated measures multiple analysis of variance (RM-MANOVA) was used to determine the relative effects of treatments and site on the abundance of algal and invertebrate species and species groupings through the duration of the experiment. Few changes in sessile invertebrate abundance occurred over the short duration of this experiment; this group will not be addressed further. Only results from major algal functional groups are reported here; please see Appendix for remainder. For most analyses, the more conservative multivariate approach was used. Univariate statistics are also reported when the results differed from multivariate. If Mauchley's criterion of sphericity was satisfied (Prob X^2>0.05), unadjusted values were reported; otherwise the Huynh-Feldt (1976) adjustment for epsilon was employed. For most analyses, the response measured was the percent cover through time. However, for slow growing corallines, which already had a high abundance, a more sensitive analysis of comparing the change from initial abundance through time was employed.

Two diversity indices were calculated for the plots through time. These included the Shannon-Wiener index of diversity (H'), and species richness (S). Repeated measures were conducted for all indices to detect the presence of a persistent pattern between plots or between sites. I also calculated the mean change in algal diversity indices from the time immediately post-press to August 1st, 2005.

RESULTS

Algal Diversity- Post-press change

At Fogarty Creek, diversity (both H’ and S) increased in +shade +trim plots and decreased in –shade-trim plots (Fig. 3.2). In contrast, at Strawberry Hill richness increased in both treatments but much more in –shade-trim plots. A similar trend was seen for H’ (Fig. 3.2). The effect of the –shade +trim treatment on diversity was intermediate to the other treatments within sites and was not different between sites.

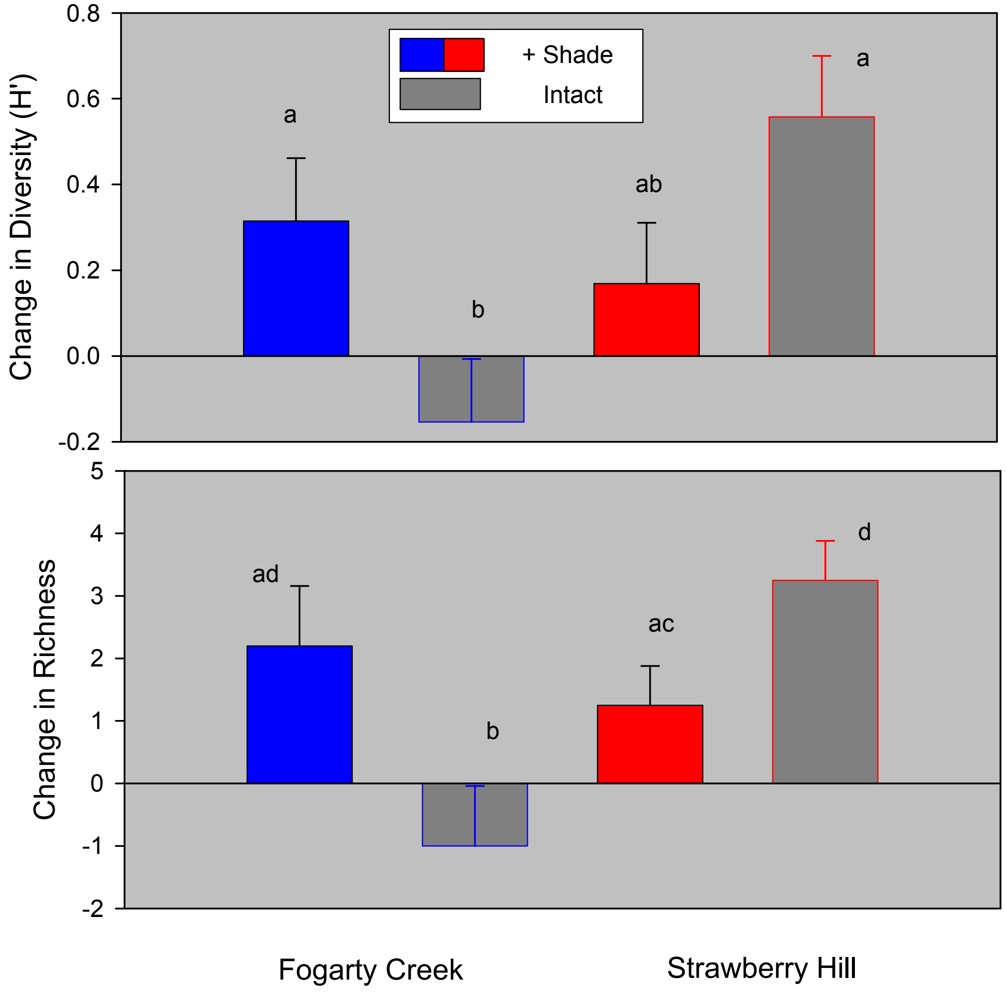


Figure 3.2. Comparing Algal Species Richness and Diversity in experimentally shaded (+shade, + trim) and intact canopy (- shade, -trim)plots at Fogarty Creek and Strawberry Hill, Oregon. Bars denote group means + SEM. Distinct letters denote statistically distinct means at $p<0.05$.

Understory Algal Abundance

There was no wholesale increase of understory algal abundance across sites beneath the shades (Table 3.1, Fig. 3.3). Repeated measures analysis revealed different effects of shading and intact canopy on total understory algal abundance between sites. At Fogarty Creek, shading had a strongly positive effect on understory abundance, increasing percent cover by an average of 22.5 percent (Table 3.1 Artificial shade: p=0.038). Total understory abundance also changed through time (Univariate analysis; Time effect: p=0.022) though the influence of shading was not dependent upon time (Time X shade effect: p>0.7). No effect of shading nor time was seen at Strawberry Hill.

TABLE 3.1. REPEATED MEASURES ANALYSIS OF THE EFFECT OF SHADING ON TOTAL UNDERSTORY ABUNDANCE BETWEEN SITES

FC= Fogarty Creek, SH= Strawberry Hill. Values bolded denote significant effect at $p<0.05$. NS= Not significant. PE= Parameter estimates; (Intercept) +/- shade effect. MC= Mauchley's criterion of sphericity.

Source of Variation	PE	MS	F	DF	Prob>F
Between Subjects- FC					
Shade	(91.83) +22.5	0.412	5.350	1	**0.038**
Error				13	
Within Subjects- FC Multivariate					
Time		0.597	3.582	2	0.060
Time*Shade		0.060	0.362	2	0.704
Error				12	
Within Subjects- FC Univariate Unadjusted					
Time		1	4.412	2	**0.022**
Time*Shade		1	0.339	2	0.716
Error				26	
Sphericity Test		MC	X^2	DF	Prob $>X^2$
		0.967	0.399	2	0.819

Source of Variation	PE (intercept)	MS	F	DF	Prob>F
Between Subjects- SH					
Shade	(108) -2.733	0.005	0.063	1	0.806
Error				13	
Within Subjects- All NS					

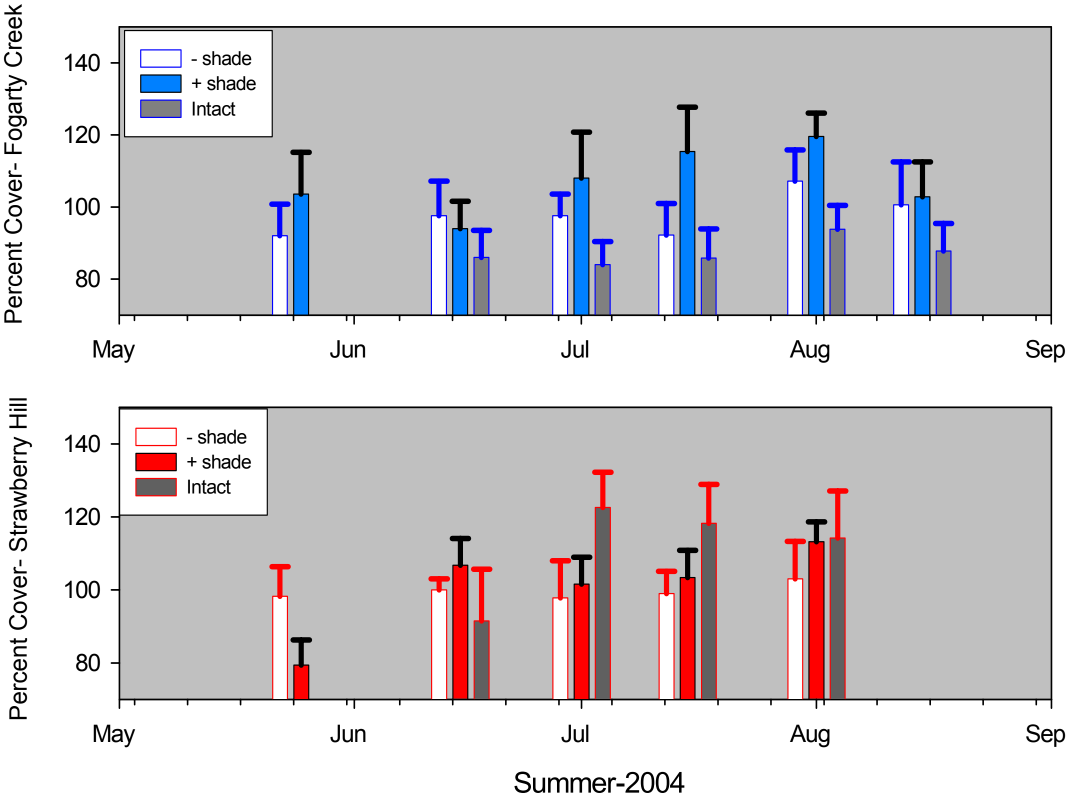


Figure 3.3. Changes in understory algal abundance in shading experiments at Fogarty Creek and Strawberry Hill, Oregon.

Algal groups- foliose red algae

Individual algal groups and algal species responded in a context-dependent fashion to the treatments at the different sites. Compared to –shade +trim plots, foliose red algae in +shade +trim plots increased at Fogarty Creek but not at Strawberry Hill (Fig. 3.4, Table 3.2: site x shade interaction, p=0.047). In contrast, compared to –shade +trim plots, foliose red algae in intact (-shade-trim) plots did not change at Fogarty Creek but increased at Strawberry Hill (Fig. 3.4, Table 3.3: site x intact canopy interaction, p=0.037). The abundance of foliose red algae also changed through time at Fogarty Creek (Time effect: p=0.02) but not at Strawberry Hill (F =0.90; DF= 2,12; p= 0.43).

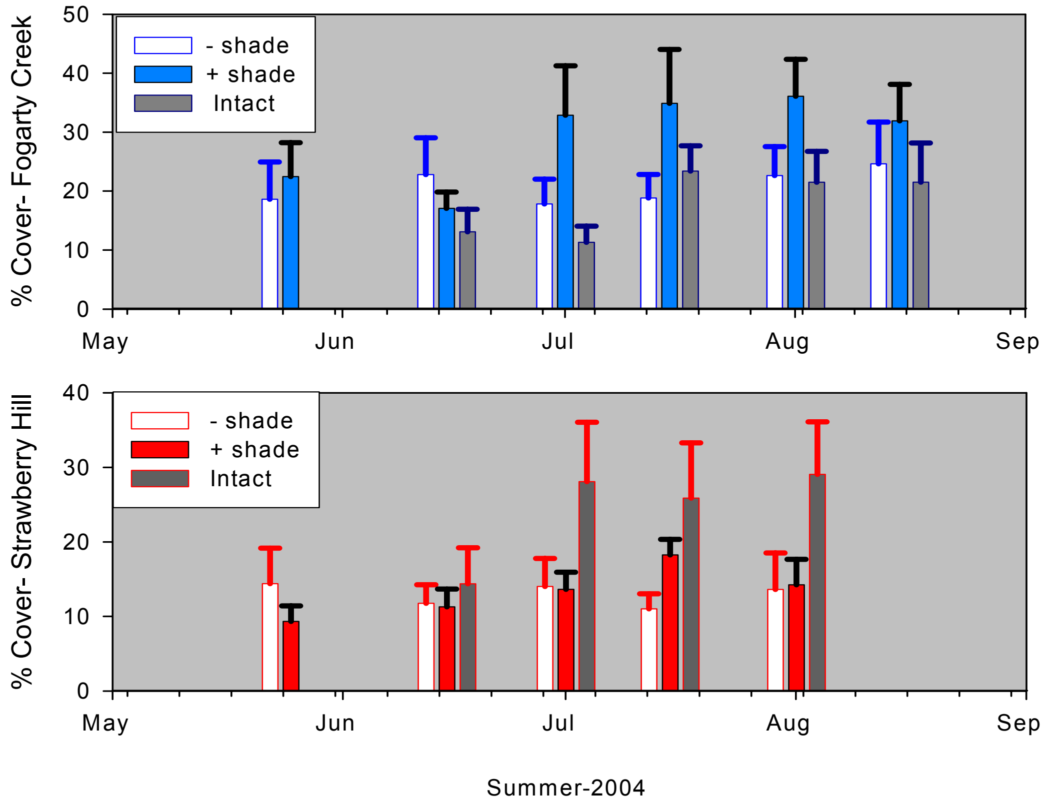


Figure 3.4: Mean Abundance (+/- SEM) of Foliose Red Algae in shading experiments at Fogarty Creek (FC) and Strawberry Hill (SH), Oregon.

TABLE 3.2. REPEATED MEASURES ANALYSIS OF THE EFFECT OF ARTIFICAL SHADES AND SITE ON FOLIOSE RED ALGAE ABUNDANCE

Values bolded denote significant effect at $p<0.05$. Between treatment within site comparisons are shown for Fogarty Creek (FC) only.

Source of variation	MS	F	DF	Prob>F
Between Subjects				
Shade	0.052	1.288	1	0.267
Site	0.095	2.384	1	0.135
Site*Shade	0.175	4.379	1	**0.047**
Error	0.040		25	
Within Subjects				
Time	0.123	1.482	2	0.247
Time*Shade	0.073	0.872	2	0.431
Time*Site	0.170	2.042	2	0.152
Time*Site*Shade	0.168	2.022	2	0.154
Error	0.083		24	
Between Subjects- Fogarty Creek				
Shade	0.392	4.705	1	**0.050**
Error	0.083		12	
Within Subjects - FC				
Time	1.037	5.705	2	**0.020**
Time*Shade	0.129	0.711	2	0.512
Error	0.181		11	

TABLE 3.3. REPEATED MEASURES ANALYSIS OF VARIANCE ON THE EFFECT of SITE and INTACT CANOPY ON FOLIOSE RED ALGAE ABUNDANCE Intact Canopy "treatment" is merely the manipulation control (-shade, -trim). Within site comparison is also shown for Strawberry Hill (SH). NS= Not significant.

Source of Variation	MS	Exact F	DF	Prob>F
Between Subjects				
Site	0.093	2.324	1	0.140
Intact Canopy	0.018	0.448	1	0.509
Intact Canopy*Site	0.195	4.871	1	**0.037**
Error			25	
Within Subjects- NS				
Between Subjects- Strawberry Hill				
Intact Canopy	0.606	7.883	1	**0.015**
Error			13	
Within Subjects-SH				
Time	0.006	0.039	2	0.962
Time* Intact Canopy	0.026	0.155	2	0.858
Error			12	

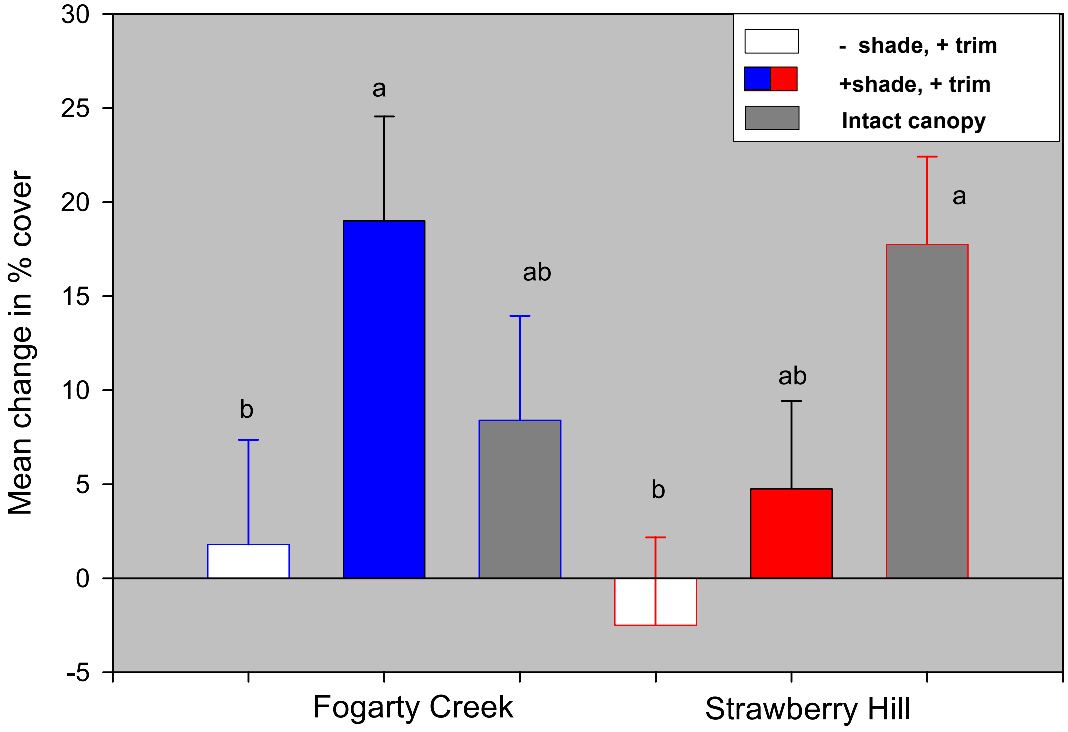


Figure 3.5. Change in Percent Cover of Foliose Red Algae during the shading experiment at Fogarty Creek and Strawberry Hill, Oregon. Distinct letters denote group means that are statistically significant at the $p<0.05$ level. The intact canopy treatment is merely the manipulation control (- shade, - trim).

The change in percent cover of foliose reds varied by site and treatment (Fig. 3.5). At both sites the –shade, +trim treatment resulted in no change in abundance (error bars overlap the 0% change line), but the relative magnitudes of the increase of foliose reds in +shade +trim and intact canopy (-shade-trim) treatments at the two sites varied inversely (Fig. 3.5).

Algal groups- Coralline algae

Coralline algae were least abundant beneath the intact canopy (-shade-trim) than in either of the other two treatments at both sites (Fig. 3.6; Table 3.4, Intact Canopy: p=0.01). Coralline algae were also more abundant at Strawberry Hill than at Fogarty Creek (Table 3.4, Site: p=0.001). Abundance changes of coralline algae through time were context-dependent, varying with both site and intact canopy (Time X Site X Intact Canopy: p =0.008). Abundance of coralline algae increased through time at Fogarty Creek but decreased through time at Strawberry Hill (Fig. 3.6).

Comparing the +shade+trim to the –shade+trim treatments, and focusing on the change in percent cover at each sample time compared to the initial cover, indicates that the effect of shade on coralline algae was context-dependent. Abundance of coralline algae beneath the shades increased at Strawberry Hill but not at Fogarty Creek (Table 3.5: Site x Shade interaction: F= 12.1, DF=1, 26;p=0.002. Within Strawberry Hill: shade F=9.69, DF 1,13 p=0.008).

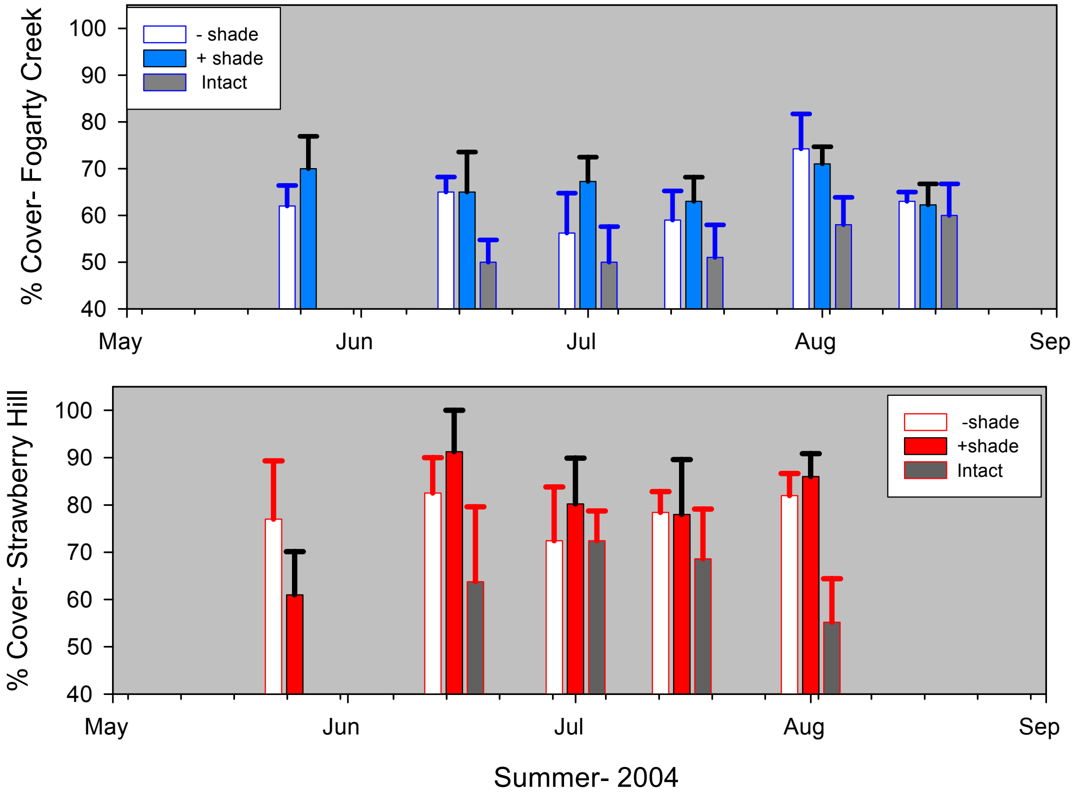


Figure 3.6. Effect of different canopy treatments on mean (+/- SEM) Coralline Algae abundances in the shading experiments at Fogarty Creek and Strawberry Hill, Oregon. See Table 3.4 for statistical analysis.

TABLE 3.4. REPEATED MEASURES ANALYSIS OF THE RELATIVE EFFECT OF INTACT CANOPY AND SITE ON CORALLINE ALGAE ABUNDANCE

Intact Canopy “treatment” is merely the manipulation control (-shade, -trim). Values bolded denote significant effect at p<0.05.

MC= Mauchley's criterion of sphericity.

Source of variation	MS	F	DF	Prob>F
Between Subjects				
Intact Canopy	0.407	8.149	1	**0.010**
Site	0.779	15.570	1	**0.001**
Site*Intact Canopy	0.004	0.083	1	0.776
Error	0.050		20	
Within Subjects-Multivariate				
Time	0.215	1.291	3	0.308
Time*Intact Canopy	0.231	1.385	3	0.280
Time*Site	0.491	2.947	3	0.061
Time*Site*Intact Canopy	0.702	4.214	3	**0.020**
Error	0.167		18	
Within Subjects-Unadjusted Univariate				
Time	1	1.312	3	0.279
Time*Intact Canopy	1	1.567	3	0.207
Time*Site	1	3.092	3	**0.034**
Time*Site*Intact Canopy	1	4.310	3	**0.008**
Error			60	

Sphericity Test	MC	Chi-Square	DF	Prob >Chisq
	0.942	1.119	5	0.952

TABLE 3.5 REPEATED MEASURES ANALYSIS OF THE EFFECT of SITE and SHADE on the RELATIVE CHANGE IN ABUNDANCE of CORALLINE ALGAE.

Responses modeled here are the increases in percent cover from initial cover, not absolute percent cover. Between treatments within site analysis is shown for Strawberry Hill only. Values bolded denote significance at $p<0.05$.

Between Subjects

Test	MS	F	DF	Prob>F
Site	0.079	2.043	1	0.165
Shade	0.083	2.167	1	0.153
Shade*Site	0.466	12.105	1	**0.002**
Error	0.083		26	

Sphericity Test

Mauchly Criterion	ChiSquare	DF	Prob >Chisq
0.581	13.423	5	0.020

Within Subjects- Multivariate

Test	MS	F	DF	Prob>F
Time	0.016	0.130	3	0.942
Time*Site	0.167	1.336	3	0.286
Time*Shade	0.075	0.596	3	0.624
Time*Shade*Site	0.186	1.490	3	0.243
Eror	0.125		24	

Within
Strawberry Hill
Between Subjects

Test	MS	F	DF	Prob>F
Shade	0.746	9.692	1	**0.008**
Error			13	

Sphericity Test

Mauchly Criterion	ChiSquare	DF	Prob >Chisq
0.517	7.730	5	0.172

Within Subjects- Multivariate

Test	MS	F	DF	Prob>F
Time	0.829	3.039	3	0.075
Time*Shade	1.421	5.210	3	**0.018**
Error	0.273		11	

DISCUSSION

In this experiment, understory algae responded differentially to shading treatments. Diversity of algal groups increased in the +shades, +trim treatment at Fogarty Creek but did not at Strawberry Hill. At Strawberry Hill, diversity increased beneath the intact canopy (-shade, -trim) treatment. Foliose red algae increased beneath the shades (+shade, +trim) at Fogarty Creek but did not at Strawberry Hill. In contrast, articulated corallines increased in dominance beneath the shades at Strawberry Hill but did not at Fogarty Creek.

Certain studies have found that understory algae responds positively to the removal or diminishment of the canopy species, i.e. they result in increases in biomass and diversity (Pierce and Hines, 1979; Kendrick, 2003). In our study, species richness and diversity (H') were greater and relative abundances of total understory algae were higher at Fogarty Creek in +shade +trim plots; i.e., in low light conditions but with reduced canopy shading. These increases were likely associated with the increase in foliose reds beneath the shades at Fogarty Creek. These responses, however, were not matched at Strawberry Hill. These between-site differences may suggest that the relative role of the canopy in generating positive or negative indirect effects varied between sites.

Increases in coralline turfs in the absence of canopy have been well documented in other studies, usually occurring in instances of high pollution and/or sedimentation (Beneditti-Cecchi, 2003; Connell, 2003; Gorgula and Connell, 2004). In this study, coralline algae were least abundant beneath the intact canopy (-shade-trim) but increased in abundance in the +shade +trim plots at Strawberry Hill. Since these are both "shaded" conditions, the increase in corallines in the +shade +trim treatments might be interpreted as dependent on factors other than light level. What these factors might be remains unknown.

Corallines are more resistant to herbivory (Nielsen 2001; van Tamelen, 1996) and possibly less prone to scour than red-bladed algae (van Tamelen, 1996). Articulated corallines are also relatively resistant to desiccation when in their natural clumps (R. Russell, pers. comm.). Strawberry Hill has more suspended sand and higher temperatures during emersion than Fogarty Creek (see Chapter 2). It is likely that the resistance of articulated corallines to desiccation and sand scour simply made them the better competitor than most foliose red species at Strawberry Hill.

Environmental Stress theory (Menge and Sutherland, 1976, 1987; Menge and Olson, 1990, Bertness and Callaway, 1994; Hacker and Gaines, 1987) gives a potential mechanism behind the differential response of the understory at the two sites. EST would suggest that across a differential stress gradient, the canopy could serve as a competitive dominant perhaps by limiting light to the understory where stress levels were intermediate. Where environmental stress levels were high (or consumer levels high) the canopy may serve a facilitative role, protecting the understory against desiccation (or herbivory).

Looking across abundances of functional groups, and relative changes in diversity indices, there appear to be consistent yet distinct interactions between the canopy species and understory assemblages at the two sites. At Fogarty Creek, the *Hedophyllum* canopy seems to act as a competitive dominant- shading the understory species and negatively affecting their abundances and diversity as reflected by the increases in foliose red algae and increases in algal diversity beneath the shades where the competitive dominant has decreased in abundance. With higher temperatures (this study; Halpin et al., 2003), greater sand loads (this study; Trowbridge, 1996), and greater variance in canopy moisture content (M. Kavanaugh, unpublished data), Strawberry Hill would seem to be a more stressful site. There the canopy also may serve a facilitative role, positively affecting understory species abundances and diversity by providing protection against desiccation and possibly photoinhibition, as reflected by the increases in algal diversity and foliose red algae beneath intact canopy treatments at that site. Complete canopy removal and further manipulation is necessary, however, to determine the nature of relationship between *Hedophyllum* and understory species as well as the mechanism underlying potential interactions. Nevertheless, compelling patterns have emerged from merely artificially shading and trimming the canopy species.

Importantly, there was no wholesale increase in understory abundance beneath the shades. Increases in relatively palatable foliose reds at Fogarty Creek were matched by increases in relatively unpalatable coralline algae at Strawberry Hill thus generating site-specific potential trophic consequences of shading. The differential response of functional groups at the two sites merits careful scrutiny also into the environmental gradient upon which species interactions occur. While many cases of canopy/understory interactions are negative within a given trophic level, this study suggests that positive interactions also are possible. Further investigation is necessary to determine whether this phenomenon will “scale-up”, and will ultimately facilitate an understanding of how community structure and production will change with disturbances that effect kelp communities.

CHAPTER 4

General Conclusions

In this thesis I have addressed the questions of what are the potential direct and indirect effects of light limitation induced by high productivity on benthic macrophytes. Several factors interacted, however, that make the modeling of this phenomenon more complex than anticipated. Phytoplankton concentrations were low in 2004 compared to the previous two years and site-level differences were also weakly reversed from what would be expected from historic observations. Regardless, results suggest that light limitation is possible during periods of moderate to high pelagic production, and that shading has context-dependent direct and indirect effects.

Direct effects of shading included decreased growth rates and accumulation of abundance of the intertidal kelp, *Hedophyllum sessile*. Although the expected between-site differences in growth rate did not occur, the experiments did reveal unexpected physiological differences between populations. At Strawberry Hill (Cape Perpetua), the shading effect was greater in strength than at Fogarty Creek (Cape Foulweather), a site of historically high macroalgal productivity- thus demonstrating potential for sun-adapted and shade-adapted populations that would respond differently to changing light regimes.

The results of the common garden experiment also suggested between-site differences in algal physiology. At low nutrient levels, growth rates were not affected by site of origin or light treatments, but at moderate nutrient levels, site of origin differences were detected. *Hedophyllum* blades from Strawberry Hill grew linearly with increasing light and at high light levels grew faster than blades from Fogarty Creek. Blades from Fogarty Creek tended to have highest growth in intermediate light levels.

As with the population level physiological response, the indirect effect of shading was context dependent and differed between functional groups. While the total understory assemblage abundance responded only weakly to artificial shading, individual functional groups changed in their relative abundance or dominance. Foliose red algae increased beneath the shades at Fogarty Creek but did not at Strawberry Hill. In contrast, articulated corallines increased in dominance beneath the shades at Strawberry Hill but did not at Fogarty Creek.

We interpret the differential understory response as the ecological role of the canopy being potentially different between sites. At Fogarty Creek, the canopy seemed to be a competitive dominant. The greatest increase in diversity and foliose reds occurred in shaded plots where the canopy had been trimmed and light availability was intermediate. At Strawberry Hill however, the greatest increase in diversity and foliose reds occurred beneath the intact unmanipulated canopy. Moreover, in unshaded Strawberry Hill plots where the canopy was trimmed, both the abundance of foliose reds and the diversity of the algal understory assemblage decreased during the course of the study.

This research suggests that increases in phytoplankton may have profound direct and indirect effects on both community structure and total community production, especially in communities where a perennial canopy-forming species exists. While many of the documented influences of algal canopies are negative, the canopy may provide several positive non-trophic effects. For example in terrestrial systems, canopies can provide protection against herbivory (Roussat and Lepart, 2000) and ameliorate environmental stress (Pugnaire et al., 1996). Algal canopies certainly provide analogous services to understory algal communities in marine environments. For intertidal communities, the canopy can ameliorate temperature stress (Burnaford, 2004) especially during the low daytime tides of summer. Furthermore, while modification of the light environment by the canopy is generally thought to be negative for subtidal species, many shallow water and intertidal species, particularly those of Rhodophyta, risk the adverse effects of too much light in the littoral zone and may exhibit photoinhibition (Lobban and Harrison, 1997) Chronic photoinhibition can result in, amongst other things, decreases in biomass accumulation (see reviews by Henley, 1993; Osmund, 1994).

There has been great progress in theoretically addressing the indirect non-trophic effects of environmental perturbations in community ecology. The Environmental Stress Models (e.g. Menge and Sutherland, 1976, 1987; Menge and Olson, 1990) brought two important testable hypotheses to community ecology. First, the models predict that interactions will change over environmental gradients or varying levels of "stress." Second, they predict that abiotic stresses can affect individual components or species differently. Certainly, this could apply also to different algal functional groups or grazer types. Bertness and Callaway (1994) and Bruno et al. (2003) modified these models by arguing that positive or facilitative effects were strong both at low environmental stress, where strong predation induced associational defenses between sessile organisms and at high environmental stress where direct stress induced facilitative associations between sessile species. At either end of this gradient, they predicted that positive interactions would shape communities through interactions that reduce consumer pressure and ameliorate abiotic stress. As in the original ESM's, they predicted that in intermediate situations, interactions will be predominately competitive. While most studies focus on species interactions, this basic theoretical framework can also serve to explain patterns of diversity (Hacker and Gaines, 1997). It has also been recognized that positive interactions can be conditional and change over space and time (Bronstein, 1994). This is especially true of non-trophic positive interactions (Bertness and Hacker, 1994; Callaway and Walker, 1997).

In Chapter 3, I proposed a model suggesting pathways via which phytoplankton shading might influence canopy and understory algae (Fig. 3.1). In light of the conditional nature of non-trophic positive and competitive interactions between canopy species and the understory assemblage, I propose that modifications of the original model (Chapter 3, Figure 3.1) should be made. These modifications also include some predictions of herbivory, the relative role of thallus scour, and how these interactions may change in an intertidal environment that may be shaded by high phytoplankton loading during immersion but also experience extremes in temperature during emersion.

The regional model (Figure 4.1) assumes that nutrient input is similar across regions and that nutrients are not limiting to kelp growth during periods of upwelling. High and low phytoplankton accumulation is caused by differential retention locally. High phytoplankton loading causes a negative direct effect as canopy-forming kelps are limited by light. In areas of low phytoplankton retention, the canopy forming kelps are neither light nor nutrient limited.

Indirect effects to the understory assume a differential stress gradient between sites. In areas of low phytoplankton retention, high environmental stress facilitates positive interactions between the canopy and understory as EST would suggest. In areas of low retention and lower stress, competitive interactions between the canopy and understory would predominate. At sites where phytoplankton accumulation is high and environmental stress is lower, the understory red assemblage would respond positively as the competitively dominant canopy decreases due to shading. In areas of high stress and high phytoplankton accumulation, however, the understory would also respond negatively, due to decreases in amelioration provided by the canopy.

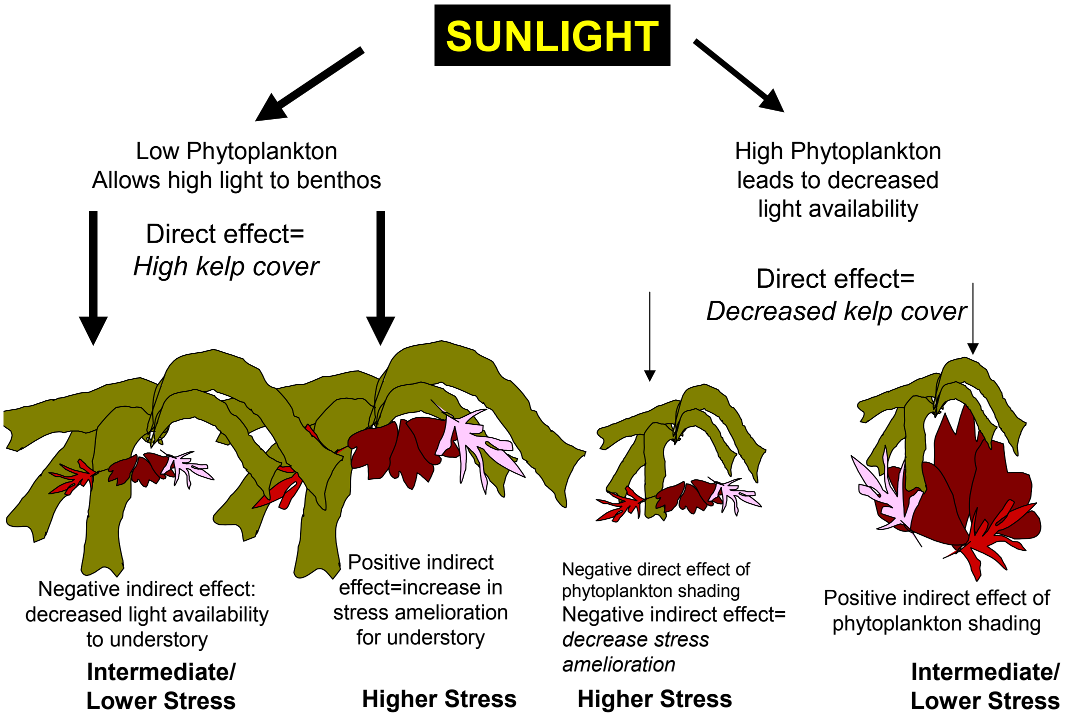


Figure 4.1: Revised model of the effect of phytoplankton shading on intertidal community structure. High and low phytoplankton concentrations are caused by similar upwelling interacting with differential localized retention (see Chapter 1); high phytoplankton is mimicked in this study by artificial shades. Nutrients are assumed to not be limiting, though more complex versions of this model may include nutrient and light co-limitation in the future. Stress is determined primarily by temperature during emersion (desiccation) and secondarily by sand scour. While photoinhibition is discussed in the text, it is not included in the model.

While many studies have investigated the effects of different canopy manipulations on the understory community structure, this study is unique in that it looks at both positive and negative indirect effects of the canopy changing in the context of high phytoplankton loading. It therefore provides a bridge by which we can investigate potential changes in intertidal community structure during the different nutrient and circulation regimes that may alter total community production.

The field and laboratory experiments investigating the effects of shading on intertidal communities revealed several ecologically important responses. First and foremost, the growth of *Hedophyllum sessile* can be limited by an ecologically relevant amount of light, that similar to what would be caused by moderate phytoplankton production. As phytoplankton concentrations during the study were atypically low, the light levels created by artificial shades suitably mimicked that which would occur during moderate production.

Secondly, site level differences in algal physiology likely exist. Sun- and shade-adapted phenotypes were suggested by a strong interaction of site and shade in the field experiments and by different responses to light in the laboratory experiments. Individuals from Strawberry Hill exhibited sun-adapted tendencies. Growth rates were more adversely affected by the experimental shade in field conditions and were positively linearly correlated to light in laboratory conditions. Individuals from Fogarty Creek exhibited shade-adapted tendencies. Growth rates were less adversely affected by the experimental shade in field conditions and maximum growth occurred with intermediate light levels in laboratory conditions.

Finally, changes in abundance in understory species did not reveal a strong compensatory response. They did, however, suggest differential responses between species and between sites. These differential responses support the notion that the kelp, *Hedophyllum*, may serve either as a competitive dominant or as a facilitator, dependent on environmental stress. This study demonstrated that canopies can either negatively and positively affect the understory algal assemblage, possibly as a function of differential environmental stress at the site level.

Further investigation is ultimately necessary to understand the relative role of herbivory and predation in affecting algal abundances in different communities. However, this study underscores the importance of indirect effects via physical modification in shaping both competitive and facilitative interactions –which could affect not only community structure but also total community production.

Literature Cited

Bakun A. (1996) Patterns in the Ocean. California Sea Grant/Centro de Investigaciones Biologicas del Noroeste, La Paz, Baja.

Benedetti-Cecchi, L, and F Cinelli. 1995. Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west coast of Italy (western Mediterranean). *Marine Ecology Progress Series* **126**: 203–212

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976-1989.

Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecology a*nd *Evolution* 9:191-193.

Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. *American Naturalist* 144:363-372.

Borum, J. and Sand-Jensen, K. 1996. Is total primary production in shallow coastal marine waters stimulated by nitrogen loading? *Oikos* 16: 406-410

Bustamante, R.H., Branch, G.M., Eekhout, S. Robertson, B., Zoutendyk, P., Schleyer, M, Dye, A., Hanekom, N., Keats, D., Jurd, M., McQuaid, C. 2005 Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia*, 102: 189 – 201

Bronstein, J.L. 1994. Conditional outcomes of mutualistic interactions. *Trends in Ecology and Evolution* 9:214-217

Bruno J., Bertness M., 2001. Habitat modification and facilitation in benthic marine communities. In: Bertness M, Gaines S, Hay M (eds) *Marine community ecology.* Sinauer Associates, Sutherland, MA, p 201–220

Burnaford, JL. 2004. Habitat modification and refuge from sublethal stress drive a marine plant-herbivore association. *Ecology*. 85:2837-2849

Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958-1965

Chow, W. S., Strid, A., Anderson, J. M. 1992. Recovery of photosynthetic functions and components after supplementary UV-B irradiation. *Photosynthesis Research* **34**:224.

Cole, J. J., M. L. Pace, S. R. Carpenter, and J. F. Kitchell. 2000, Persistence of net heterotrophy in lakes during nutrient addition and food web manipulation. *Limnology and Oceanography*. 45 1718–1730

Connell, S.D. 2003. Negative effects overpower the positive of kelp to exclude invertebrates from the understorey community. *Oecologia* 137: 1432-1939

Connell, S.D. 2003. The monopolization of understorey habitat by subtidal encrusting coralline algae: a test of the combined effects of canopy-mediated light and sedimentation. *Marine Biology* 142: 1065 - 1071

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien plants: Implications for conservation and restoration. *Annual Review of Ecology and Systematics* 34:183-211.

Dayton, P. K. 1985. The ecology of kelp communities. *Annual Review of Ecology and Systematics* 16:215-245

Dayton, P. K., and M. J. Tegner. 1984. Catastrophic storms, El Nino and patch stability in a southern California kelp community. *Science* 224:283-285

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

Dennison, W.C., 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquat.Bot*. 27, 15–26.

Dennison, W.C., Alberte, R.S., 1986. Photoadaptation and growth of *Zostera marina* L. (eelgrass) transplants along a depth gradient. *J. Exp. Mar. Biol. Ecol*. 98, 265–282.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431-451

Dethier, M. N, E. S Graham, S Cohen, and L. M Tear. 1993. Visual versus random-point percent cover estimations: ‘objective’ is not always better. *Marine Ecology Progress Series* **110**: 9–18

Drew, E. 1983. Light. In Earll and Erwin (eds), The Ecology of Sublittoral Benthos. Clarendon Press UK

Dring, M. 1987. Light climate in intertidal and sutidal zones in relatiion to photosynthesis and growth of benthic algae: a theoretical model. In Herring, Campbell, Whitfield, and Maddock (eds), Light and Life in the Aquatic and Amphibious Habitats (pp. 23-34). Blackwell Scientific, UK

Duarte, C.1992 Nutrient concentration of aquatic plants: patterns across species. *Limnology and Oceanography* 41:87-112

Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* **4**1: 87–112.

Duarte, C.M., 1991. Seagrass depth limits. *Aquat. Bot.* 40, 363–377

Falkowski, P. and Raven J. 1997. Aquatic Photosynthesis. Blackwell Scientific, UK.

Franklin, L. A. & Forster, R. M. 1997. The changing irradiance environment: consequences for marine macrophyte physiology, productivity and ecology. *European Journal of Phycology*. **32**:207 32

Gerard, V and Dubois, K.1988. Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina.* Marine Biology 97:575-580

Gorgula S.K. and Connell, S.D. 2004. Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Marine Biology* 145: 613 - 619

Gray, J., Wu, R., and Or, Y. 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Serie*s 238:249-279

Hacker, S. and S.D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* **78**: 1990-2003.

Hader D.-P.; Lebert M.; Figueroa F.L.; Jimenez C.; Vinegla B.; Perez-Rodriguez E. 1998 Photoinhibition in Mediterranean macroalgae by solar radiation measured on site by PAM fluorescence. *Aquatic Botany* 61: 225-236

Hammerstrom K, Dethier MN, Duggins DO (1998) Rapid phlorotannin induction and relaxation in five Washington kelps. *Mar Ecol Prog Ser* 165:293-305

Henley, W.J. (1993). Measurement and interpretation of photosynthetic light-response curves in algae in the context of photoinhibition and diel changes. *Journal of Phycology*., 29 : 729-739

Hurd, C. L. 2000. Water Motion, Marine Macroalgal Physiology, and Production. *Journal of Phycology* 36: 453-472.
Kirincich, A. R., J. A. Barth, B. A. Grantham, B. A. Menge, and J. Lubchenco .2005. Wind-driven inner-shelf circulation off central Oregon during summer, *J. Geophys. Res.*, 110, C10S03, doi:10.1029/2004JC002611.

Kirk, J. 1983, Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, UK

Larkum AWD (1986) A study of growth and primary production in *Ecklonia radiata* (Laminariales) at a sheltered site in Port Jackson, New South Wales (Australia). *J Exp Mar Biol Ecol* 96:177–190

Lauenroth, W.K. and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2, 397-403.

Littler and Arnold, K. E. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. - *Journal of Phycology*. 18: 307-3 1
Littler M.M and and Littler, D. **S.** 1984. Relationships between macroalgal functional form groups and substrata stability in subtropical rocky-intertidal system. - *J. Exp. Mar. Biol Ecol.* 74: 13-34.

Littler, MM., Martz, DR., Littler, DS., 1983. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Marine Ecology Progress Series* 11, 129-139.

Lobban CS, Harrison PJ (1994) *Seaweed ecology and physiology*. Cambridge University Press, Cambridge

Lowell RB, Markham JH, Mann KH (1991) Herbivore-like damage induces increased strength and toughness in a seaweed. *Proc R Soc Lond Ser B* 243:31-38

Luning, 1981. Light. In Lobban, Harrison, and Wynne (eds), *The Biology of Seaweeds* (pp326-355) Blackwell Scientific, UK

Mann KH, Kirkman H (1981) Biomass method for measuring productivity of *Ecklonia radiata*, with the potential for adaptation to other large brown algae. *Aust J Mar Freshw Res* 32:297–304

Mann, KH. Seaweeds: Their productivity and strategy for growth. *Science*. 182, 4116, pp. 975-981.

Maxwell, K., and Johnson, G. 2000. Chlorophyll fluorescence- a practical guide. *Journal of Experimental Botany* 51:659-668

Menge BA, Berlow EL, Blanchette CA, Navarrete SA, Yamada SB. The keystone species concept: Variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs 64:* 249-286, 1994

Menge BA, Daley BA, Wheeler PA, Strub PT, 1997. Rocky intertidal oceanography: An association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography 42 (1): 57-66

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65: 21–74.

Menge, B. A. 1997. Detection of direct versus indirect effects: were experiments long enough?. *American Naturalist* 149: 801–823.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. A*merican Naturalist* 110: 351–369.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition and predation in relation to environmental stress and recruitment. *American Naturalist* 130: 730–757

Menge, B. A., and. Olson, A. M. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution*, 5: 52-57

Menge, B. A., Daley, B. A., Wheeler, P. A., Dahlhoff, E., Sanford, E. & Strub, P. T. (1997) Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proc. Natl. Acad. Sci. USA* 94, 14530-14535

Moujet, J; Tremblin G; Morant Manceau, A,;Morancais, M and Robert, M. 1999. Long-term photoacclimation of *Haslea ostrearia* (Bacillariophyta): effect of irradiance on growth rates, pigment content and photosynthesis. *Eur. J. Phycol*. 34 : 109-115

Nielsen, K.J. 2001. Bottom-up and top-down forces in tide pools: Test of a food chain model in an intertidal community. *Ecol. Monogr*., 71, 187–217.

Nielsen, K.J. 2003. Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. Proceedings of the National Academy of Science 100:7660-7665

Osmond, C.B. 1994. What is photoinhibition ? Some insights from sun and shade plants. In Photoinhibition of Photosynthesis : From the Molecular Mechanisms to the Field (Baker, N.R. and Bowyer, N.R., eds) BIOS Scientific Publishing, Oxford

Paige KN, Whitham TG. 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *Am. Nat.* 129:407−16

Pavia H, Toth GB (2000) Inducible chemical resistance to herbivory in the brown seaweed *Ascophyllum nodosum*. *Ecology* 81:3212-3225

Philander, SG .1990. *El Nino, La Nina and the Southern Oscillation.* Academic Press. San Diego, USA

Pugnaire, F., P. Haase, J. Puigdefábregas, M. Cueto, S.C. Clark, and L.D. Incoll. 1996, Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain: *Oikos*. 76 455–464

Pugnaire, F.I., and M.T. Luque. 2001, Changes in plant interactions along a gradient of environmental stress: *Oikos*. 93 42–49

Rabouille C, Mackenzie FT, Ver LM. 2001. Influence of the human perturbation on carbon, nitrogen, and oxygen biogeochemical cycles in the global coastal ocean. *Geochimica et Cosmochimica Acta* Vol. 65, no. 21, pp. 3615-3641

Ramus 1982. Engelmann's theory: The compelling logic. In Srivistava (ed), Synthetic and Degradative Processes in Marine Macrophytes (pp.29-46). De Gruyter, Berlin

Reed, D and Foster, M . 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. *Ecology* 65: 937-948

Rousset, O., and J. Lepart. 2000. Positive and negative interactions at different life stages of a colonizing species (Quercus humilis). *Journal of Ecology* 88:401-412

Sand-Jensen, K., and J. Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* 41:137–175.

Stabeno and Monahan, 1983. The influence of whitecaps on the albedo of the sea surface. In Whitecaps and the marine atmosphere, Report 5 (pp-78-93). University College Galway, Ireland.

Tegner, M. J., P. K. Dayton, P. B. Edwards, and K. L. Riser.1997. Large-scale, low-frequency effects on kelp forest succession: a tale of two cohorts. *Marine Ecology Progress Series* 146:117–134

Tilman D. 1988. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton,New Jersey, USA.

Tilman D.1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.

Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. *Nature* 367:363–365.

Valiela, I; McClelland, J; Hauxwell, J; Behr, PJ; Hersh, D; Foreman, K .1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography*. 42:1105−18.

Van Alstyne KL (1988) Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology* 69:655-663 van Tamelen, P. G. 1996. Algal zonation in tidepools: experimental evaluation of the roles of physical disturbance, herbivory, and competition. Journal of Experimental Marine Biology and Ecology 201:197–231.

Van de Pol, W; Eggert, A; Buma, A, and Breeman, A. 2001. Effects of UV-B-induced damage and photoinhibition on growth of temperate marine red macrophytes: habitat-related differences in UV-B tolerance. *Journal of Phycology* 37: 30-42

Vitousek, P., and R. Sanford, Jr. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17:137-167

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. Annu. Rev. Ecol. Syst. 30, 257-300

Williams, S.L. and M.N. Dethier. 2005. High and dry: variation in net photosynthesis by the intertidal seaweed, *Fucus gardneri*. Ecology 86:2373-2379.

Zangerl AR, Arntz AM, Berenbaum MR (1997) Physiological price of an induced chemical defense: photosynthesis, respiration, biosynthesis, and growth. Oecologia 109:433-441

APPENDIX 1. Light manipulation in field and lab experiments

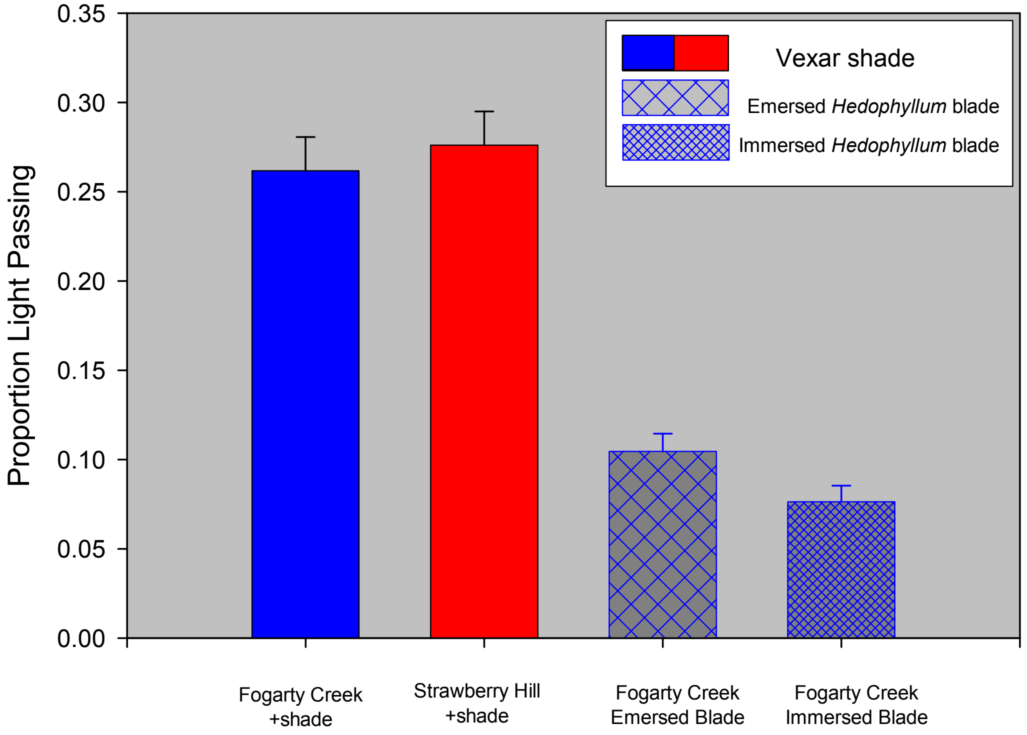


Figure A1.1 Relative percent shading afforded by artificial shades at Strawberry Hill and Fogarty Creek by *Hedophyllum* blades at Fogarty Creek during emersion and immersion.. Values were assessed using a hand-held quanta meter during mid-morning (between 8.30 and 9 am) on different days at the two sites (N= 5 per site). Quanta meter was held at substrate level normal to shades (N= 5/site) and at 10 cm below an outstretched blade in air (emersion, N=5) and under water in minor surge channel (immersion, N=6).

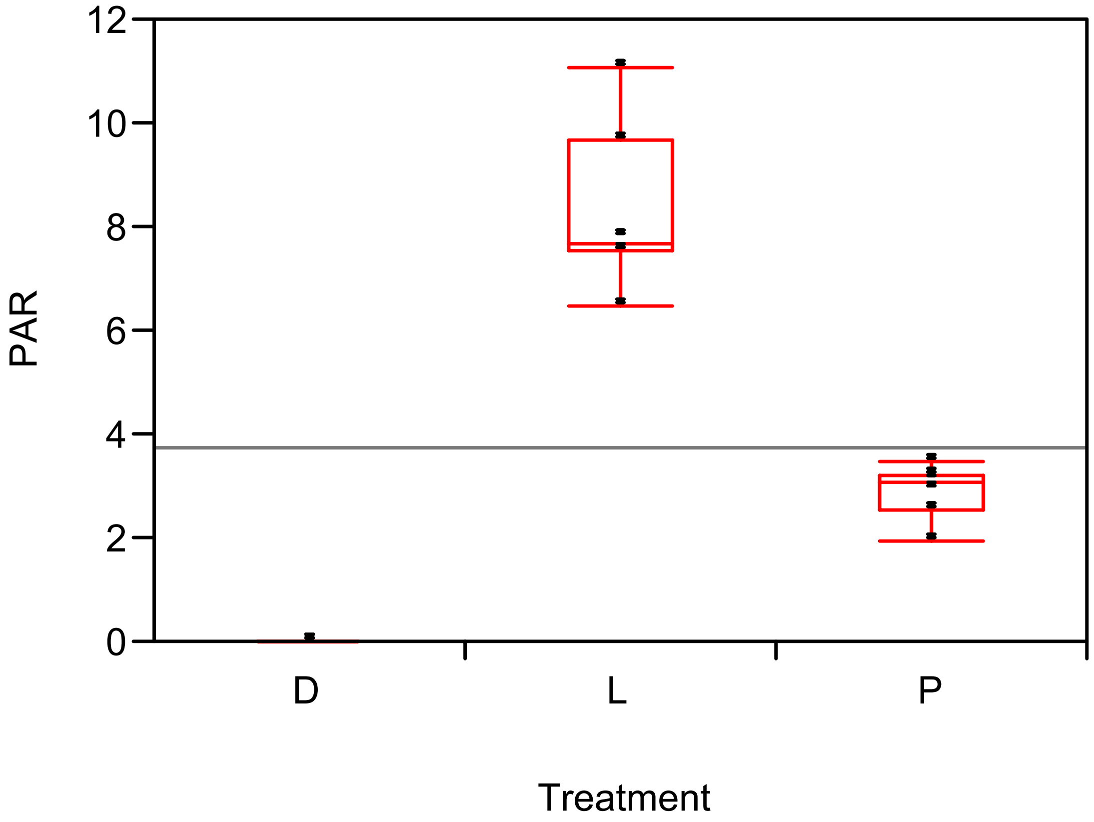


Figure A1.2 Light levels for common garden mesocosm experiment.
PAR indicates level of Photosynthetically Active/Available Radiation (~400-700 nm) in **moles of photons/m^2/day**. D= Dark, P=Partial Shade, L= Light treatments. The dark treatments are below the detectable scale of the figure.

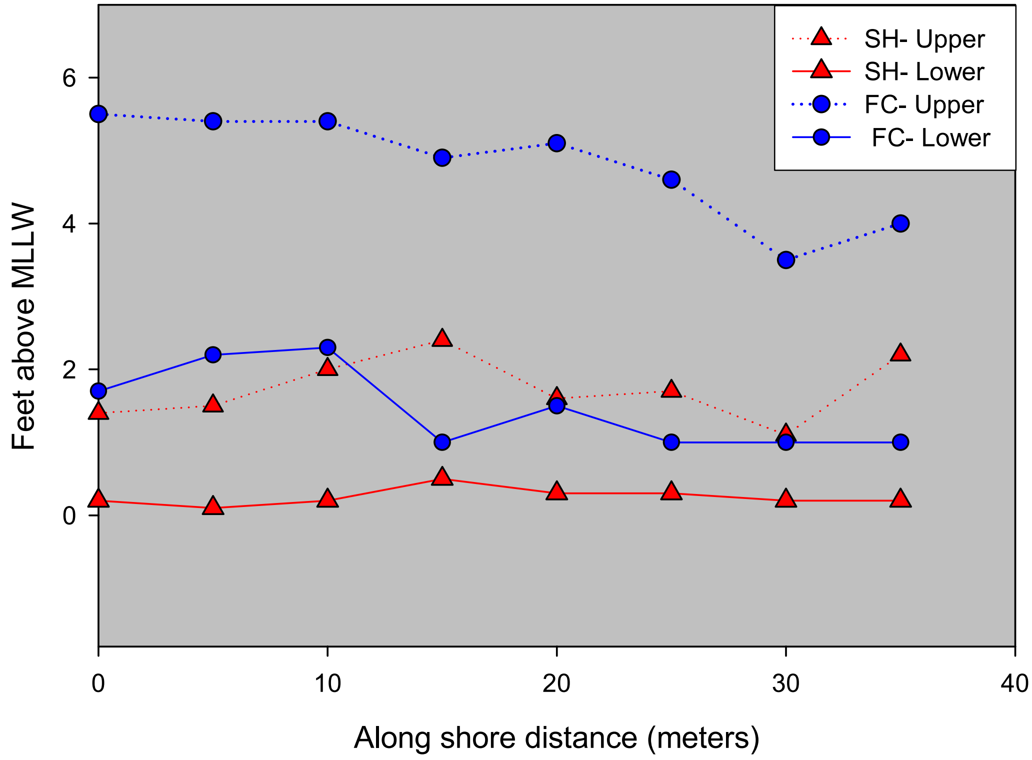


Figure A2.1 Elevations of the Hedophyllum bed at study benches at Fogarty Creek and Strawberry Hill, Oregon. Upper extents are shown with dashed lines, lower in solid lines. Alongshore distance is determined every five meters from North to South at study areas.

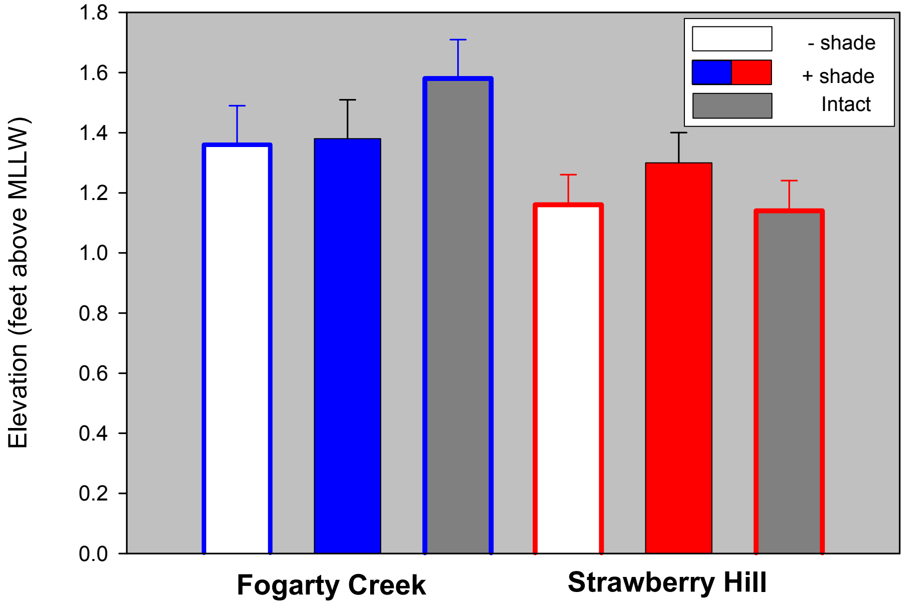
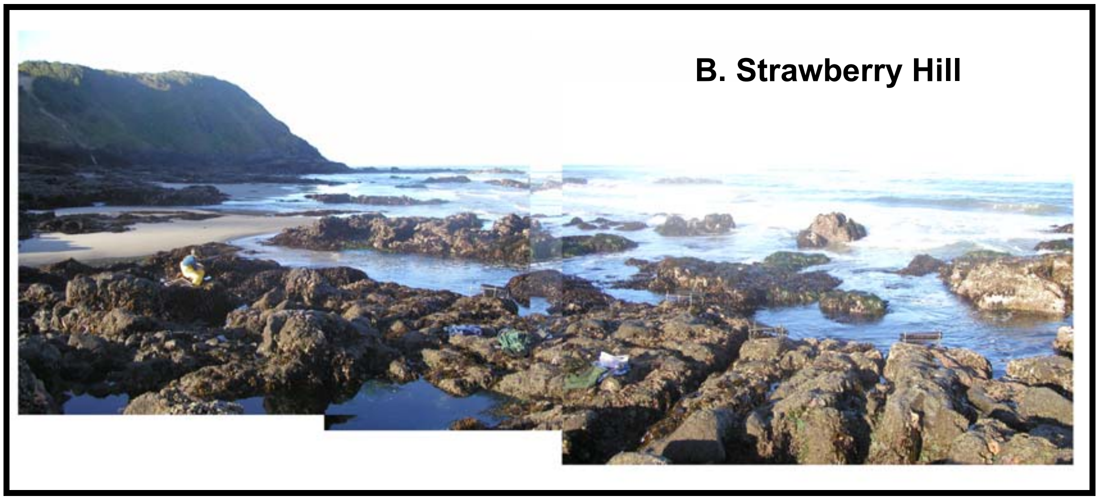


Figure A2. 2. Elevations of study plots at Strawberry Hill and Fogarty Creek, Oregon. Mean elevation (+SEM) of artificially shaded plots (N=5), -shade plots (N=5) and manipulation control plots (N=5) are reported for each site (total N= 30).

Figure A2.3. Images of study sites showing extent of *Hedophyllum* bed, study design, and community context at Fogarty Creek (A) and Strawberry Hill (B), Oregon. Figures are not shown at the same scale. Experimental shades are 70 cm x 70 cm for reference. Image from Fogarty Creek is shown looking toward the north; for Strawberry Hill the direction is southwesterly.



APPENDIX 3. Taxonomic resolution of field study

Nearly 80 species or taxa were found consistently found in the plots at both sites. Table 1 shows the species list for the study, the taxonomic resolution at which organisms were classified, and the total percent of plots through time in which the organism was observed. We identified nearly 40 groups of non-*Hedophyllum* algae, 12 herbivores, 12 carnivores, and 16 taxa of sessile filter-feeding invertebrates, including bivalves, barnacles, tube-dwelling polychaetes, sponges and tunicates.

Articulate and crustose corallines were present in nearly all plots through the duration of the experiment (percent occurrence= 0.98 and 0.95 respectively). Algal species that appeared in over half of the measurements included (in rank percent occurrence): *Microcladia borealis*, *Dilsea californica*, Fleshy Red Crusts, *Ulva* Complex, *Cryptopleura* Complex, and *Mazzaella splendens*.

The chiton *Katharina tunicata* had the highest percent occurrence through the duration of the experiment, appearing in 72 percent of all plot measurements. The limpet category, lumped into *Lottia sp*. due to the high frequency of un-identifiable juvenile limpets, was found in approximately 70 percent of all plots. The herbivorous snails, *Littorina sp*. were found in 61.3 percent of plots.

The barnacle species *Balanus glandula* appeared quite frequently, as did *Chthalamus sp.* (0.847). *Mytilus californianus*, another intertidal dominant, appeared relatively infrequently- less than one quarter of all observations. Its primary predator, the star, *Pisaster ochraceous*, appeared in over one half of the surveys.

TABLE A3.1: TAXONOMIC RESOLUTION OF STUDY

Species or species groups are listed according to trophic level affinities. Percent occurrence is the percentage of quadrats in which the organism was observed. Species or genera are italicized. Complexes consist of multiple genera that cannot be readily distinguished in the field.

Trophic Group	Type	Name	Percent occurrence	Trophic Group	Type	Name	Percent occurrence
Primary Producer	Brown Other	*Leathesia/Colpomenia*	0.020	Herbivore	Amphipod	amphipod Complex	0.100
	Coralline	Crustose Corallines	0.953		Chiton	*Katharina tunicata*	0.720
	Coralline	Erect Corallines	0.980		Chiton	*Lepidochiton Complex*	0.467
	Diatom	*Navicula sp.*	0.013		Chiton	*Mopalia sp.*	0.140
	Grass	*Phyllospadix sp.*	0.047		Chiton	*Tonicella lineata*	0.293
	Green	*Halicystis ovalis*	0.007		Crab	*Pachycheles* Complex	0.107
	Green	*Ulva* Complex	0.540		Isopod	*Cirolana harfordi*	0.020
	Laminarian	*Alaria marginata*	0.020		Isopod	*Idotea sp.*	0.360
	Laminarian	*Egregia menziesii*	0.033		Limpet	*Lottia* Complex	0.707
	Laminarian	*Laminaria sp.*	0.027		Snail	*Littorina* Complex	0.613
	Red Blade	*Cryptopleura* Complex	0.573		Snail	*Tegula funebralis*	0.007
	Red Blade	*Dilsea californica*	0.833		Urchin	*S.purpuratus*	0.213
	Red Blade	*Erythrophyllum sp.*	0.013	Filter-feeder	Barnacle	*Balanus glandula*	0.793
	Red Blade	*Mazzaella flaccida*	0.140		Barnacle	*Balanus nubilus*	0.227
	Red Blade	*Mazzaella linearis*	0.287		Barnacle	*Chthamalus sp.*	0.847
	Red Blade	*Mazzaella splendens*	0.500		Barnacle	*Pollicipes polymerus*	0.240
	Red Blade	*Porphyra sp.*	0.080		Barnacle	*Semibalanus cariosus*	0.393
	Red Blade	*Schizymenia* Complex	0.373		Bryozoan	*Bryozoan Complex*	0.020
	Red Branch	*Callithamnion sp*	0.033		Bryozoan	*Flustrellidra corniculata*	0.100
	Red Branch	*Farlowia sp*	0.007		Clam	clam Complex	0.193
	Red Branch	*Mastocarpus* Complex	0.053		Mussel	*Mytilus californianus*	0.220
	Red Branch	*Microcladia borealis*	0.873		Mussel	*Mytilus trossulus*	0.073
	Red Branch	*Neorhodomela* Complex	0.007		Polychaete	Calcareous Tube Complex	0.147
	Red Branch	*Odonthalia* Complex	0.013		Polychaete	*Dodecaceria fewkesi*	0.193
	Red Branch	*Osmundea spectabilis*	0.053		Polychaete	*Pista elongata*	0.073
	Red Branch	*Plocamium sp.*	0.273		Polychaete	Sandy Tube Complex	0.740
	Red Branch	*Polysiphonia* Complex	0.087		Sponge	Sponge Complex	0.380
	Red Branch	*Prionitis* Complex	0.053		Tunicate	Colonial Tunicate Complex	0.047
	Red Branch	*Pterosiphonia sp.*	0.007		Worm	Peanut Worm Complex	0.153
	Red Branch	*Ptilota* Complex	0.120	***Carnivore***	Anemone	*Anthopleura elegantissima*	0.813
	Red Crust	Fleshy Crusts	0.767		Anemone	*A. xanthogrammica*	0.293
	Red Crust	*Hildenbrandia sp.*	0.073		Anemone	*Epiactis prolifera*	0.033
	RedOther	*Halosaccion glandiforme*	0.247		Crab	*Cancer sp.*	0.033
Omnivore	Crab	*Pachygrapsus crassipes*	0.007		Fish	Sculpin Complex	0.007
	Crab	*Pagurus hirsutiusculus*	0.053		Star	*Leptasterias hexactis*	0.647
	Crab	*Pugettia sp.*	0.013		Star	*Pisaster ochraceus*	0.553
					Whelk	*Nucella canaliculata*	0.240
					Whelk	*Nucella ostrina*	0.020
					Whelk	*Ocenebra sp.*	0.040
					Worm	Nemertean Complex	0.520
					Worm	Platyhelminthes Complex	0.007

APPENDIX 4: Effect of shading on individual algal species and invertebrate species groups.

The effect of shading on individual species of red bladed algae was different between sites and for different species. See body of thesis for methods and statistical analysis. Abundance of *Dilsea californica* varied with both shade and site, with abundances at Fogarty Creek being 2-3 times that at Strawberry Hill (Table 13, p<0.005). Accounting for site differences, shading still had a persistent effect on *Dilsea*, adding up to 6.7 percent cover to the relative abundance of the species (p=0.040). Both the effect of site (p=0.042) and the interaction between site and shade (0.022) varied through time.

TABLE A4.1. EFFECT OF SITE AND ARTIFICIAL SHADE ON *Dilsea californica* ABUNDANCES

Source of variation	MS	Exact F	DF	Prob>F
Between Subjects				
Site	0.449	10.335	1	**0.004**
Shaded	0.207	4.755	1	**0.040**
Shaded*Site	0.085	1.956	1	0.175
Error	0.043		23	
Within Subjects				
Time	0.037	0.262	3	0.852
Time*Site	0.467	3.268	3	**0.042**
Time*Shaded	0.214	1.499	3	0.244
Time*Shaded*Site	0.565	3.953	3	**0.022**
Error	0.143		23	

The effect of shading on the suite of *Mazzaella* species, however, was not as clear. Shading did not have an overall effect (F=0.001, p=0.92). However, at Strawberry Hill, natural canopy affected the abundance of *Mazzaella sp*. (Table 10, p=0.05). Natural canopies can ameliorate the negative effects of desiccation during emersion periods which may be more important for the persistence of *Mazzaella* than that of *Dilsea*. The intact canopy effect was not apparent for *Mazzaella* at Fogarty Creek (p=0.602), likely indicating different interactions of environmental stressors at the two sites.

TABLE A4.2 EFFECT OF INTACT CANOPY ON *Mazzaella sp.* ABUNDANCES BETWEEN SITES

FC= Fogarty Creek, SH= Strawberry Hill. NS= No within subject or within/ between subject interactions were significant.. MC= Mauchley's criterion of sphericity.

Source of Variation	MS	Exact F	DF	Prob>F
Between Subjects-Fogarty Creek				
Intact Canopy	0.022	0.286	1	0.602
Error	0.077		13	
Within Subjects-FC				
Time	0.592	3.552	2	*0.061*
Time*Intact Canopy	0.025	0.152	2	0.861
Error	0.167		12	
Within Subjects-FC, Univariate Unadjusted				
Time	1	3.921	2	**0.033**
Time*Intact Canopy	1	0.166	2	0.848
Error			26	
Sphericity Test	MC	ChiSquare	DF	Prob >Chisq
	0.990	0.126	2	0.939
Source of Variation	MS	Exact F	DF	Prob>F
Between Subjects- Strawberry Hill				
Intact Canopy	0.355	4.614	1	**0.051**
Error	0.077		13	
Within Subjects- SH				
Time	0.025	0.148	2	0.864
Time*Intact Canopy	0.060	0.359	2	0.706
Error	0.167		12	

Algal groups- Non-calcified red crusts

Fleshy red crusts such as Petrocelis and *Hildenbrandia sp.*were more abundant in +artificial shade plots (Table 12, Shaded:p=0.027) but did not differ in abundance between sites (Site:p=0.697). For this category, neither abundances of fleshy crusts nor shade varied through time (Time: p=0.146; Time X Shaded: p=0.309).

TABLE A4.3. EFFECT OF ARTIFICIAL SHADES AND SITE ON FLESHY RED CRUST ABUNDANCES

Source of variation	MS	Exact F	DF	Prob>F
Between Subjects				
Shaded	0.212	5.518	1	**0.027**
Site	0.006	0.155	1	0.697
Site*Shaded	0.021	0.550	1	0.465
Error	0.038		26	
Within Subjects				
Time	0.167	2.081	2	0.146
Time*Shaded	0.098	1.231	2	0.309
Time*Site	0.083	1.034	2	0.370
Time*Site*Shaded	0.087	1.084	2	0.354
Error	0.08		25	

Herbivores

Herbivores were more abundant at Fogarty Creek than at Strawberry Hill (Figure 9; Table 13, p<0.001), and their abundances decreased dramatically through the course of the experiment (Time effect: p=0.009). Herbivores were less abundant in natural canopy plots than in manipulated plots (Table 13, Intact canopy: p=0.011) though the magnitude varied significantly through the duration of the experiment (p<0.045). Shading did not have an effect on the abundance of herbivores.

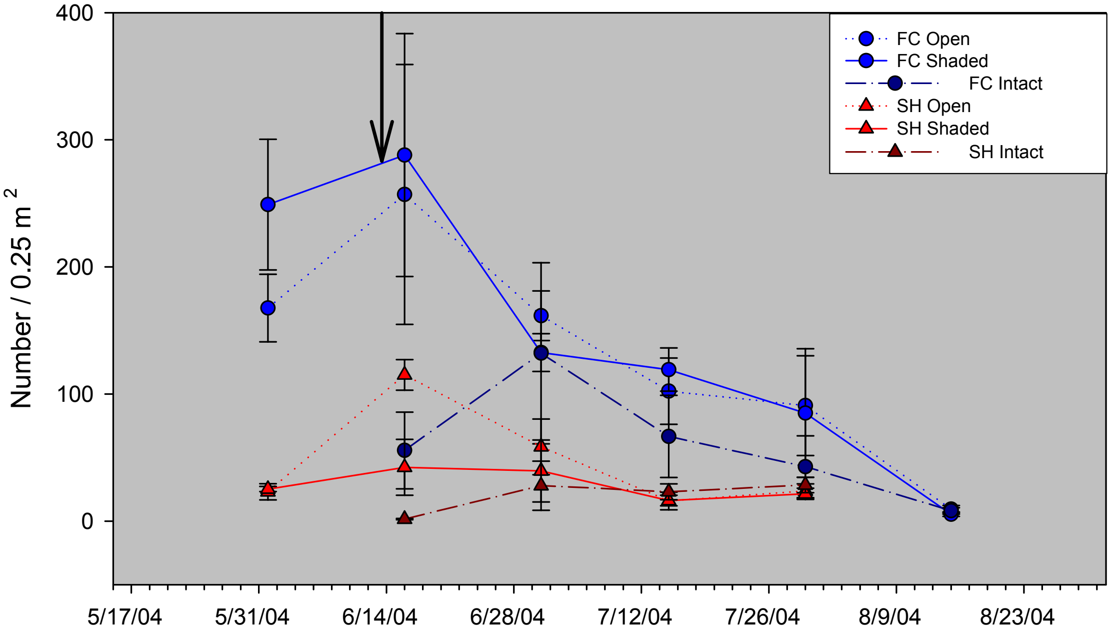


Figure A4.1: Changes in total herbivore abundance in artificially shaded, -shade, and intact canopy plots at Fogarty Creek and Strawberry Hill, Oregon.

TABLE A4.4. EFFECT OF INTACT CANOPY AND SITE ON HERBIVORE ABUNDANCES

MC= Mauchley's criterion of sphericity.

Source of variation	MS	Exact F	DF	Prob>F
Between Subjects				
Site	0.694	14.580	1	**0.001**
Intact Canopy	0.367	7.712	1	**0.011**
Intact Canopy*Site	0.029	0.612	1	0.443
Error	0.048		21	
Within Subjects				
Time	0.820	5.192	3	**0.009**
Time*Site	0.145	0.921	3	0.450
Time*Intact Canopy	0.327	2.073	3	0.138
Time*Intact Canopy*Site	0.136	0.860	3	0.479
Error	0.158		19	
Within Subjects- Unadjusted Univariate	MS	Approx. F	DF	Prob>F
Time	1	4.992	3	**0.004**
Time*Site	1	0.977	3	0.409
Time*Intact Canopy	1	2.837	3	**0.045**
Time*Intact Canopy*Site	1	0.801	3	0.498
Sphericity Test	MC	X^2	DF	Prob $>X^2$
	0.611	9.706	5	0.084

Herbivore groups- Lottia sp.

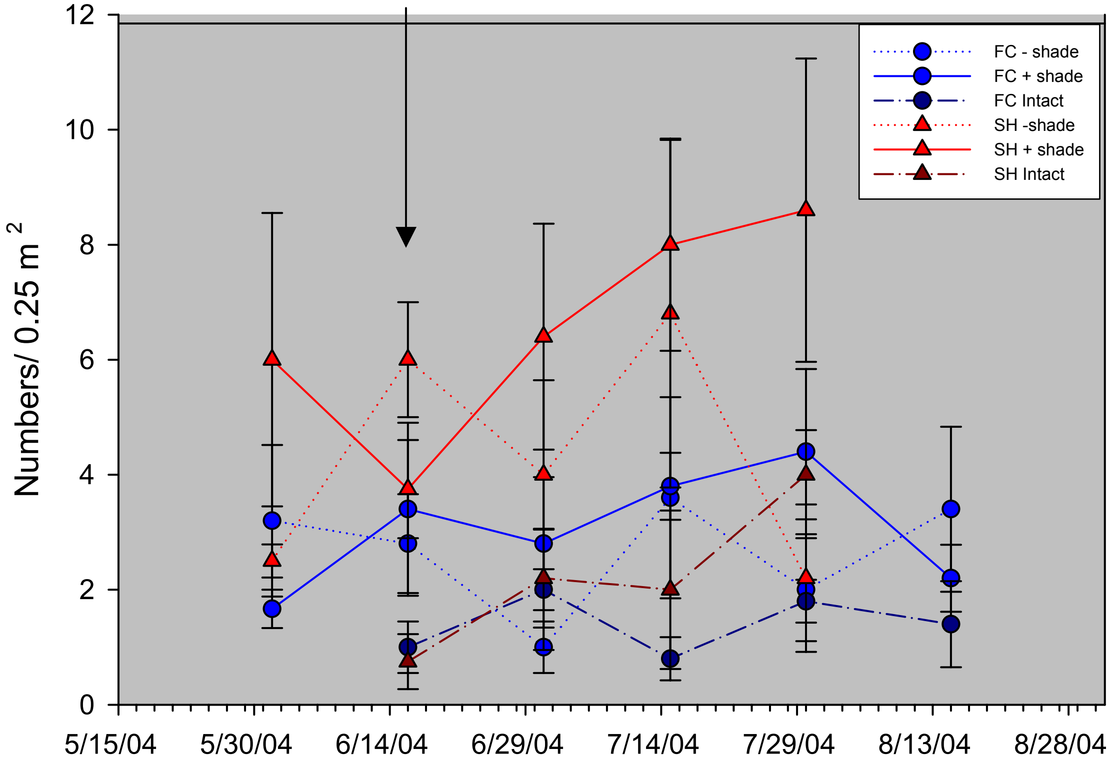
Consistent with the general herbivore pattern, limpet abundances were lower in plots with intact canopies than in the other plots (Table 15, Intact canopy: p=0.032). Limpet abundances were much higher also at Fogarty Creek than at Strawberry Hill (p<0.0001) and it is likely that the within site dynamics at FC carried the statistical relationship between the intact canopy and the common intertidal herbivore. Calculating the repeated measures within each site yielded a different result in that relationship was only strong and persistent at Fogarty Creek (Within FC Intact Canopy: F=5.46, dF= 1,13, p<0.036). Within Strawberry Hill alone, there was no effect of canopy (p=0.4) on the abundances of limpets.

TABLE A4.5. EFFECT of SITE and INTACT CANOPY on LIMPET ABUNDANCES

Source of Variation	MS	Exact F	NumDF	Prob>F
Between Subjects				
Intact	0.251	5.268	1	**0.032**
Site	2.391	50.221	1	**<.0001**
Site*Intact	0.086	1.808	1	0.193
Error			21	
Within Subjects				
Time	0.521	3.298	3	**0.043**
Time*Intact	0.278	1.760	3	0.189
Time*Site	0.150	0.950	3	0.437
Time*Site*Intact	0.053	0.333	3	0.801
Error			19	

Carnivores.

While abundance of the sea star *Pisaster ochraceus,* the whelks *Nucella ostrina* and *Nucella canaliculata*, and other less common predators was recorded through the duration of the experiment, sea stars far outnumbered whelks and carnivorous crabs at both sites. Strawberry Hill had far more sea stars than Fogarty Creek (Table 17, p=0.008). The effect of shading was positive (+2.4), was not site-dependent (Shaded X Site: p=0.208), and did not vary through time (Time X Shaded: p=0.144) . The effect of the intact canopy was negative (-1.13) albeit not statistically significant (p=0.287) through the duration of the study. The effect of the intact canopy did change through time (Time X Intact Canopy, p=0.04), likely playing a greater role in July than in early August when abundances of stars dropped in all plots except for the artificially shaded plots at Strawberry Hill (Figure 10).



FigureA4.2: Changes in mean number of sea stars in 3 treatments at Fogarty Creek and Strawberry Hill, Oregon. Fogarty Creek plots are shown in blue; Strawberry Hill plots in red. The arrow denotes the successful installation of the shades and thus the initiation of the experiment.

TABLE A4.7. RELATIVE EFFECTS OF SITE, INTACT CANOPY, AND ARTIFICIAL SHADING ON SEASTAR ABUNDANCES

FC= Fogarty Creek, SH= Strawberry Hill. NS= No within subject or within/ between subject interactions were significant. PE= Parameter estimates: (Intercept) and Artificial shade or Intact Canopy effect. MC= Mauchley's criterion of sphericity.

Source of Variation	PE	MS	Exact F	DF	Prob>F
Between Subjects					
Site (SH-FC)	1.22	0.330	8.258	1	**0.008**
Intact	-1.13	0.047	1.184	1	0.287
Shaded	2.4	0.212	5.307	1	**0.030**
Shaded*Site	-1.16	0.067	1.672	1	0.208
Error				25	
Within Subjects-Multivariate					
Time		0.196	2.349	2	0.117
Time*Site		0.007	0.083	2	0.921
Time*Intact		0.206	2.476	2	0.105
Time*Shaded		0.175	2.104	2	0.144
Time*Shaded*Site		0.008	0.091	2	0.914
Error				24	
Within Subjects- Univariate Unadjusted					
Time		1	3.424	2	**0.040**
Time*Site		1	0.122	2	0.886
Time*Intact		1	3.428	2	**0.040**
Time*Shaded		1	2.101	2	0.133
Time*Shaded*Site		1	0.067	2	0.935
Error				50	

Sphericity Test	MC	ChiSquare	DF	Prob >Chisq
	0.831	4.439	2	0.109

APPENDIX 5: Effects of shading on biomass of intertidal assemblages

Method

At the end of the experiment, a 100 cm^2 sub-sample of the plot was collected for biomass estimates. Sub-samples were taken from the approximate center of each plot, and were removed from the rock surface using a combination of metal putty knives, standard screwdrivers, and a crowbar. Crusts, however, are difficult to remove by any means and remained mostly intact so are therefore underrepresented in the samples. Sub-samples were sorted in the lab to the highest taxonomic resolution possible. Individual taxa were separated before drying. Samples were dried at 67° C in a laboratory drying oven for 24 hours to obtain dry weights. Calcareous and chitonous material such as barnacle plates and crab carapaces were included in total weights.

Analysis of variance on dry mass of individual taxa was performed using JMP software to test for treatment effects. Linear regression was also performed to test the relationship between groups within a given treatment. Analyses were conducted at three different taxonomic groupings: individual taxa, taxa type (such as "barnacle" or "foliose red algae") and trophic level.

TABLE A 5.1: ORGANISMS FOUND in 100 cm ^{2} SUBSAMPLE of PLOTS AT END OF EXPERIMENT at FOGARTY CREEK and STRAWBERRY HILL, OREGON.

Trophic Group	Species	"Type"	Resolution	Total
Primary Producer	corallines	red coralline	genus	**11**
	Cryptopleura sp	red blade	genus	
	Dilsea californica	red blade	species	
	Farlowia mollis	red branch	species	
	Mazzaella sp	red blade	genus	
	Phyllospadix	grass	genus	
	Plocamium sp	red branch	genus	
	Polysiphonia/Ceramium	red branch	genus	
	Porphyra sp	red blade	genus	
	Ptilota sp.	red branch	species	
	Ulva	green	genus	
Herbivore	amphipod	amphipod	taxa	**11**
	Cirolana sp	isopod	genus	
	Idotea sp	isopod	genus	
	Lepidochiton sp.	chiton	genus	
	Littorina sp.	snail	genus	
	Lottia sp	limpet	genus	
	Macron sp.	snail	genus	
	Mopalia sp.	chiton	genus	
	P_ hirsutiusculus	crab	species	
	Pugettia sp	crab	genus	
	Tonicella lineata	chiton	species	
Filter-feeder	*Balanus sp.*	barnacle	genus	**7**
	clam	clam	taxa	
	Flustrellidra	bryozoan	genus	
	Mytilus sp	bivalve	genus	
	oyster	bivalve	taxa	
	Pollicipes polymerus	barnacle	species	
	Polychaete tubes	worm	taxa	
Carnivore	*Leptasterias hexactis*	star	species	**5**
	N. canaliculata	whelk	species	
	nemertean	worm	taxa	
	nereid	worm	taxa	
	Pachycheles	crab	genus	
Other	*Halichondria sp.*	sponge	genus	**2**
	peanut worm	worm	taxa	

TABLE A5.2: COMPARISON OF MEAN BIOMASS of TAXA BETWEEN TREATMENT and BETWEEN SITES.

Analysis of variance was conducted on individual species and taxonomic groups. These data represent a subset. For between treatment analysis, shared letter or no letter denotes no significant difference at $p<0.05$. For between site analysis, *=$p<0.05$; **=$p<0.01$. All values are grams dry weight per 100cm2

	Open	Shaded	Intact	Fogarty Creek	Strawberry Hill
Primary producers	5.9168	5.9998	4.2862	5.0622	5.7396
Articulated corallines	5.6291	5.7240	3.8448	4.6914	5.4405
Foliose reds	**0.0134**^{a}	**0.26049**^{ab}	**0.36967**^{b}	0.3205	0.1085
Branched reds	0.2750	0.0201	0.0725	0.0514	0.1937
Non-coralline (pooled)	0.2878	0.2758	0.4414	0.3709	0.2991
Herbivores	0.1085	0.1286	0.1739	0.1183	0.1557
Snails	**0.02528**^{b}	**0.06259**^{a}	**0.02008**^{b}	0.0420	0.0300
Limpets	0.0018	0.0038	0.0002	**0.0038****	**0.0001****
Chitons	0.0147	0.0023	0.0708	0.0533	0.0053
Filter-feeders	0.8488	0.1782	0.3626	0.6373	0.5715
Barnacles	0.0988	0.0377	0.0771	0.1194	0.0231
Bivalves	0.4682	0.1641	0.1075	**0.4442***	**0.0490***
Polychaetes	0.2818	0.3853	0.1176	**0.0637****	**0.4994****
Carnivores	0.0783	0.0558	0.1234	0.1000	0.0717
Whelks	0.0007	0.0092	0.0004	0.0064	0.0005

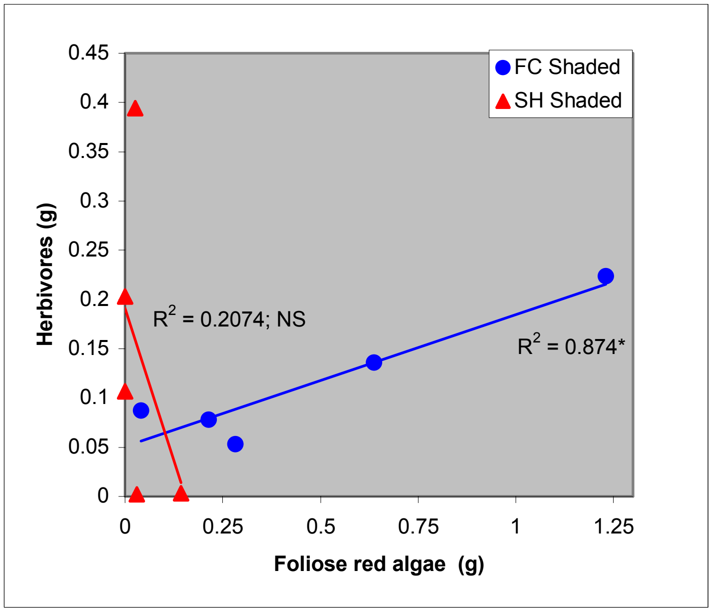


Figure A5.1. Relationship between the biomass of palatable red blades and herbivores beneath experimental shades at Fogarty Creek and Strawberry Hill, Oregon. Biomass calculated as grams dry weight/100 cm ^{2}. * Denotes p<0.05, NS= not statistically significant.

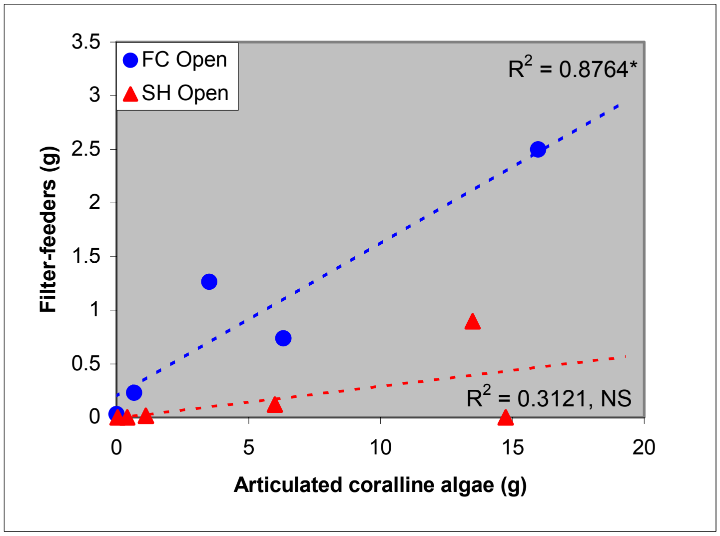


Figure A5.2. Relationship between the biomass of articulated corallines and filter-feeders in Open plots at Fogarty Creek and Strawberry Hill, Oregon. Biomass calculated as grams dry weight/100 cm ^{2}. * Denotes p<0.05, NS= not statistically significant.

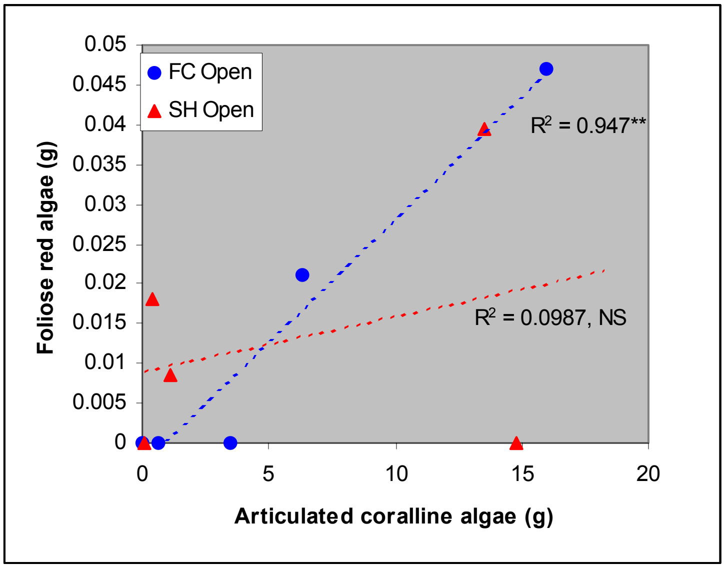


Figure A5.3. Relationship between the biomass of articulated corallines and foliose red algae in Open plots at Fogarty Creek and Strawberry Hill, Oregon. Note scale of foliose red algae. Biomass calculated as grams dry weight /100 cm ^{2}**.** ** Denotes p<0.01, NS= not statistically significant.

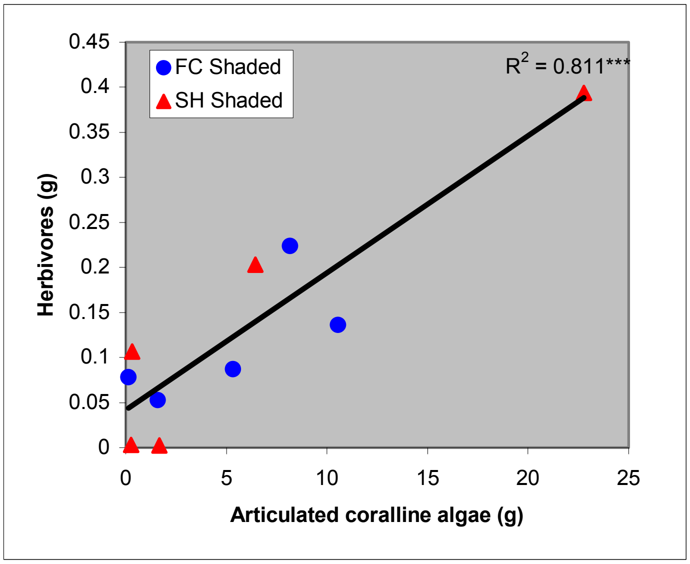


Figure A5.4. Relationship between the biomass of articulated corallines and herbivores beneath experimental shades at Fogarty Creek and Strawberry Hill, Oregon. See Table X for correlation coefficients for individual sites. Biomass calculated as grams dry weight /100 cm ^{2}. ***Denotes p<0.001

APPENDIX 6: Repeated Measures Analysis

Repeated measures analysis of variance was used to determine the relative magnitude and persistence of the effects of treatment and site on several responses throughout the duration of the study: the growth rate of *Hedophyllum sessile,* the abundance of different species or groups of macroalgae, and the abundance of different species or groups of invertebrates. Because these responses were taken from the same plots at different times throughout the experiment, there is a lack of statistical independence between these observations. Any statistical analyses must account for lack of independence; repeated measures analysis of variance was the logical choice.

The analysis is separated into two components:

1. *Between subject effects* are modeled by fitting the sum of the columns (responses at time 0, 1, 2, 3 etc) to the model effects. These are the overall effects of the treatment, site, or interactions between the two on the response and account for lack of independence.

2. *Within subject effects* (repeated or time effects) are modeled with a response function that fits differences between columns. These model how the differences in explanatory variables and interactions vary across time.

Importantly, if one is interested in how environmental factors that vary with time may affect the strength of the treatment or site effect, repeated measures is preferable to a simple before/after analysis (comparable to a before/after/control/impact “BACI” with replication). For example, along the Oregon coast, wind-driven upwelling brings in high levels of nutrients that are made available to macroalgae and other autotrophs. Upwelling is not constant during the summer and its intensity may vary. Because light (measured) and nutrients (not directly measured) may interact to co-limit the growth of macroalgae, understanding the interactions of treatment (light) and time is critical to understanding the overall effect of the treatment in its environmental context.

Repeated measures analysis does not differ structurally from multivariate analysis. Both have dependent observations. The difference lies in the response by time orientation. In repeated measures the *same response* is measured over *multiple times*; in multivariate models, the multiple dependent variables are measures of *multiple responses* measured at the *same* point in time. These responses usually are different metrics (sex, weight, reproductive index of a single individual) but can be the same metric considering individual species (species A, B, C found in an individual collecting unit).

Therefore, the model follows the general multivariate structure:

$$Y_{1:i,j}\ Y_{2:i,j}\ Y_{3:i,j\ldots\ldots} = \text{treatment} + \text{site} + \text{treatment*site}$$

Where Y_1 is the response at time 1 for an individual receiving the ith treatment at site j, Y_2 is the response at time 2 etcetc.

There are cases in a repeated measures model, that allow transformation of a multivariate problem into a univariate problem (Huynh and Feldt 1970). Several criteria need to be met in order to use univariate tests in a multivariate context, the most operational is that the sphericity criterion be met. The sphericity test checks the appropriateness of an unadjusted univariate F test for the within-subject effects using the Mauchly criterion to test the sphericity assumption of equal variances- a chi-square test (Anderson 1958). In practice, most researchers interpret the sphericity test as

- If the sphericity chi-square test is not significant, you can use the unadjusted univariate F tests;
- If the sphericity test is significant, use the multivariate or the adjusted univariate tests (JMP Help Manual, 2000).

There is debate regarding the use of the univariate approach compared to the multivariate. If you can use the univariate output, you may have more power (thus decrease the probability of a Type 2 error). However, the univariate approach is appropriate only when the sphericity assumption is not violated. If the sphericity assumption *is* violated, then some researchers opt to adjust the univariate degrees of freedom. JMP prints two different *correction factors*: the Greenhouse-Geisser Epsilon (G-G) and the Huynh-Feldt Epsilon (H-F). However, neither Mauchley's test nor the two correction factors are robust with small sample sizes and where there are missing observations.

For most analyses, the more conservative multivariate approach was used in our study. Univariate statistics are also reported when the results differed from multivariate. If Mauchley's criterion of sphericity was satisfied (Prob X^2>0.05), unadjusted values were reported; otherwise the Huynh-Feldt (1976) adjustment for epsilon was employed.