

AN ABSTRACT OF THE THESIS OF

Alyssa L. Harris for the degree of Bachelor of Arts in International Studies in Biology presented on November 29, 2007. Title: Predicting the effects of climate change: effects of thermal stress on seaweeds in the Galapagos rocky intertidal.

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Because global warming is predicted to increase the severity of El Niño events in the future, understanding how warmer temperatures affect seaweed growth and the animals associated with seaweeds is important for predicting how marine ecosystems will change. The Galapagos Islands of Ecuador are considered a living laboratory for studying climate change and served as the experimental site for this study. An artificially induced average increase in temperature by 1.45°C significantly decreased seaweed biomass in the intertidal of Tortuga Bay, Santa Cruz Island. The experiment utilized a block design with six treatments. Treatments consisted of 15cm x 15cm black (warm) and white (cool) plates to cause differential thermal stress, cross-factored with herbivore exclusion cages to study the effects of grazing, and a natural substratum control. Thermal stress (plate color) and grazing were both significant factors reducing seaweed biomass. Abundance, richness, and diversity of invertebrate animals living among the seaweeds showed declines in warmer treatments. Effects on small animals could reflect intolerance to thermal stress, loss of habitat (seaweed), or both, and future studies should investigate these factors. These results indicate that warmer conditions due to human induced climate change can decrease seaweed growth and affect animals that rely on seaweeds for food or habitat, possibly including the Galapagos marine iguana. Insight from the Galapagos might help predict seaweed response to climate change in other regions including the temperate Pacific Northwest.

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**Predicting the effects of climate change:
Effects of thermal stress on seaweed growth in the Galapagos rocky intertidal**

by

Alyssa L. Harris

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Approved:

Dr. Mark A. Hixon, Thesis Advisor (Zoology Department)

Dr. Robert Mason, Head or Chair (Biology Department)

Dr. Joseph G. Hoff, Academic Coordinator, International Degree Program

I understand that my thesis will become part of the collection of Oregon State University. My signature below authorizes release of my thesis to any reader upon request. I also affirm that the work represented in this thesis is my own work.

Alyssa L. Harris, Author

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Note: Honors College students will require seven signature lines: three committee members, Department Head/Chair, Director of the Honors College, Director of the International Degree Program and student signature.

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Introduction

The rocky intertidal has served as an experimental model for understanding ecosystem interactions, from biotic factors, such as keystone species (e.g., Paine, 1966) to abiotic factors, such as physical and physiological stressors (e.g., Menge and Sutherland, 1987). The history of marine ecology is rich in studies examining how such environmental factors affect species distributions and zonation in the rocky intertidal (Lewis 1964, Stephenson and Stephenson 1972). The spatial theory of marine ecology suggests that upper distributional boundaries are due to physiological stress, imposed by the rigor of physical factors such as desiccation (drying), while lower boundaries are due to inter-specific (between-species) and intra-specific (within-species) interactions, including predation and competition (Connell, 1972). Although Cubitt (1984) suggested more complex interactions for explaining the upper limits of zonation, it is generally concluded that the flora and fauna of the rocky intertidal, living at the interface of marine and terrestrial environments, experience the extreme bounds of their thermal tolerance limits (Davenport and Davenport 2005, Helmuth et al. 2002).

The Galapagos Islands of Ecuador have served as a living laboratory of ecology and evolution from Darwin to the present day (Darwin 1959, Grant 1999). Because of the archipelago's unique location along the Eastern Pacific equator, these islands are considered a test bed for climate change (Barrett, 2007, Vinueza et al. 2006) and served as the experimental site for this study. Seaweeds, important food and habitat of a variety of other organisms can experience severe desiccation when exposed at low tides (Connell 1972, Dethier et al. 2005). Due to their susceptibility to thermal stress and their important ecological roles, it is critical to understand how seaweeds will be affected by

increasing temperatures associated with human induced global warming and climate change.

The roles of seaweeds in ecosystems are important at local and global scales. On the local scale, seaweeds can act as habitat for organisms (Lilley and Schiel, 2006), and as food for local herbivores such as sea urchins in the Pacific Northwest (e.g., Dayton, 1975), marine iguanas, Sally Lightfoot crabs, and fish in the Galapagos Islands (Vinueza et al., 2006, Rubenstein and Wikelski, 2003). Seaweed growth is usually limited by grazing under variable conditions and nutrients when light and temperature are stable (Kaiser et al., 2005). While grazing, a top-down effect, is strong in the Galapagos (Vinueza et al., 2006), bottom-up (e.g., nutrients) and temperature effects on seaweed growth and abundance appear to strongly influence the timing of marine iguana reproduction and survival (Rubenstein and Wikelski, 2003). This evidence suggests a need to understand the effects of both grazing and thermal stress on seaweed growth, and recent studies by Vinueza (2006) are investigating these roles at longer temporal scales.

On the global scale, annual productivity of seaweeds and seagrasses can be equal to or greater than that of rainforests, playing a major role in atmospheric carbon dioxide (CO₂) uptake (Kaiser, 2005). Seaweeds generally obtain carbon needed for photosynthesis from bicarbonate (HCO₃⁻) in the water. During low tides and exposure to air, they can only obtain carbon from atmospheric carbon dioxide (CO₂). Due to what can be long periods of exposure, seaweed can still photosynthesize in the air, although at lower rates, as long as they do not desiccate (Kaiser et al., 2005).

At the Galapagos Islands, an oceanographically unique system for tropical regions (Vinueza et al. 2006, Kaiser, 2005), I focused this study, a subset of L. Vinueza's

dissertation, on understanding how thermal stress and grazing effects impact seaweed growth, the scientific literature for understanding these effects in temperate regions, and how these regions may demonstrate impacts of human-induced climate change. Before exploring the question of thermal effects on seaweeds in the Galapagos, I believe it appropriate to explain the context of global climate change linked to these ecologically important regions.

Climate Change: Links to oceanic cycles

The Intergovernmental Panel on Climate Change (IPCC) defines climate change as statistically significant variations in climate-weather of all temporal and spatial scales (IPCC, 2007, Synthesis Report Question 3). One global scale prediction for climate change is a co-occurrence of global warming and ocean-atmospheric linked cycles, including the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (IPCC, 2001, Fedorov and Philander, 2000). This co-occurrence may have dramatic effects on primary productivity in both temperate and tropical regions.

In the tropics, El Niño (hereafter EN) occurs when trade-winds influenced by sea surface temperatures (SST) around the equator slacken, changing current patterns, eventually resulting in a movement of warmer western-pacific waters towards the cooler, eastern Pacific region. The opposite pattern, La Niña, involves a strengthening of tradewinds, with stronger upwelling and greater concentrations of nutrients in the east Pacific. Generally, such events have happened on a 2-7 year intervals over the last 5,000 years, which Kerr (1999) suggested is double the rate than during the previous 10,000 years. This horizontal shift of water mass directly results in warmer SST, greater rainfall, and overall warmer marine and terrestrial conditions in the eastern Pacific region,

including the Galapagos Islands (McPhaden et al. 1998, Fedorov and Philander, 2000; Pierrehumbert, 2000). It is not clearly understood how EN will be affected in frequency and severity in the next 100 years (IPCC, 2001), but the impact of global warming combined with EN fluctuations could have strong effects on the global scale. For example, Wolter and Timlin (1998) reported an increase in rainfall and thermal anomalies, or extremes, during EN within the last twenty years, clearly coinciding with increased greenhouse gases and global warming. Scientists predict changes in these cycles, but there is great difficulty involved with understanding the bounds of EN's natural fluctuations (Chapin, 1996). Perhaps insight may come from the strongest El Niño events ever recorded in 1982-83 and 1997-98.

These two events greatly affected global communities causing 23,000 human deaths and \$33 billion of damage in 1998 alone (Kerr, 1999). However, these EN events especially affected the Galapagos ecological community (Glynn 1988, Robinson 1985, Valle 1985, Snell and Rae 2006) including possible impacts to the growing eco-tourism based human population of the islands. The Galapagos archipelago, located 600 miles off the coast of Ecuador, is situated at the convergence of many currents, consequently subjecting the islands to a complex dynamic of cooler, more productive environments than other tropical regions (Vinueza et al., 2006). During normal years, areas of the islands experience upwelling of nutrient rich waters due to a shallow layer of warm water, called a thermocline, which is easily penetrated by deeper, cooler currents. Upwelling is a process induced by winds that cause warm waters on the surface to move off-shore, consequently pulling deep cold waters to the coastal surface. Under these conditions and in the drier La Niña events, marine life thrives (Snell and Rae, 2006). El

Niño conditions increase SST, deepen the thermocline thereby impeding upwelling events and nutrient inputs, and increase precipitation, run-off, and thermal extremes, all negatively affecting marine life. Conversely, terrestrial life thrives in the wetter seasons of El Niño because the rains increase productivity in the arid regions (Vinueza, 2007 personal communication, Snell and Rae, 2006, Barret, 2007). This strong dichotomy between marine and terrestrial life was not seen during the harsh conditions of the 1982-83 and 1997-98 El Niño events.

During these El Niños (hereafter EN) both marine and terrestrial species suffered greater mortality and lowered success (Snell and Rae, 2000). For marine species, warmer conditions have killed 95% of Galapagan coral reefs and the Galapagos Damsel fish (*Azurina eupalama*) has gone extinct (Barrett, 2007). Local fur seal populations declined due to disease and food shortages. More than 30% of the female population and non-territorial males died, while mortality for territorial male seals was nearly 100%. The four youngest year classes were also lost, reducing the population's chance for recovery (Trillmich and Limberger, 1985). Food shortages affected 18 sea bird populations resulting in the complete loss of reproductive success that year (Glynn, 1988). ("Reproductive success" is the survival of young offspring to reproductive maturity, a major factor for maintaining a population.) Penguin populations have still not recovered from the 1983 event (Snell and Rae, 2006). Marine iguana populations experienced severe starvation, resulting in 60-70% mortality (Laurie and Brown, 1990). All these population declines in higher trophic-level animals were related to declines in food availability directly related to declines in primary productivity, including seaweeds. There appears to be strong effects of thermal-stress and lower nutrients acting on

seaweeds during strong ENs, consequently affecting higher-trophic level animals in the complex Galapagos food web.

Clearly the evidence suggests that compounding effects of global warming and EN events may strongly impact primary productivity in the Galapagos region, but how about more temperate regions that already experience large, seasonal variations? The Pacific Decadal Oscillation (PDO) plays an important role in these seasonal variations of the Pacific Northwest and is tightly related to Niño cycles (Kerr, 1999). With global warming, PDO may be affected as well. The PDO is a shift in the velocity between the California current, that runs southwards along the US west-coast, and the Alaska Current that runs northward towards the Alaskan Gulf. The shift is characterized by wind changes that may be linked to changes in the Great Ocean Conveyor (GOC). The GOC is a globally linked connection between the thermohaline circulation and surface currents (Hixon personal communication, 2007). The thermohaline circulation involves vertical currents that result from temperature and salinity differentials that cause cold, dense waters from the poles to sink to deeper levels and re-circulate towards the equator. Along the way, these currents are linked to surface currents at specific locations resulting in the Great Ocean Conveyor. The GOC is what connects all of the world's oceans and human induced climate change may cause a break down in its cycle (Broecker, 1999). Changes in the GOC could correspond with shifts in the PDO (Bondi et al., 2001). During fast GOC, the PDO enters a cool phase driving a strong California current along the western US coast resulting in upwelling events along the Pacific Northwest. These upwelling events result in large pulses of nutrients, reaching intertidal areas, increasing productivity, and boosting populations throughout the food-web (Bosman, A.L. et al., 1987). During

slow GOCs, the PDO enters a warmer phase and productivity off the NW coast drops resulting in huge ramifications for local salmon populations (Hixon personal communication, 2007). While PDO and EN differ in the regions they directly impact and time scale with which they act, PDO acting on a decadal oscillation in the North East Pacific and EN acting every few years in the tropics, both are interconnected by the GOC. With global warming resulting in warmer SST and overall warmer oceans, the GOC could slow down resulting in a shift to the warmer conditions of PDO. If this happens and the PDO warms resulting in a weaker and warmer California current, strong El Niño events could have more powerful impacts on a larger scale (Fiedler, P.C. 1984, Kerr 1999).

Evidence of thermal stress and grazing in temperate Pacific Northwest

To understand what lessons from the Galapagos could be applied to the Pacific Northwest, we first must understand the roles temperature and grazing play in this temperate region. While the main seaweed of interest in this study was the green seaweed *Ulva* sp., the most dominant species at the experimental site in the Galapagos, I did not restrict the literature review to only experiments investigating *Ulva* because it is not the most preferred food source for many common herbivores in the Pacific Northwest. For example, the common purple sea urchin, *Strongylocentrotus purpuratus*, preferentially feeds on brown seaweeds (Leighton, 1968; Gaines, 1985; Lafferty and Kushner, 2000).

Compared to tropical regions, temperate regions tend to be characterized by higher primary productivity due to complex seasonal changes of light and thermal

stratification (Keiser et al., 2005). Theoretically, complex seasonal changes result in the evolution of eurytolerant species at higher latitudes. This hypothesis is consistent with the pole to tropics species diversity gradient theory that suggests species diversity decreases as distance increases from the tropics. However, Santelices and Marquet (1998) showed that areas of high diversity in temperate regions are characterized by species with small geographic ranges like all highly diverse areas and is consistent with areas of higher primary productivity and upwelling like the Oregon coast. A recent study by Helmuth et al. (2006) also suggested that complex thermal mosaics of temperature can act regionally through areas rather than on simple latitudinal gradients. This study stressed the need to understand species reactions to thermal stress at local levels for predicting impacts of climate change across species range. Therefore studying thermal stress effects on species in temperate regions may also give insight into possible impacts of global warming and climate change.

The temperate region of the Pacific Northwest is characterized by strong vertical zonation with seaweeds dominating the rocky intertidal throughout the year with variable fluctuations between seasons (Schiel, 2004). Due to their latitudinal range this region experiences a wide range of seasonal changes from the cold wet winter months to dry, hot summer days. Seaweeds along the Oregon shores experience a decline in survival during the summer months and a surge of life in winter months. Until Cubit's (1984) study, these observations were believed to be due to thermal stress alone and that grazing acts strongly only when physical conditions are benign. However, Cubit discovered that the decline in seaweed in summer months was due to combined effects of thermal stress and increased rates of grazing by limpets directly affected by variations in the rates of

seaweed production. From this study a new perspective of interactions between rates of herbivory and rates of seaweed production developed. Cubitt concluded that the community structure of the Oregon rocky intertidal is sensitive to changes in annual patterns of physical conditions (influenced by the PDO) and small changes could change the abundance of seaweeds and herbivores. Shortly after Cubitt's study, Menge and Sutherland (1987) proposed a model of community regulation that incorporated the complex patterns of variation in disturbance, competition, and predation to environmental stress and recruitment.

A later study by Dethier et al (2005) showed that for the seaweed *Fucus gardneri*, stress and herbivory acted independently and suggested that effects in changes in the intertidal physical environment and herbivory could be simpler than suggested by Cubitt. Dethier's study showed that stress affected phlorotannins (an important molecule for seaweed which may play an anti-oxidant role) more than growth and herbivory influenced growth and reproduction. She discovered that herbivory strongly affected seaweed growth across all stress gradients. While her study suggests a less complex interaction of grazing and stress effects on seaweed growth, grazing effects being stronger than thermal effects, this may be a reflection of their experimental design since they were unable to manipulate stress and herbivory simultaneously. Their conclusions indicated a need to explore different levels of stress and herbivory. Given the need to understand these effects simultaneously, the experimental design of this study was aimed toward understanding this interaction better.

The experimental design of this study focused on the following questions: First, how does thermal stress affect the seaweed growth in the Galapagos rocky intertidal, then

how are other animals living among the seaweeds affected, and finally, what principles of climate change from the Galapagos can we apply to the Pacific Northwest?

Methods

To determine the roles of temperature and herbivory on seaweed growth, we utilized both field experiments and laboratory analysis. The field work was at two intertidal sites at Tortuga Bay on Santa Cruz Island, Galapagos (0°, 99°W).

Field Experiment

At each site two experimental treatments were established: plates of different color (dark or light) to cause differential thermal stress at low tide and caged or un-caged plates to test the effect of herbivory. Plates were constructed from 15cm x 15cm squares of high density polyethylene (HDPE) with a small 4cm x 4cm clear acrylic plate centered on the colored plates. The acrylic plates were sandblasted to facilitate the settlement of algal spores. We glued ibutton (Maxim #DS1920) temperature loggers inside the colored plate located directly under the acrylic plate. To exclude herbivores, we covered the acrylic on half of the plates with 10cm x 10cm cages constructed of black stainless steel mesh (2cm² holes).

Thirty plates were placed into the low-intertidal at each site in an area mostly dominated by *Ulva* sp. Plates were randomly assigned to five blocks per site, each block included 6 different treatments with 10 replicates each: caged black plates, caged white plates, un-caged black plates, un-caged white plates, caged rocky substratum, un-caged rocky substratum. The rocky intertidal substratum, characterized by dark black lava-rock, acted as a natural control in this experiment. Each replicate set was grouped within meters of the others so as to experience similar environmental conditions including wave

force, nutrients, exposure time, and solar radiation intensity. Effects of wave force, nutrient analysis, and cages are currently being undertaken (L. Vinueza, personal communication).

Plates were deployed in mid November 2006. Temperature loggers in both black and white plates recorded the temperature of the plate every hour of the day throughout the three-month duration. Plates were maintained throughout the experiment by manually removing any growth on the colored plate outside of the designated growth area (i.e., acrylic plate). Cage and plate durability was also checked during this time. Plates were removed in late January 2007 and taken to the lab for analysis.

Lab Analyses

Seaweed growth is defined by Kaiser (2005) as the net balance between energy gains through photosynthesis and energy loss from respiration, nutrient uptake, and reproduction. Because growth can be measured in mass terms, biomass was our measurement of seaweed growth. I measured biomass as dry weight because wet weights are known to vary between seasons (Zemke-White and Ohno, 1999). Biomass was measured after seaweed fronds were manually removed from the plates, strained in water to separate all other organisms and sand particles, and dried in an oven at 61°C for 48 hours. Dry weight was estimated using an electronic precision balance. During manual seaweed extraction, numbers and species of macros-invertebrate animals were also recorded.

Statistical Analysis

Since seaweeds are primary producers, they can be very important for the survival of many organisms at different stages in their life cycle. Seaweeds provide food for

immature and mature animals like iguanas (Rubenstein and Wikelski 2003) and refuge for small animals during juvenile and adult stages (Lilly and Schiel 2006). As such, I explored analyses of organisms found within the seaweeds including: the number of individuals (abundance), species richness, and the Shannon-Wiener Biodiversity Index (H'). The abundance and species richness are both aspects of understanding diversity. Species richness is the total number of different species present in a sample. Through it we can assess what types of animals were affected by temperature and herbivory. Together with the abundance and the biodiversity index H' , which combines species richness and evenness into the calculation, we have a more thorough understanding of how temperature and herbivory impact overall invertebrate biodiversity (evenness is how equally proportioned the abundances of species are).

We used S-Plus statistical software to explore our dependent variables (biomass, species richness) across all factors (sites and experimental treatments). The three factors possibly affecting seaweed biomass in this study included site, herbivory, and plate color (relative thermal stress). Since a three-way ANOVA indicated that site was not a significant factor affecting seaweed biomass ($P = .182$) we ran a 2-way ANOVA across both sites using plate color and herbivory as the independent variables. We used Tukey multiple comparisons to test differences among treatments. The Bonferroni correction was applied to give a new significance level of 0.017. This correction allows for a more conservative analysis of the data. The same process was applied when exploring the effects of factors on species richness, abundance, and Shannon-Wiener (H') diversity.

The difference in hourly temperatures between black and white plates, graphed during low tides of less than 0.4 meters, represents the times when thermal stress was

actively affecting the plates. We assume that tides above 0.4m do not expose the plates. Therefore, there would be no detectable thermal difference between the plates while submerged underwater. The difference in temperature between black and white plates was graphed along a temporal scale starting the hour of low tide and including the temperature difference of the plates for two hours after low tide. Positive values indicated that black plates were warmer than white plates and negative values indicated the opposite. While temperatures were recorded each hour every day, I graphed only the values associated with times of exposure at low tide. S-Plus t-test of difference in mean temperatures between black and white plates was used to assess if one group of plates was warmer than the other.

Results

Plate Temperature

Between November 4, 2006 and January 28, 2007, black plates were usually hotter than white plates (Fig. 1). For example, 77% of all between-plate comparisons recorded black plates as hotter than white plates (Fig. 1A). The time series examining the magnitudes of differences in temperature between black and white plate shows a strong tidal cycle, with black plates ranging up to 13°C hotter than white plates during low tides (Fig. 1B.). On average black plates were 1.45°C warmer than white plates (Fig. 1C; t-test of difference between means, $P = 0.002$).

Seaweed Biomass

There was a trend for biomass to decrease with warmer temperatures for both grazing treatments (Figure 2a). Both grazing and plate color were significant factors affecting seaweed biomass ($P < 0.001$, $P = 0.003$ respectively). Seaweed biomass was less

when herbivores were present than when they were absent ($P < 0.001$). Tukey multiple comparison (Fig. 2b) showed that at a 5% alpha level, white plates contained significantly more biomass than control plots (confidence interval (CI) between: control-whites [-1.430, -0.2844]), black plates and control plots were comparable (CI: b-c [0.213, 0.937]), and a difference between white and black plates although marginal, may suggest that white plates had more biomass than black plates (CI: b-w [-1.070, 0.0778]). A confidence interval that includes zero implies that there is no significant difference between the two groups of interest. Finally, site was not a significant factor affecting biomass in this study ($P > 0.05$).

Number of Individuals (Abundance)

Site and plate color were both significant factors affecting the number of animals per plate ($P < 0.0002$, $P = 0.0004$ respectively). The total number of animals on average for white plates was 0.83 animals per cm^2 (x/cm^2) with as many as $3/\text{cm}^2$ on one plate. For black plates, the average number of individuals was approximately $0.30//\text{cm}^2$ with as many as $1.2/\text{cm}^2$ on one plate. There was an average of $0.2/\text{cm}^2$ found in control plots with, as many as $1.23/\text{cm}^2$ found in one plot. Figure 3a shows that regardless of herbivore treatment, animals were more abundant on white plates compared to black plates and control plots. Tukey comparisons show that the total number of animals/ cm^2 was greater at the second site (Figure 3b) and greatest on white plates. At a 5% alpha level, white plates held more individuals than control plots (CI: c-w[-0.85,-0.113]) and marginally, although not significantly, more than black plates (CI: b-w[-0.638, 0.0988]).

Table 1 shows a list of all the animals found and their corresponding proportions. Of all animals present, amphipods, the mollusk *Collumbela* (Dove shells), Polychaetes

and an un-identified white crustacean persisted throughout the experiment in the highest quantities. Figure 6 shows changes in relative proportions of taxa between black and white plates. Amphipods persisted of the largest group at 35% of all organisms in all plates, 41% in black plates, and 30% in white plates. The unknown white crustacean consisted of 25% of all organisms in all plates, 8% in black plates, and 32% in white plates. There were differences in proportions associated with the unknown crustacean, barnacles, and a much smaller Mollusk (Epitoniidae Family) between black and white plates. The proportion of white crustaceans dropped from 32% in white plates to 8% in black plates while epitoniids and barnacles dropped from 4% each in white plates to 1% each in black plates. Furthermore, some organisms including *Thais melons* (a predatory snail), mollusk Family Nassariidae, mollusk Family Hipponicidae, an unidentified mollusk, a worm, and mollusk eggs were found in white plates, but never in black plates. While proportions of animal taxa shifted, an overall trend for total animal abundance was a decline in numbers from white plates to black plates ($P=0.0102$).

Species Richness

In this study species richness was significantly different between sites ($P<0.002$), grazing treatments ($P<0.0001$), and between plate groups ($P<0.001$). Figure 4a shows a general trend to associate caged treatments and white plates with higher species richness. Tukey comparisons (Figures 4b, 4c) show that at a 5% alpha level, site 2 had more species than site 1 ($P<0.002$). White plates held more species than both control and black plates (CI: c-w[-6.77, -2.13], b-w[-5.27, -0.634]). There was no difference in richness between black plates and control plots (CI: b-c [-0.816, 3.820]), even though black plates

had greater mean animal abundance in caged plots. Overall there is a general trend to see higher species richness in caged treatments, on white plates, and at the second site.

Composite Species Diversity

Grazing ($P < 0.0001$) and plate color ($P = 0.0102$) were both important factors affecting composite species diversity (H') in this experiment, while site was not ($P = 0.456$). The general trend of higher diversity among the white plates can be observed in Figure 5a, although the trend is not as strong among plates that experienced intense grazing. Across all grazing treatments, white plates supported greater invertebrate diversity than control plots (CI: c-w [-0.85, -0.113]) and marginally greater biodiversity than black plates (CI: b-w [-0.638, 0.0988]). On average white plates showed $H' = 1.2448$, black plates showed $H' = 0.9754$, and control plots showed $H' = 0.76329$. The lack of a difference in H' between black and white plates experiencing intense grazing could indicate that the loss of seaweed biomass from grazing may be more significant factor affecting diversity than thermal stress alone at this time (white plates $H' = 0.83154$, black plate $H' = 0.8741$).

Discussion

Although the El Niño (EN) we expected to occur during this experiment did not fully manifest, the conditions of the experimental sites still experienced warmer conditions that reflect mild EN fluctuations. Oceanic Niño Index (ONI) data from NOAA's Climate Prediction Center recorded warmer conditions during the time of the experiment which generally occur during EN patterns. However, ocean-atmospheric conditions did not result in the expected EN. Even so, conditions were still warm and

allow us to use this study as a reflection of ways in which future climate change could affect local ecosystems.

The field experiment demonstrated that both thermal stress and grazing play important roles on seaweed growth, consequently affecting other animals in the Galapagos rocky intertidal. Thermal stress reduced seaweed standing-crop between warmer black and cooler white plates, as well as between white and control plates. Black plate and control plot biomass were most similar, probably because they were about the same color and so absorbed about the same amount of solar heat. Therefore any difference between black-white and white-control comparisons may reflect the plates acting as artifacts of the experimental design. This could mean that herbivores prefer a natural substratum compared to plate cover and therefore the biomass of seaweed would be less in control plots than black plates, even though they are both black and we assume experienced similar temperatures. If this is the case, the degree of lava rock preference would have to be considered in future studies. Less biomass in control plots than black plates could also reflect difficulty in removing all of the seaweed biomass from control plots in the field than from the plates in the laboratory.

The trend of reduced biomass in black plates across both grazing treatments is consistent with an aspect of Dethier's (2005) study in Washington, USA, which found that grazing slowed seaweed growth and that stressed seaweeds tended to grow slower than unstressed seaweed, although not significantly. However the effects of temperature and grazing acting simultaneously in this study, which Dethier was unable to explore, suggests that interactions between the two can impact seaweed growth to a greater degree than she suggested. For example, the mean biomass on black plates exposed to grazing

was less than that on black plates without grazing, indicating that grazing and temperature when acting together can reduce seaweed growth. The lack of an interaction between thermal stress and grazing in Dethier's study could be a reflection of the short 3-month duration of the project and the lack of simultaneously manipulating grazing and thermal stress effects. Although this study was also short in its duration, we were able to see effects of grazing and thermal stress acting on the same subjects over a short period of time. This study is also part of a longer term dissertation of Luis Vinueza, who has been working at this site for many years. His future publications will clarify the long-term impacts of this study.

The parallel effects of grazing and thermal stress from this study deepen our understanding of Vinueza's (2006) five-year study on the interaction between top-down and bottom-up effects. He found that the effects of grazers varied through three distinct phases: during El Niño, in the late stages of El Niño, and in stable normal conditions. These responses implied that during low productivity, seaweeds are limited by physicochemical conditions and algal diversity can not benefit from grazing (whereas some previous studies had shown grazing could increase diversity). El Niño conditions reduce upwelling, limit nutrient availability, cause a bottom-up effect and reduce seaweed abundance, negatively impacting consumers. This effect was also documented in marine iguana studies by Laurie and Brown (1990) and Rubenstein and Wikelski (2003), where mortality rates were directly related to the lack of preferred seaweed availability during El Niño events. When normal conditions returned, grazing effects on seaweeds increased. Our study shows that thermal-stress acts strongly with or without grazers during even mild El Niño conditions. With a decline in abundance from

desiccation, grazers will feed heavily on what remains of *Ulva*, resulting in an increased loss of biomass. The removal of biomass could also reduce habitat and increase thermal stress for smaller animals that live among the *Ulva* sp. canopy.

Our results show a trend associated with seaweed loss that resulted in a decline in species abundance and diversity of invertebrates. Grazing, thermal stress, and, although unexpected, site influenced invertebrate abundance and species richness. The total number of individual animals, species richness, and diversity all declined in black or control plates compared to white plates for both grazing treatments. This trend indicates that warmer conditions reduce seaweed biomass and the ability for animals to survive in the remaining crop. It is unclear whether this result reflects thermal intolerance of groups or a response to habitat loss. Both factors could be important.

Some species were never found on black plates. These species included *T. melons*, whelks of the Family Nassariidae, another gastropod of the Family Hipponicidae, an unidentified mollusk, and mollusk eggs. These animals may be particularly susceptible to thermal stress because they were never found on black plates, although other factors like plate color, texture, and the mobility of animals affected by stress could also be important. Fluctuating proportions of the abundance of other animals such as the amphipods, white crustaceans, and other mollusks, may reflect different factors, including habitat loss, spatial competition, or predator-prey interactions. One possibility is that a reduction in the abundance of some animals might have opened more space for more tolerant species, such as amphipods that were found folded inside a mucus-like sack inside seaweed fronds. Further manipulations of different factors in isolation could

provide a better idea of the potential roles these factors may have on the patterns observed in our study.

Overall, animal abundance and species richness were greatest in white plates and lowest in black plates and control plots alike, even though the latter was somewhat marginal for species richness. This marginality in richness between black and control plots could be due to the fact that collecting animals from control plots was more difficult and fast mobile animals like crabs could have easily escaped during seaweed removal. Similarly, because control plots were situated on the lava-rock substratum, the possibility of greater spatial dimensions for the animals to hide in during collection may have influenced this result (i.e., cracks, rock burrows, etc.).

Differences in species richness and abundance between site 1 and site 2 were unexpected, although possible factors causing these differences did not appear to affect seaweed biomass during this study. The number of animals per plate and species richness was greater at the second site. Densities of grazers appeared to be greater at the first site than the second site (personal observation). With more grazers, I would speculate that site 1 would have spottier seaweed cover although this was not measured directly. Site 2 was slightly rockier than site 1, which may also provide more spatial complexity for various species to inhabit. Site 2 was lower in the intertidal which could result in less exposure time and greater productivity. While factors influencing animal abundance between sites may also include variations in competition, predation, wave force, and nutrients, we should not underestimate the impacts of human interactions. Site 1 was much closer to a nature trail while site 2 was not directly visible and/or accessible from any trail. Human disturbance may be a factor causing between-site differences,

although this was not measured in this study and future studies should investigate this factor more.

Even though differences between sites existed for invertebrate abundance and species richness, site was not a factor affecting overall animal diversity (H'). Grazing and plate color both affected diversity. For all grazing treatments, white plates showed the highest H' values than did both black plates and natural plots. Although I could not identify to the species level for all organisms, each organism was placed into some taxonomical grouping, sometimes as high as phylum. While this calculation of biodiversity is not as rigorous as it could be if identification was to the species level, in context with richness and animal abundance it can help show that animals at all sizes are affected by the direct or indirect effects of thermal stress.

The deleterious effects of thermal stress most likely occur during the extreme temperatures at low tide (e.g., when black plates recorded temperatures that were 13 °C warmer than white plates). At these times, photosynthesis is greatly limited by temperature (Mann, 1973). As a result, seaweeds produce less food storage for themselves and lose biomass. This implies that warmer, longer ENs could have more dramatic effects and recovering from these events will be more and more difficult when communities experience them in closer successions. To generate more accurate predictions, future studies should investigate the influence of differences between sites such as nutrients, wave force, biotic interactions, temperatures at the organism's level (as in Helmuth's 2006 study), the resilience response of organisms over longer time periods, and the effects of extreme temperatures at low tide.

Broader implications of this study

The results of this study are consistent with previous work demonstrating the importance of bottom-up effects during El Niño events (Menge, 2000; Vinuela et al., 2006; Snell and Rea, 1999; Rubenstein and Wikelski, 2003). With global warming expected to magnify the severity of El Niño, thereby reducing productivity, understanding the impacts will allow us to expect, if not prepare for, events like 1982-83 and 1997-98. If we are using the Galapagos as a laboratory for studying climate change, similar results may be expected in the temperate Northwest of the United States if the PDO falls into a longer warm phase. Although analyzing seaweeds along the Pacific Northwest is more complex, a study by Dayton (1999) showed that areas of the kelp beds were changed after the El Niño cycle. For the US coast Helmuth et al.'s (2006) study on the mosaic patterns of thermal stress showed that mussel body temperatures can be associated with areas that are hotter or colder than expected for their latitude. This signified that areas within regions along the west coast can experience unexpected "hot spots" or "cold spots" that could result in localized extinctions during thermal anomalies. Although Helmuth's study was conducted on mussels, similar results could be expected for other intertidal organisms, including seaweeds. Local extinctions could be expected in both the Galapagos and Pacific Northwest. For the most adequate comparison between the two regions, we would need to conduct this experiment in the Pacific Northwest.

A large list of studies and literature on predictions, impacts, and consequences of climate change is continually growing and developing in complexity because of the significant relevance to declining biodiversity and impacts to human society (Chapin 2000, Scavia et al., Thompson et al. 2002, Winder and Schindler 2004, Schiel et al. 2004,

Helmuth et al. 2006, MEA 2005, Harley et al. 2006 to name only a few). These studies all connect biodiversity loss and human activities that are leading to the Earth's 6th mass-extinction. While I think it is important to concretely understand ecological losses we will experience in the next generation, and of which I will briefly describe, it is worth mentioning the importance of a cyclic relationship between human development, in this case the Galapagos, and climate change that permeates all societies, albeit in different ways, and of which we have the capacity to improve. Our activities will determine this relationship.

Human activities have undoubtedly altered earth's ecosystems (IPCC, 2001; ESA, 2005). Ecosystem changes are impacting biodiversity and ecosystem functioning upon which our global civilization depends (IPCC 2001, MEA 2005, ESA 2005). Ecosystem functioning includes the inherent properties, goods, and services that an ecosystem offers. Properties are the natural materials (e.g., carbon) and processes (e.g., energy flow) within a system. The goods are marketable properties (food, raw materials) and services are those that directly or indirectly benefit human activities (ESA 2005, MEA 2005 are good sources for more information). Coastal marine ecosystems alone are estimated to provide \$14 trillion of goods (raw materials and food) and services per year. That is 43% of the global economy (Costanza et al. 1997, Harley et al. 2006). Clearly we heavily rely on our coastal ecosystems yet at the same time our unsustainable practices are resulting in their demise.

Pollution, water declines, habitat loss, and spread of invasive species all reflect how human activities cause or magnify this demise. Chapin's (2000) paper on the consequences of changes in biodiversity summarizes activities that are contributing to

species loss and the ramification this has for ecosystems and human society. He shows that our fossil fuel consumption and increased indiscriminant travel, both of which contribute to global warming and spread of invasive species, are causing global-scale changes affecting ecosystem functioning.

The Ecological Society of America's (ESA) annual committee report adapted a diagram from Chapin's paper clearly defining the links between human activities, global change, and ecosystem functioning (refer to Figure 7). The diagram reflects a natural feedback system that relays information from one group to others that eventually affects all groups. This study predicts changes in seaweed growth with warmer El Niño conditions and reflects one part of this feedback system.

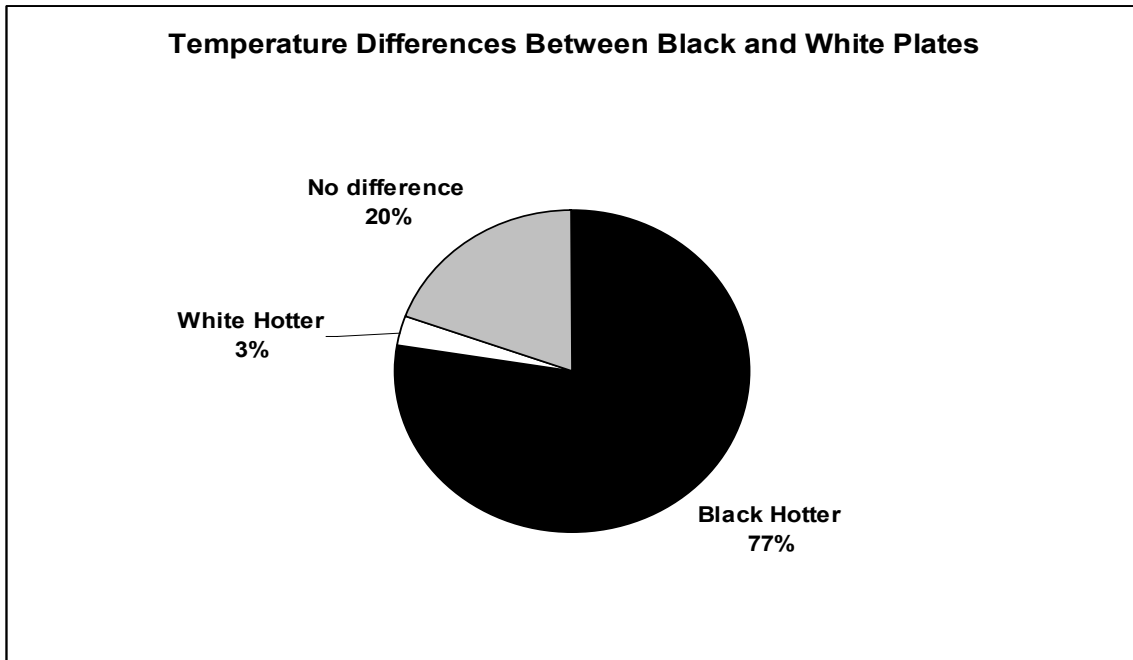
The context of this study in the cycle goes something like this: First, increased burning of fossil fuels has resulted in increased global warming (IPCC, 2005). Global warming will cause many alterations to the abiotic environment, including increased sea surface temperatures, raised water levels, and warmer conditions. Increases in SST can affect abiotic controls like El Niño. Stronger ENs will change the properties and biotic communities of an ecosystem through bottom-up effects like those seen in this study and confirmed in others (previously listed). Changes in ecosystem properties will affect ecosystem goods and services. In the Galapagos, which is heavily reliant on its ecosystem-based tourist trade, declines in primary productivity will directly affect the most charismatic animals that bring in the lucrative tourists. The cycle starts with unsustainable human activities and ends by negatively impacting human endeavors. Areas that experience upwelling events, here both the Galapagos and Pacific Northwest, could see drastic changes in ecological communities with climate change.

This cycle from Chapin and ESA is clearly reflected in the cycle of human development and growth for the Galapagos proposed by the Charles Darwin Foundation's (CDF) "Socio-economic Analysis of the Situation in the Archipelago" (2007). The report states that the current development in the Galapagos, based on a "frontier mentality", is following an unsustainable cycle that screams impending crisis if things do not change. The last 15 years reflect this attitude through drastic economic, cultural, and ecological changes caused by economic growth driven by the lucrative tourist trade. The Gross Income in the Galapagos has increased by 14% each year due to a rise in the number of visitors from 40,000 in 1990 to more than 145,000 people in 2006. Tourism brings in US\$418 million dollars. Yet only \$63 million enters the local economy. The presence of multi-national corporations raise the standard of living making the Galapagos look more and more attractive to both national and international travelers, investors, and immigrants. This all contributes to increasing the population and demands for natural resources. With most of the money leaving the islands, there are not sufficient funds to provide services needed to sustain a human population negatively impacting both humans and local diversity through forcing harmful practices like illegal fishing and increased pollution to persist.

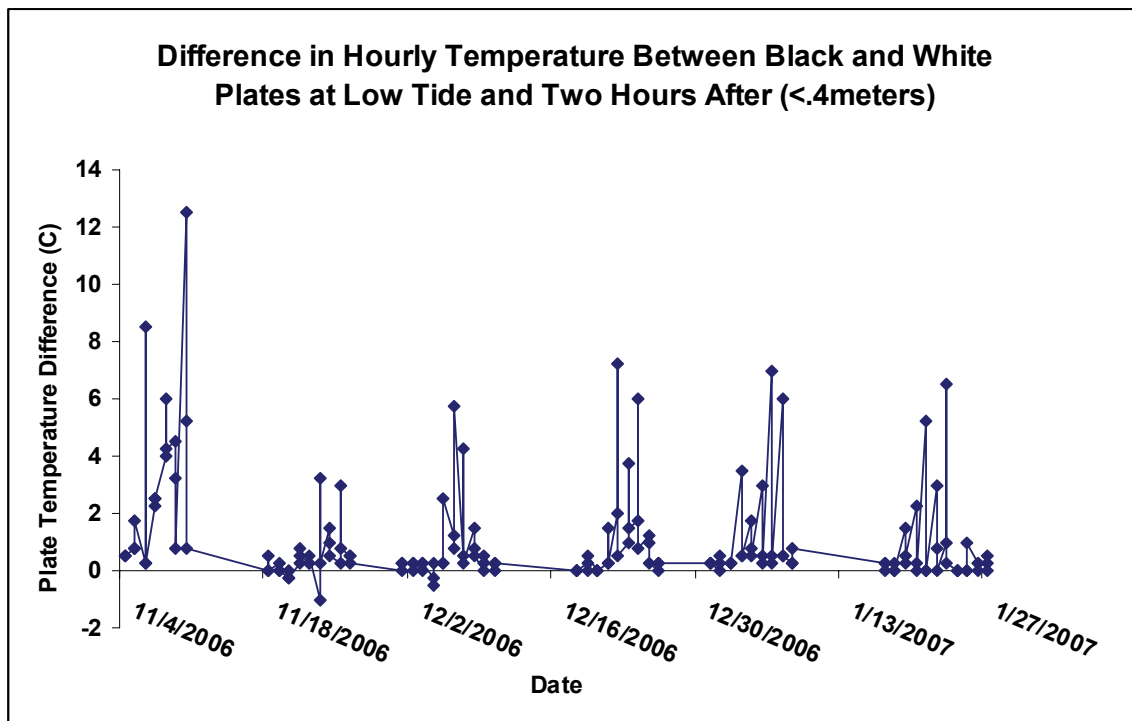
Incorporating the implications of this study with the two models of Chapin and CDF we can see a more complete picture of how climate change will affect an ecosystem, in this case the Galapagos Islands. Bottom-up effects reducing primary productivity could possibly affect the tourist trade in the Galapagos and the people living there. Biodiversity loss, caused by human activities and occurring during changes in EN, will directly and indirectly harm the developing Galapagos society.

The situation in the Galapagos is cause for great concern both economically and ethically. The islands are the last oceanic archipelago that still retains 95% of its original biodiversity (29% are endemic as compared to 13% in Hawai'i [Garske, 2002]) and which has had substantial impact on science and philosophy since Darwin. Biodiversity is the economic basis of these islands and a source of pride to both Ecuador and the world. UNESCO and the World Conservation Union (aka International Union for the Conservation of Nature) have declared the Galapagos as one of the World Heritage Sites in danger. Even the President of Ecuador has declared the islands at risk and of national priority. Eco-tourism is a valuable trade and a strong proponent in well-implemented areas for conservation of biodiversity. However, poorly implemented eco-tourism, as seen in the Galapagos can be harmful. Should we fail to develop a sustainable cycle of growth in the microcosm of the islands in Galapagos, what does this suggest for a global society? The social development along the United State's West Coast is not exactly the same as in the Galapagos, but the principles of Chapin's diagram apply everywhere and point toward solutions based on changes in human behavior. Although changes in human behavior are difficult to achieve regardless of culture, a change is possible and necessary in order for future global generations, both human and ecological, to survive.

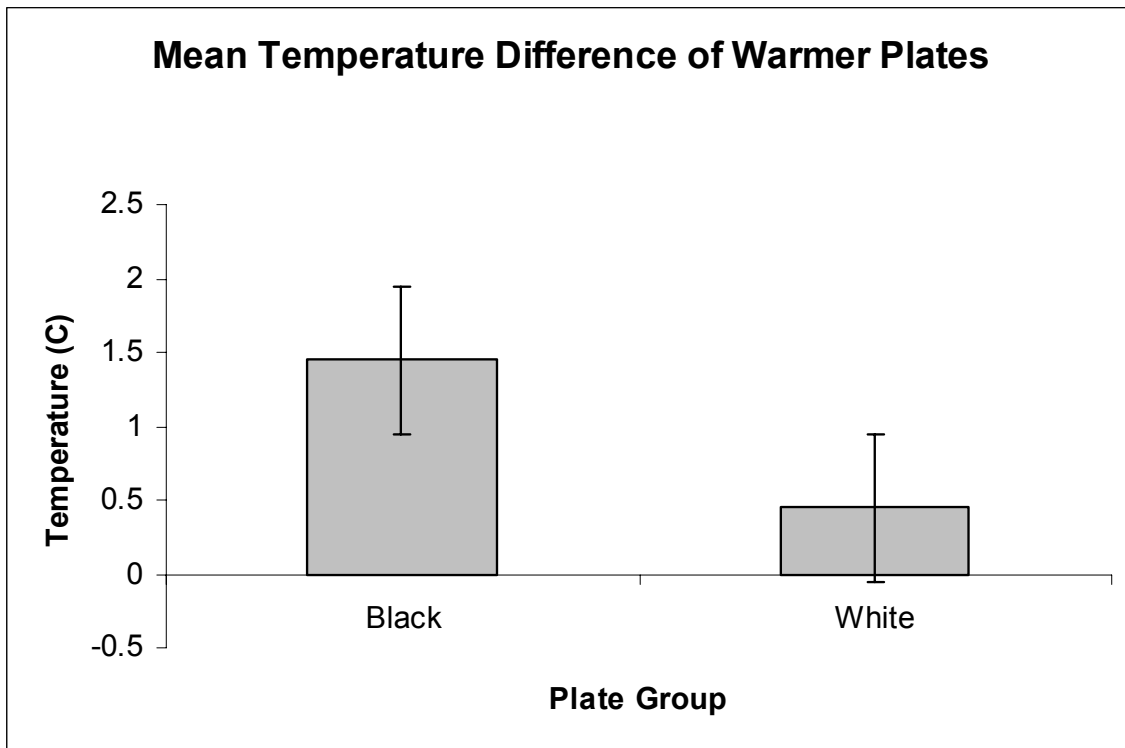
Figure 1



- A. Proportions of plate groups that recorded warmer temperatures. No difference indicates the proportion of plates that did not register any temperature differences.

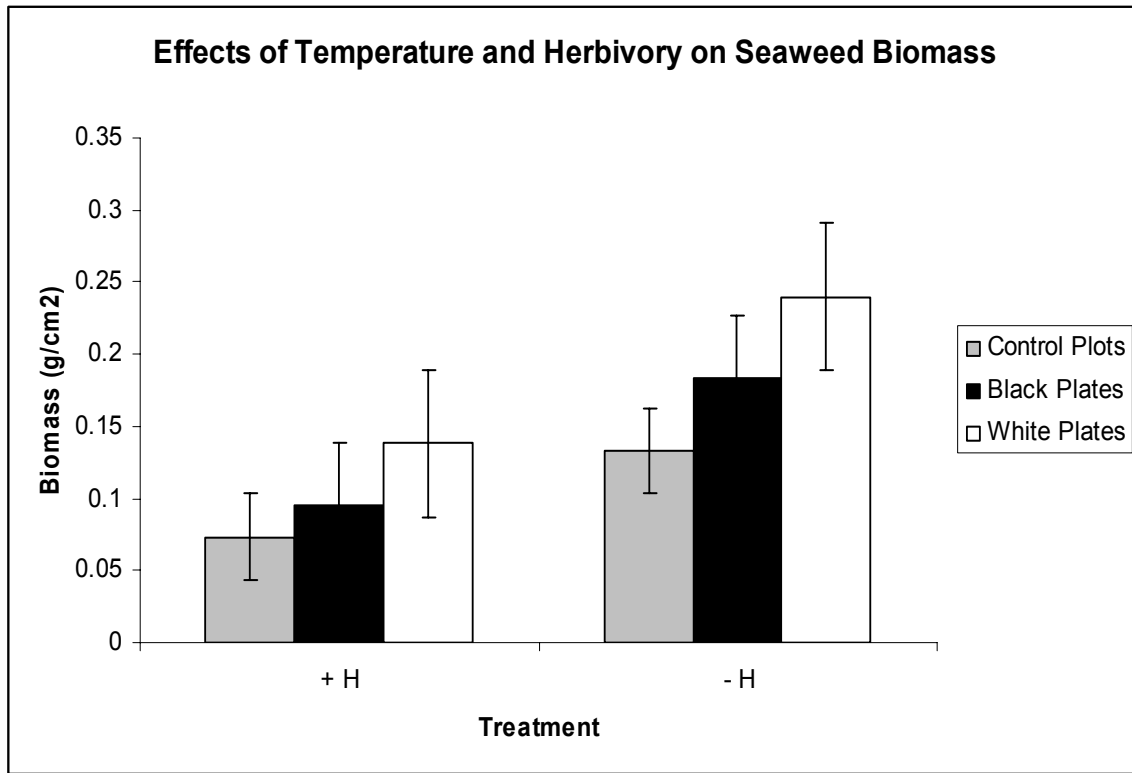


- B. Difference in temperatures between plate groups during low tide and two hours after. Positive values dictate when black plates were warmer and negative values indicate white plates were warmer.

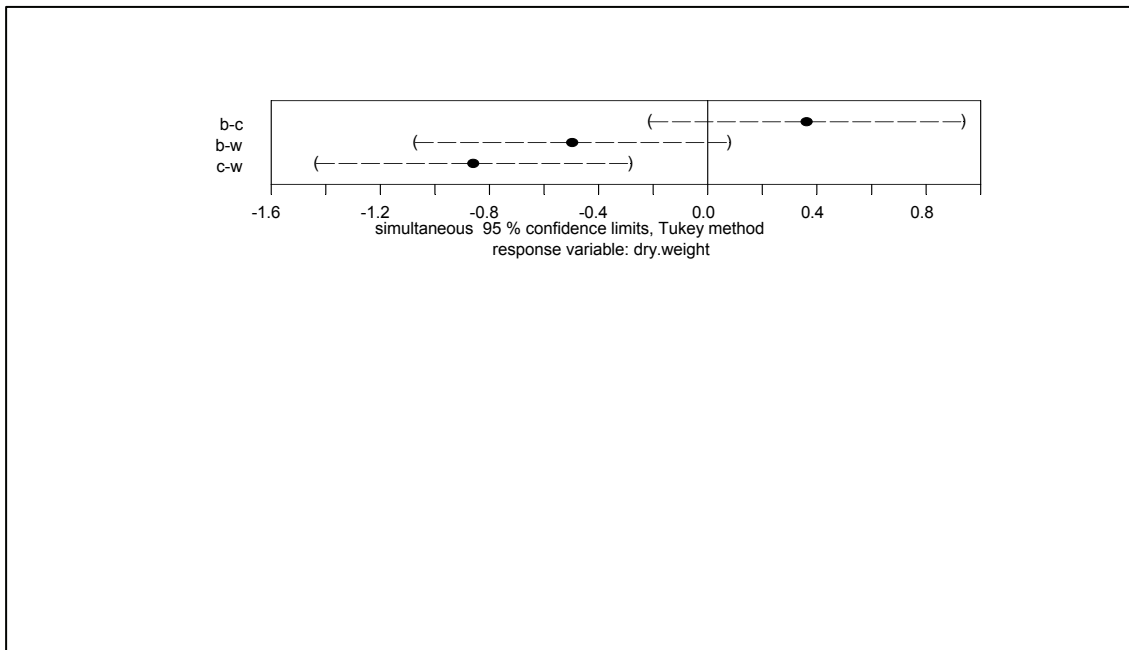


C. When warmer, black plates were warmer on average by 1.45 °C. When warmer, white plates were warmer by 0.44°C.

Figure 2

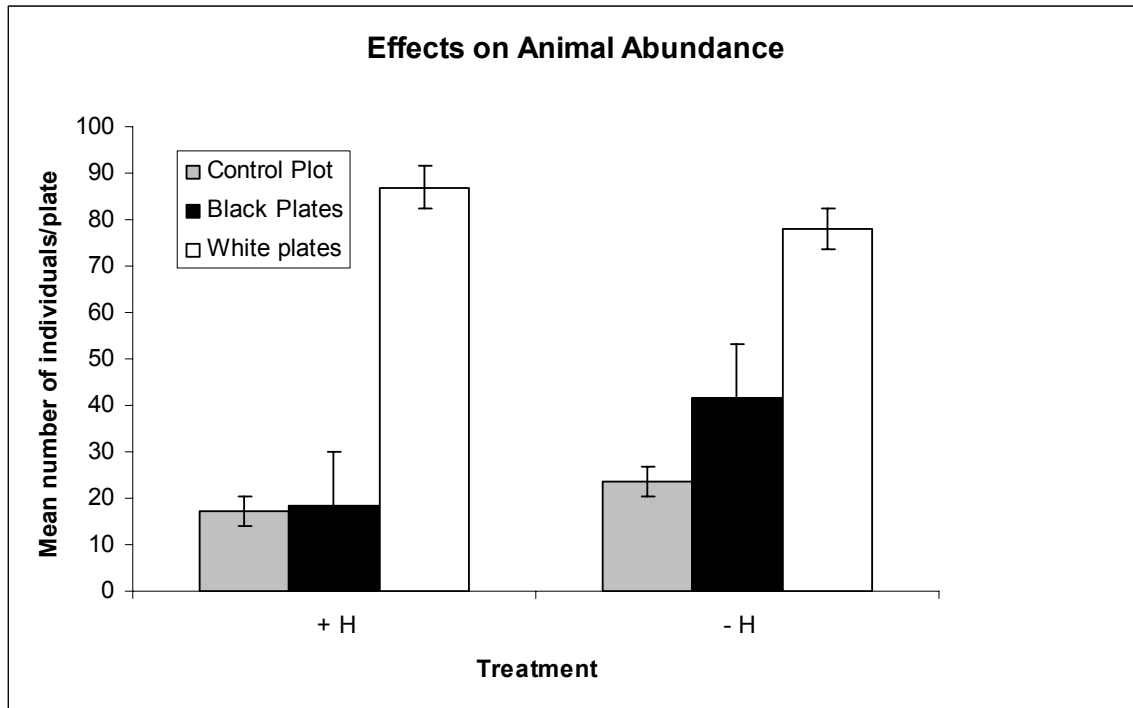


A. Effects of temperature (plate color) and herbivore presence (+H) or absence (-H) on algal biomass.

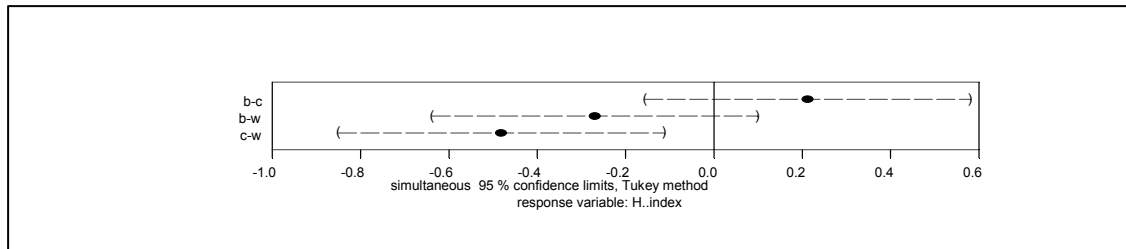


B. Tukey multiple comparison to determine differences between groups (b=black plates, w= white plates, c=natural substratum). White plates held more biomass.

Figure 3

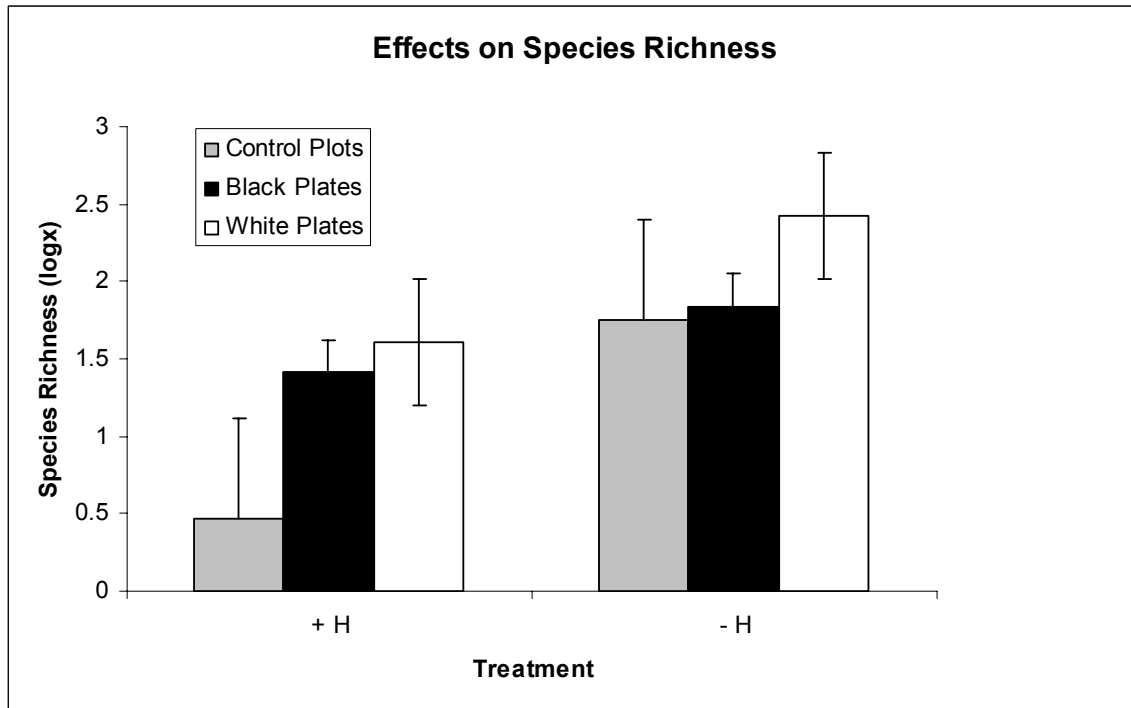


A. Effects of temperature (plate color) and herbivore presence (+H) or absence (-H) on invertebrate abundance. White plates had significantly more abundance than black and control plates across both grazing treatments.

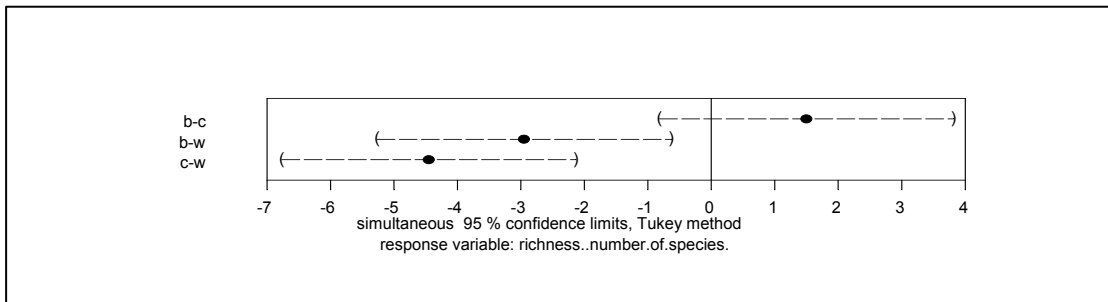


B. Tukey multiple comparison to determine the difference between plate groups (b= black plates, w= white plates, c= natural substratum).

Figure 4

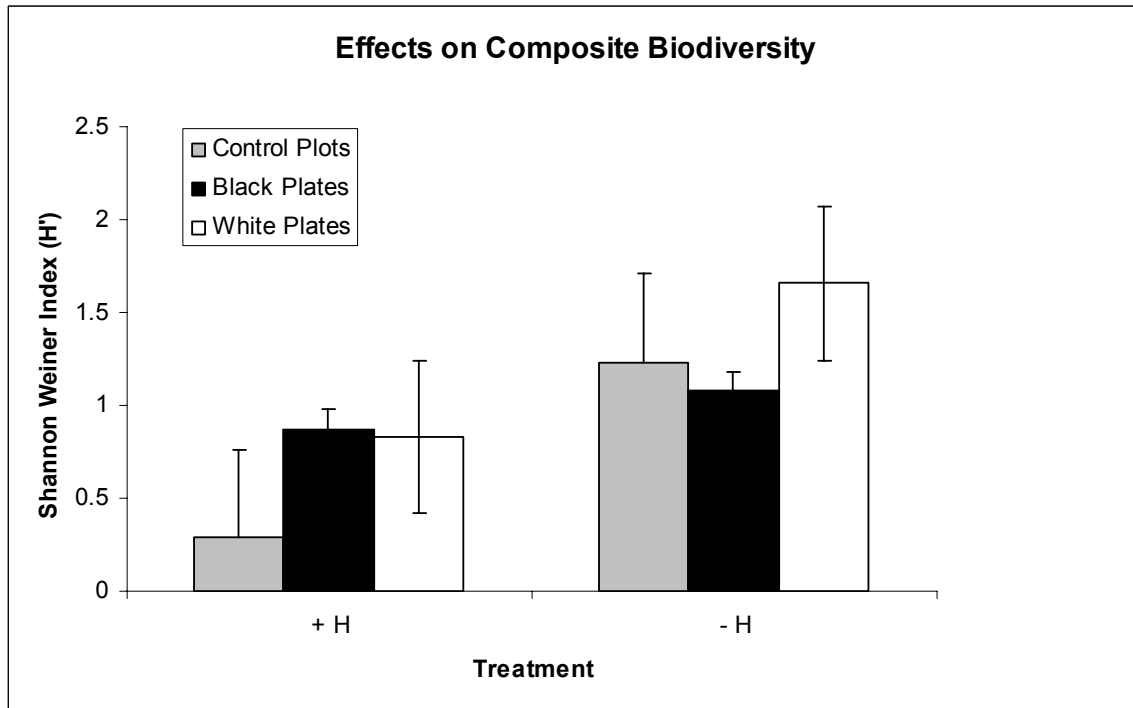


A. Effects of temperature (plate color) and herbivore presence (+H) and absence (-H) on invertebrate species richness.

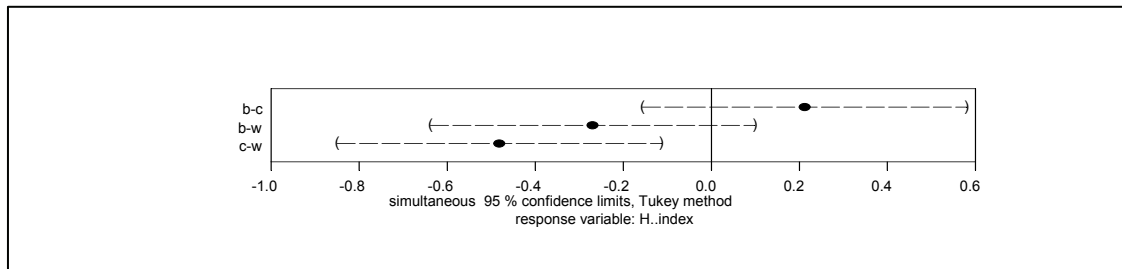


B. Tukey multiple comparison to determine differences between plate groups (b= black plates, w= white plates, c= control substratum plates). White plates had more invertebrate species richness than both black and control plates.

Figure 5

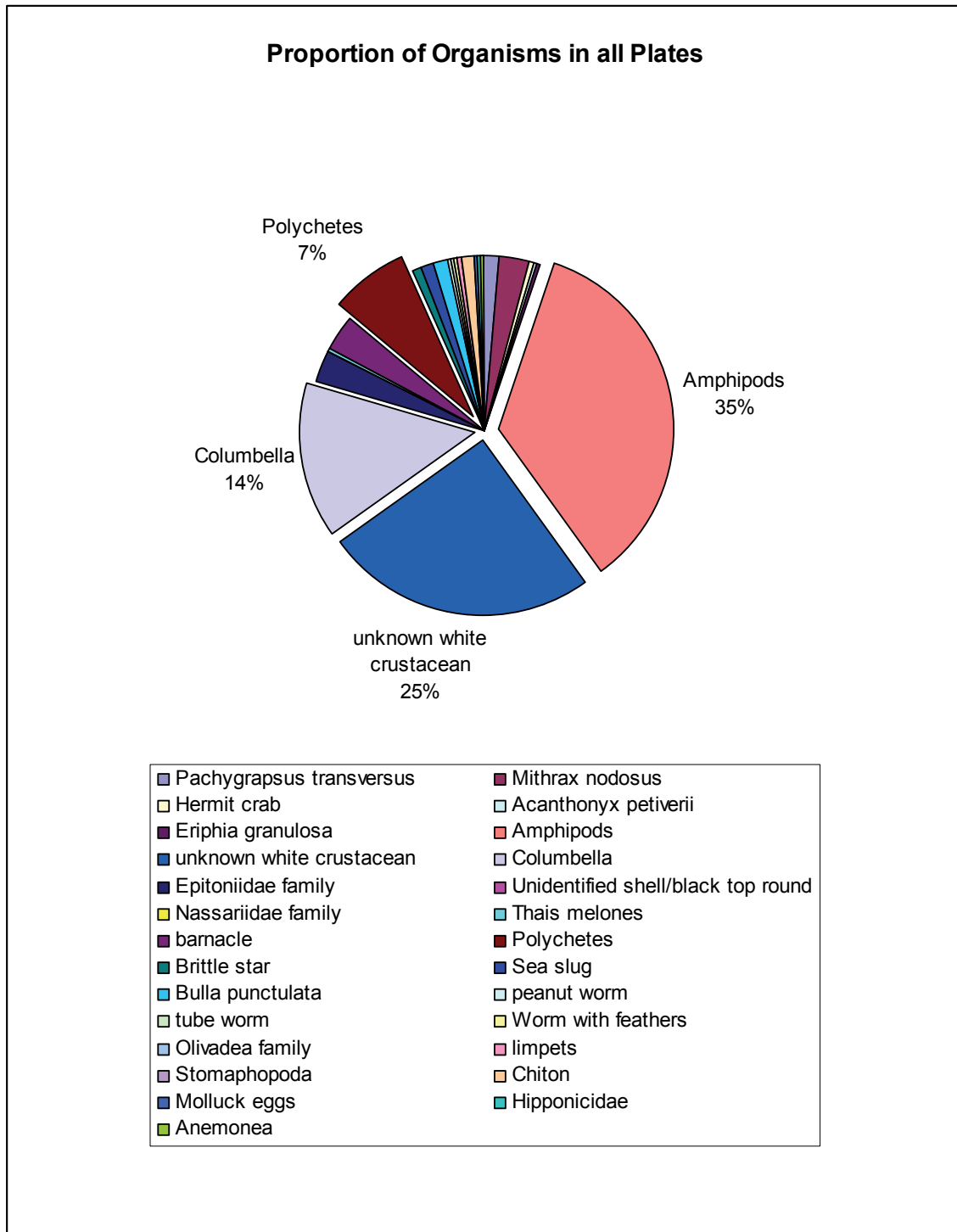


A. Effects of temperature (plate color) and herbivore presence (+H) or absence (-H) on invertebrate composite diversity.

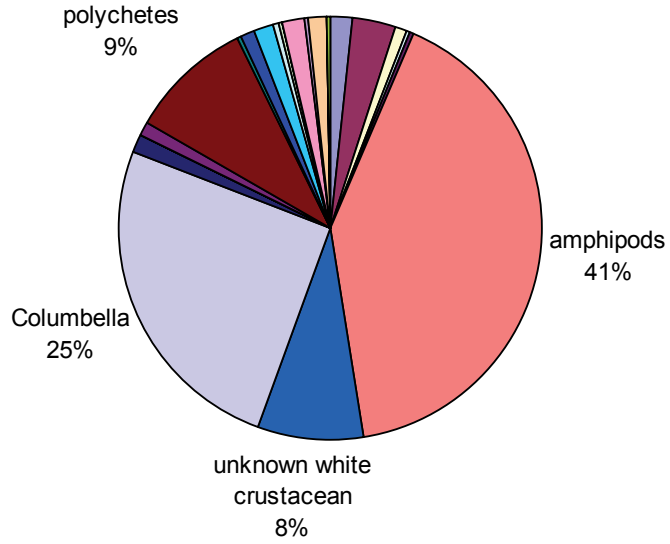


B. Tukey multiple comparisons to determine differences between plate groups (b=black plates, w= white plates, c= natural substratum). White plates had more biodiversity than control plots.

Figure 6

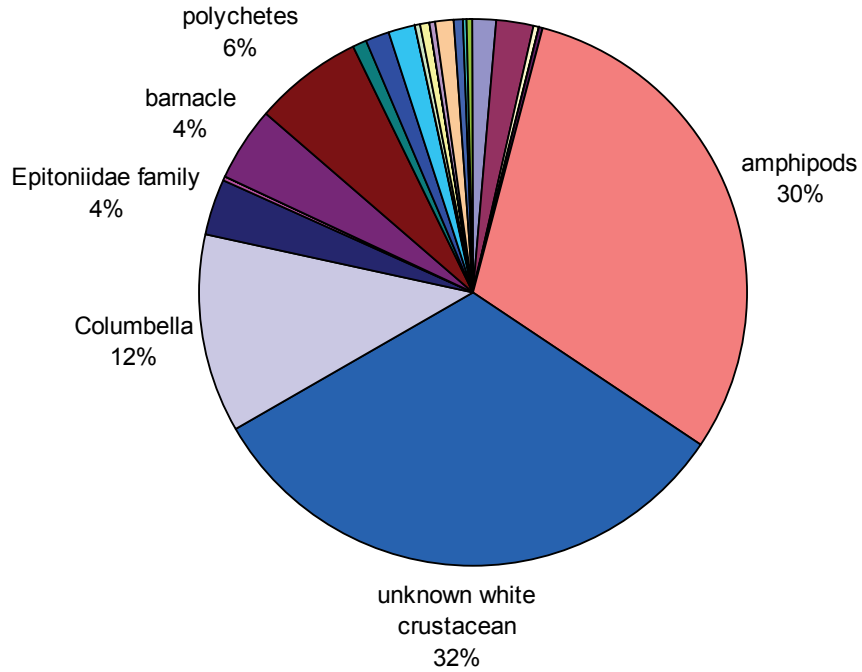


Proportions of Organisms in Black Plates



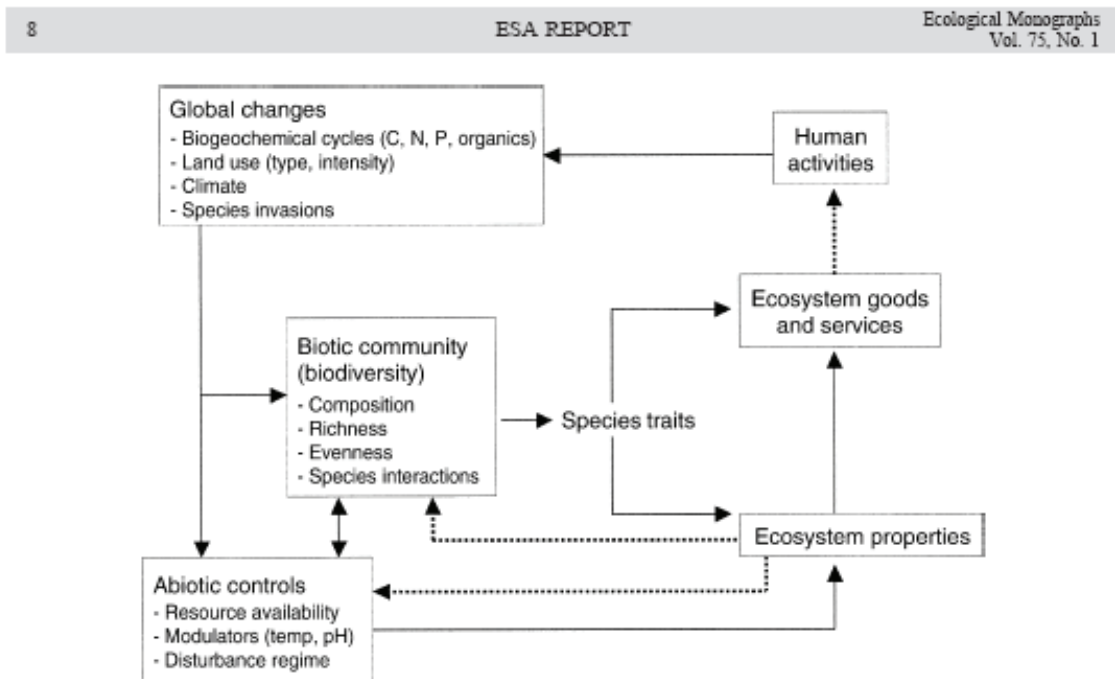
- | | |
|----------------------------|--------------------------------------|
| ■ Pachygrapsus transversus | ■ Mithrax nodosus |
| ■ Hermit crab | ■ Acanthonyx petiverii |
| ■ Eriphia granulosa | ■ amphipods |
| ■ unknown white crustacean | ■ Columbella |
| ■ Epitoniidae family | ■ Unidentified shell/black top round |
| ■ Nassariidae family | ■ Thais melones |
| ■ barnacle | ■ polychetes |
| ■ brittle star | ■ sea slug |
| ■ Bulla punctulata | ■ peanut worm |
| ■ tube worm | ■ worm w/long feathery appendages |
| ■ Olivadea family | ■ limpets |
| ■ Stomaphopoda | ■ Chiton |
| ■ Mollusk eggs | ■ Hipponicidae |
| ■ Anemonea | |

Proportions of Organisms in White Plates



- | | |
|----------------------------|--------------------------------------|
| ■ Pachygrapsus transversus | ■ Mithrax nodosus |
| ■ Hermit crab | ■ Acanthonyx petiverii |
| ■ Eriphia granulosa | ■ amphipods |
| ■ unknown white crustacean | ■ Columbella |
| ■ Epitoniidae family | ■ Unidentified shell/black top round |
| ■ Nassariidae family | ■ Thais melones |
| ■ barnacle | ■ polychetes |
| ■ brittle star | ■ sea slug |
| ■ Bulla punctulata | ■ peanut worm |
| ■ tube worm | ■ worm w/long feathery appendages |
| ■ Olivadea family | ■ limpets |
| ■ Stomaphopoda | ■ Chiton |
| ■ Mollusk eggs | ■ Hipponicidae |
| ■ Anemonea | |

Figure 7



ESA Report: “Feedback between human activities, global changes, and biotic and abiotic controls on ecosystem properties.” (adapted from Chapin et al., 2000)

Table 1. List of animals and corresponding proportions between plate groups

Organism	Black	White	Total proportion
<i>Pachygrapsus transversus</i>	0.016639	0.014537	0.013904547
<i>Mithrax nodosus</i>	0.033278	0.020594	0.02893649
Hermit Crab	0.008319	0.00424	0.004885381
<i>Acanthonyx petiverii</i>	0.001664	0.000606	0.001503194
<i>Eriphia granulosa</i>	0.004992	0.000606	0.00263059
Amphipods	0.409318	0.304058	0.349492672
unknown white crustacean	0.081531	0.321018	0.24990605
<i>Columbella</i>	0.251248	0.116899	0.142803457
Family Epitoniidae	0.014975	0.03513	0.03156708
unidentified shell/black top round	0	0.000606	0.000375799
Family Nassariidae	0	0.000606	0.000375799
<i>Thais melones</i>	0	0.001211	0.00263059
Barnacle	0.011647	0.044821	0.030815483
Polychaetes	0.094842	0.062386	0.072904923
Brittle Star	0.003328	0.009691	0.008267569
Sea Slug	0.009983	0.013931	0.012777151
<i>Bulla punctulata</i>	0.013311	0.015142	0.012401353
Peanut Worm	0.004992	0.000606	0.00263059
Tube Worm	0.003328	0.003634	0.003006389
worm w/long feathery appendages	0	0.005451	0.003382187
Olivadea	0.001664	0	0.000375799
Limpets	0.016639	0.000606	0.004133784
Stomaphopoda	0.001664	0.001817	0.001503194
Chiton	0.014975	0.010297	0.010898159
Mollusk Eggs	0	0.004846	0.003006389
Family Hipponicidae	0	0.003028	0.001878993
Anemonea	0.001664	0.003634	0.003006389

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