EFFECTS OF SPATIOTEMPORAL TEMPERATURE VARIATION ON BENTHIC
COMMUNITY DYNAMICS IN THE GALAPAGOS ISLANDS

Lindsey Anne Carr

A dissertation submitted to the faculty at the University of North Carolina at Chapel Hill in
partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department
of Biology.

Chapel Hill
2016

Approved by:

John F Bruno

James Umbanhowar

Robert Peet

F Joel Fodrie

Jon Witman

ABSTRACT

Lindsey Anne Carr: Effects of spatiotemporal variation on benthic community dynamics in the
Galapagos Islands
(Under the direction of John F Bruno)

Temperature can affect population and community level processes, via strong and
predictable effects on individual metabolism. Metabolic Scaling Theory (MST) 1) describes
how individual metabolic rates scale with temperature, and 2) generates mechanistic predictions
based on how this response to temperature variation will drive ecological pattern and process.
For example, temperature can influence trophic interactions via differential metabolic scaling of
predator and prey metabolic rates. More specifically, metabolic theory and experiments indicate
warmer temperatures can increase the top-down effects of herbivores on plant biomass, resulting
in depleted standing plant biomass. Yet there are few studies that have tested metabolic scaling
theory in the ocean across natural, *in situ*, environmental gradients.

The Galapagos Islands is the ideal system for testing metabolic scaling theory *in situ*
because the Archipelago is at the center of several different oceanographic currents (tropical,
subtropical and upwelled water), resulting in enormous variation in water temperature (11°C -
31°C). Upwelling is the wind-driven process of cold, nutrient-rich subsurface water replacing
warm, nutrient-poor surface water. Also, even though community composition differs across the
Archipelago due to oceanographic conditions, there is a suite of organisms that are present across
the Islands throughout the year.

For my doctoral dissertation research, I quantified benthic community patterns across the Islands and related community composition and biomass to temperature. I also tested metabolic scaling theory in the Galapagos Islands via lab experiments, *in situ* grazing assays, and a long-term exclusion experiment. Further, to examine the generality of temperature variation in upwelling systems, I analyzed *in situ* temperature data from five upwelling regions and examined differences in thermal regimes between the regions. I then related this temperature variation to local grazer-algal interactions. Overall, my findings provide evidence for a mechanistic link between temperature and grazing rates and suggest temperature-mediated herbivory could be important in influencing benthic community patterns in upwelling systems.

TABLE OF CONTENTS

.

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: WARMING INCREASES THE TOP-DOWN EFECTS AND METABOLISM OF A SUBTIDAL HERBIVORE

Introduction

The strength of herbivore-plant interactions determines the composition and distribution of primary producers in many marine communities (Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983, Paine 1992, Duffy & Hay 2000, Burkepile & Hay 2006). Several studies have found that this interaction is influenced by sublethal changes in environmental temperature, via alterations to metabolic rates (O'Connor 2009, Kratina et al. 2012). For example, higher temperatures often cause increases in both primary production and consumption rates; however, due to differential temperature scaling of photosynthesis and respiration, consumption is predicted to increase relative to production at warmer temperatures (Allen et al. 2005, O'Connor 2009, O'Connor et al. 2009). In some circumstances, this could lead to lower standing plant biomass due to stronger top-down effects.

A growing body of literature demonstrates that in a warming world the relative strength of top-down effects increases (within a non-lethal or non-stressful thermal environment), in freshwater, marine and terrestrial systems (O'Connor 2009, Barton et al. 2009, O'Connor et al. 2009, Yvon-Durocher et al. 2010, Hoekman 2010, Kratina et al. 2012). To date, these experimental studies were conducted with relatively small but relevant changes in temperature (from ambient to +6°C). It is unclear to what degree temperature influences species interactions in systems where organisms experience higher temperature variation. For example, it is possible that high natural temperature variability selects for physiological tolerance of temperature

change (i.e., plasticity). Hoekman (2010) used the wide range of temperatures (10°C - 35°C) experienced by the inquiline community in pitcher plants to determine how temperature influences the top-down effects of mosquito larvae on protozoa. He found mosquito larvae developed faster at the warmer temperatures, and consequently, had higher energy demands and fed on protozoa at a faster rate relative to slowly developing mosquito larvae. Yet there are few other studies that quantified the effect temperature has on top-down control in environments with highly dynamic temperature regimes.

I used the nearshore system in the Galápagos Islands to determine how temperature affects the metabolism and the strength of top-down effects of a common subtidal grazer, the green sea urchin (*Lytechinus semituberculatus*). Ocean temperature in the Galápagos is highly variable in space and time, ranging from 11°C - 31°C due to upwelling and downwelling of internal waves, El Niño-Southern Oscillation (ENSO) events and seasonality. Sea urchins are a key grazer on macroalgae in marine systems and can regulate the benthic algal community productivity and structure (Paine 1980, Witman 1985, Hereu et al. 2005, Brandt et al. 2012). They are the most significant invertebrate grazer guild in the Galápagos Islands (Irving & Witman 2009, Brandt et al. 2012), and at high densities can convert macroalgal assemblages to urchin barrens or pavements of encrusting algae (Ruttenberg 2001, Edgar et al. 2009). Therefore, if urchins exert strong top-down control in a system with large spatial and temporal variation in environmental temperature, warmer temperatures should strengthen the top-down effect of urchins on macroalgal assemblages and possibly result in increased urchin barrens.

I manipulated temperature in outdoor mesocosms and measured the effects on urchin grazing rate and metabolism, as well as plant photosynthesis. My findings suggest warming strengthens the top-down effects of urchins and results in lower algal standing biomass.

Methods

The Galápagos Islands are located 965 km off the coast of Ecuador and are centered at the confluence of several oceanographic currents leading to a high degree of variability in ocean temperature and phytoplankton biomass. The Equatorial Undercurrent runs from west to east across the Pacific Basin and drives major upwelling as it collides with the western islands, resulting in cold and nutrient-rich waters around these islands (Houvenaghel 1978, 1984). The cool Humbolt Current delivers nutrient-rich water to the southern edge of the archipelago (Kessler 2006). The northeast region of the archipelago is strongly influenced by the warm, nutrient-poor waters of the North Equatorial Countercurrent (NECC, or the Panama current) (Kessler 2006). Both of these currents contribute to the South Equatorial Current (SEC), a westward flowing current that strongly influences the central region of the archipelago (Houvenaghel 1984) (Fig. 1.1).

The dominant influence of the SEC changes seasonally, depending on the location of the Intertropical Convergence Zone (ITCZ) (Houvenaghel 1984). The ITCZ is north of the equator during the *Garùa* (fine mist) season (May to December), and the Humbolt Current is the major contributor to the SEC. During the wet season (December to May) the ITCZ shifts towards the south and the dominant influence to the SEC is the NECC. This results in fluctuating gradients of temperature and resource availability throughout the central archipelago.

The maximum average SST across the archipelago occurs in February and March, with the minimum usually occurring in August or September (Houvenaghel 1978, Schaeffer et al. 2008) (Fig. 1.2). Temperature data were collected from two sites on San Cristobal (the easternmost island in the archipelago). During 2011, there was a cold season low of 13°C in November 2011 and a high of 25°C in July 2011. In 2012, there was a warm season high of

30°C in February 2012 and a low of 20°C in May 2012 (Fig. 1.2). This annual cycle is interrupted during ENSO events (Barber & Chavez 1983, Chavez et al. 1999).

During the warm ENSO phase (El Niño), the easterly trade winds weaken resulting in a deeper EUC thermocline, warmer waters and decreased upwelling. This results in low standing stock of primary producers in the euphotic zone (Pennington et al. 2006); and, ultimately marine consumer populations, such as seabirds, marine iguanas, and sea lions, decrease in abundance (Valle et al. 1987, Laurie & Brown 1990). In contrast, the cold ENSO phase (La Niña) occurs as the easterly trade winds strengthen, sea surface temperatures decrease, and upwelling intensifies resulting in higher standing stock of primary producers (Izumo et al. 2002). During La Niña, ocean temperature in the western islands can be as low as 11°C (Wellington et al. 2001).

In addition to regional-scale spatiotemporal variability in temperature and resource availability, the upwelling and downwelling of internal waves result in extreme and rapid temperature changes over smaller spatial and temporal scales (Witman & Smith 2003). For example, over a 53-week period on a rocky subtidal wall in the central archipelago at depths between 3-12m, 20 cold water events were recorded where temperature dropped by 3-9ºC over a 25 hr period (Witman & Smith 2003).

I tested the effect of temperature on the common subtidal herbivore *Lytechinus semituberculatus* (green sea urchin) and the green macroalga *Ulva* sp. *Lytechinus*, *Tripneustes depressus* (white sea urchin), and *Eucidaris galapagensis* (slate pencil urchin) are the three most common urchin species in the Galápagos Islands and together comprise 91% of urchin biomass (Brandt & Guarderas 2002, Brandt et al. 2012). In rocky subtidal habitats throughout the archipelago at depths between 1-5m, *Lytechinus* and *Eucidaris* are the two most common urchins, while *Tripneustes* is rare (Table 1.1). Further, *Lytechinus* is a strong interactor and

capable of converting algal turfs (brown filamentous turf, order Ectocarpales: *Giffordia* sp., *Ectocarpus* sp.) to urchin barrens in relatively short time periods, while *Eucidaris* does not have any detectable effect on the abundance of algal turfs (Irving & Witman 2009).

Ulva sp. was chosen as a food item for *Lytechinus* for several reasons: 1) *Ulva* sp. are one of the most abundant macroalgal species, along with turf, crustose coralline algae, and *Sargassum*, in the Galápagos nearshore habitats (Vinueza et al. 2006, Vinueza 2009); 2) ephemeral species, like *Ulva*, are highly palatable for herbivores (Carpenter 1986); and 3) sea urchin fronts in the Galápagos appear to consume all macroalgal species except for brown species (e.g., *Padina*) (L. Carr *personal observation*) and damselfish turfs (Irving & Witman 2009).

Urchins and *Ulva* were haphazardly collected from the southern part of San Cristobal Island (89°36'41.85"W, 0°55'39.36"S), and were immediately transported to the laboratory in buckets filled with seawater. All urchins were collected from a depth of ~1.5 m. Study organisms were maintained in culture tanks indoors at 23ºC (ambient sea water temperature) for two days prior to beginning water temperature adjustments. Assays were conducted in a shaded, outdoor facility at the joint UNC/USFQ Galápagos Science Center (San Cristobal Island, Galápagos).

I conducted feeding rate assays in July 2012 to test the effect of two different temperatures (14ºC or 28ºC) on green urchin grazing rates on *Ulva*. Water temperature in the culture tanks was adjusted from ambient (23ºC) to either 14ºC or 28ºC over a four-day period. This is within the time period of shallow subtidal temperature changes of this magnitude in the Galápagos (Witman & Smith 2003).

Ulva and urchins were placed in 4-L plastic container mesocosms and received a fresh supply of temperature-conditioned seawater every 12 hours. Temperature treatments were maintained with either Visi-Therm submersible individual heaters (Marineland, Blacksburg, Virginia, USA) or ice baths. Feeding assays were replicated twice (*n* = 5 replicates for each trial). Herbivore presence and absence treatments were randomly assigned in water tables. Each mesocosm was equipped with an iButton Thermochron datalogger (Dallas semiconductor, Dallas, Texas, USA) and water temperature was recorded every 5 minutes. Eight mesocosms were equipped with a HOBO Pendant temperature/light sensor (HOBO, Bourne, Massachusetts, USA) and relative light intensity was measured every 5 minutes.

Starting conditions for each mesocosm were 2.50 ± 0.004 g of wet mass *Ulva* tissue and either three urchins or no urchins (control to test for autogenic loss). The average test size for the urchins in the mesocosms was 3.55 ± 0.08 cm, which is representative of the green sea urchin populations in southern San Cristobal (*n* = 120 from two sites measured in May and June 2011: minimum 2.75 cm, maximum 5.8 cm. Mean ± 1 SE of 3.79 ± 0.61 cm).

Assays were terminated and final algal biomass was measured after 48 hrs (when ~ 50% of algal tissue was consumed (Tomas et al. 2011)). Biomass consumption was estimated as ($[H_i \times C_f/C_i] - H_f$), where H_i and H_f were the initial and final wet weights of algal tissue in the presence of herbivores, and C_i and C_f were initial and final wet weights of the controls. Relative light intensity levels did not vary between mesocosms and was 326.06 ± 19.7 lumens/ft^2. These light levels are less than the average relative light levels at 1.5 m depth in the field (886.86 ± 74.07 lumens/ ft^2), but are within the range of light conditions experienced throughout the tidal cycle at the southern sites of San Cristobal Island during the month of June (Table 1.1).

Feeding rate assays were initially analyzed using a mixed model ANCOVA with one level of nesting. The analysis tested for one fixed effect (temperature treatment), covariate (urchin test size), and one random effect (temporal block). Consumption data were log transformed to meet the assumption of homogeneity of variances. The random effect was not significant ($p = 0.183$). Therefore, results were pooled and the random effect was dropped, for final analysis of treatment effects. All statistical analyses were performed in R (v. 2.15.2).

To estimate the temperature response of metabolic pathways (net photosynthesis and respiration), I measured oxygen production and consumption rates for *Ulva* and green urchins in 0.6L containers under conditions identical to the feeding rate assays. Initial and final oxygen concentrations were measured for *Ulva* (5 ± 0.08 g of leaf tissue) and paired blanks (seawater only) ($n = 20$ replicates) using a YSI-200 oxygen sensor (Yellow Springs Instruments, Yellow Springs, Ohio, USA). Samples of *Ulva* tissue (5 ± 0.08 g) were obtained by using three *Ulva* "rosettes" plucked from the substrate by the holdfast. Rosettes used were similar sizes and no cutting or tearing was necessary. After the initial measurement, aquaria were covered with plastic to minimize oxygen exchange with the air and left for 2 hrs. Net photosynthesis rates were estimated by subtracting measurements of dark oxygen consumption from light oxygen production.

Lytechinus oxygen consumption rates were measured according to methods described in Siikavuopio et al. (2008). Urchins were held at 23°C prior to oxygen consumption trials. One randomly selected urchin was placed into an airtight, closed-system respirometry chamber (0.6L) and water temperature was gradually adjusted over a 10 hour period to 14°C and then back up to 28°C over a 30 hour period. Within the chamber was a mounted YSI 200 dissolved oxygen probe to measure oxygen concentrations (mg/L) and a pump for water circulation to prevent the

18

development of strong oxygen and temperature gradients. The chamber was placed into a water bath to maintain temperature treatments. An individual urchin was then placed into the chamber and oxygen concentrations were measured every five minutes for one hour at each temperature treatment (14°C and 28°C). Trials were repeated for 11 urchins. The mean weight specific oxygen consumption rate (Q, mg O_2 kg^{-1} h^{-1}) was calculated with the equation of Karamushko and Christiansen (2002):

$$Q = (C_0 - C_t)V/WT$$

C_0 and C_t are the initial and final oxygen concentration (mg O_2 l^{-1}), respectively. V is the volume (l) of the chamber minus the test urchin volume (test urchin volume was estimated from their biomass). W is the biomass of the urchin in kg. T is the measurement time in hours.

Oxygen consumption and production test were analyzed with a t test on change in O_2. All statistical analyses were conducted using R (version 2.15.2).

Results

Temperatures in the cold mesocosms were maintained at 14.01 ± 0.08°C and 14.03 ± 0.07°C for trials 1 and 2, respectively. Warm mesocosms for trials 1 and 2 were 28.06 ± 0.09°C and 28.00 ± 0.04°C, respectively. The range of temperatures maintained across both trials was $13.54 - 14.47$°C for the cold treatment and $27.56 - 28.5$°C for the warm treatment (Fig. 1.3). Green urchin consumption was 46% higher at the warmer temperature ($p < 0.0001$) (Fig. 1.4A). Urchin test size was not a significant covariate ($p = 0.87$).

Green urchin metabolism was significantly higher at 28°C than at 14°C ($p < 0.001$, Fig 1.4B). *Ulva* oxygen consumption was greater at 28°C (at 14°C, 2.55 ± 0.11 g O_2•g tissue^{-1}•hr^{-1};

at 28ºC, 3.24 ± 0.13 g O_2•g tissue^{-1}•hr^{-1}; p = 0.004). Oxygen production was also greater at 28ºC

(at 14ºC, 3.88 ± 0.09 g O_2•g tissue^{-1}•hr^{-1}; at 28ºC, 4.74 ± 0.15 g O_2•g tissue^{-1}•hr^{-1}; p = 0.01).

However, net photosynthesis rates did not vary with temperature (p = 0.45, Fig 4C).

Discussion

Consistent with the predictions based on metabolic theory and a growing body of literature, my results indicated that sublethal warming significantly increases the strength of top-down effects. Specifically, I found a 14°C increase in temperature resulted in a 46% increase in grazing rate and lower standing plant biomass. Similar results have been found in other marine systems (O'Connor 2009: with herbivores there was a nearly 100% decrease in algal net growth at high temperatures compared to growth at low temperatures with or without herbivores) and grasslands (Barton et al. 2009: warming of 1°C increased the strength of top-down indirect effects on grasses and forbs by 30-40%).

One limitation of my study was that the urchins and algae might have acclimated to the ~5°C temperature change had I warmed the treatment tanks more slowly or maintained the experiment for longer. Thus, it is difficult to extrapolate to how slower or longer-term changes in temperature will affect urchin-algal interactions and, consequently, larger spatial scale changes in ecological patterns. However, the rate of temperature change during the acclimation period and experiment is similar to temporal patterns of temperature fluctuation experienced by urchins around San Cristobal and the Galápagos Archipelago in general (Palacios 2004, Vinueza 2009, Witman et al. 2010). In this dynamic system, urchins rarely spend more than several days to a few weeks at the same temperature, suggesting that my experimental treatments were representative of the natural temperature regime.

While there was a significant temperature effect on consumer metabolism and feeding rates, there was not a significant temperature effect on algal photosynthesis rates following the 4-day acclimation period in this study. It is possible that this was because light, nutrients, carbon dioxide, or some other resource was limiting and thus warming could not stimulate photosynthesis. Further, the positive effect of increased temperature on algal photosynthetic rate can be reduced or reversed at sub-saturating light levels because warming can increase the light level needed to reach the compensation point (Davison 1991). Light conditions in the experiment were within the range of light levels in the nearshore habitats in the Galápagos (Table 1) and further, most populations of subtidal algae are subject to subsaturating light conditions (Davison 1991); therefore the experimental conditions likely reflect algal performance in the field. My results are consistent with O'Connor (2009) which found no temperature effect for *Sargassum* with a 4°C temperature change.

Organisms throughout the nearshore habitats of the Galápagos Islands experience large and frequent temperature fluctuations (Witman & Smith 2003, Palacios 2004, Vinueza et al. 2006, Schaeffer et al. 2008, Vinueza 2009, Witman et al. 2010, Vinueza 2010). Therefore, populations in this environment could be less metabolically sensitive to extreme temperature changes due to adaptation, resulting in metabolic responses that deviate from the predicted outcomes of metabolic theory. For example, in the rocky intertidal, adaptive regulation results in reduced snail metabolic rates at warmer temperatures (Marshall & McQuaid 2011). However, my results provide evidence that in a dynamic system where organisms experience relatively large variation in environmental temperature, metabolism and consumption still scale with temperature, which is consistent with metabolic theory (Allen et al. 2005, O'Connor 2009, O'Connor et al. 2009).

At the upper range of species' thermal tolerances metabolism and consumption are predicted to scale differently and metabolic demands should outpace increased grazing intensity (Rall et al. 2010). Lemoine and Burkepile (2012) found *Lytechinus variegatus* consumption and metabolism scaled differently at temperatures beyond 29°C, a 9°C increase from the starting temperature treatment (20°C). Ultimately, urchin ingestion efficiency was decreased at the higher temperature, resulting in possible reduced consumer fitness. Because shallow subtidal temperatures around San Cristobal reach 30°C, future work should focus on understanding *Lytechinus* metabolism/consumption ratios at the highest temperatures in the Galápagos and the implications for species interactions and the strength of top-down effects under these conditions.

My finding that warming increased urchin metabolism, even in a thermally variable system, provides further support for a mechanistic link between environmental temperature and feeding rates. Additionally, my findings indicate warming increases grazing intensity, which could in turn affect ecological patterns, such as primary producer community composition and biomass. For example, if these grazing rates are maintained over longer time-scales (i.e., days to weeks), warmer temperatures may increase the prevalence of urchin barrens in areas of the Galápagos with high densities of sea urchins because of the increased relative strength of top-down effects. This study focused on one algal species and thus I cannot extrapolate to how temperature would affect other algal-urchin interactions. Furthermore, macroalgal primary production is highly seasonal in the Galapagos nearshore habitats (Vinueza et al. 2006, Vinueza 2009) and it is unclear what effect this could have on urchin-plant interaction strength. I also recognize that other factors influence urchin-plant interactions and primary production. Future work should focus on elucidating the stability of this interaction under larger temporal and

spatial scales, and various environmental conditions (i.e., different seasons, ENSO cycles, varying light intensities, etc.) and with different algal species.

The absence of macroalgae in intertidal and shallow subtidal habitats during warm periods (e.g., El Niño) in the Galápagos Islands is generally attributed to the decreased strength of bottom-up forcing (i.e., upwelling) and subsequent lack of nutrients (Vinueza et al. 2006). However, temperature stress (i.e., desiccation) does play a minor role in regulating intertidal algal biomass in the Galápagos (Vinueza 2009). Therefore, future work should focus on understanding the constraints of physical stress on macroalgal growth in the Galápagos Islands, as stress is known to alter the relative importance of bottom-up and top-down effects (Thompson et al. 2004).

Low macroalgal biomass in warm seasons and years could also be due in part to increased grazing intensity due to higher temperature (e.g., O'Connor et al. 2009). Both mechanisms could be operating (i.e., changes in top-down and bottom-up control), although the relative strength of these mechanisms in influencing large-scale ecological patterns in upwelling systems is unknown. In freshwater pond systems, Kratina et al. (2012) found a negative interaction between warming and nutrient input on total phytoplankton biomass in freshwater systems, suggesting a shift toward stronger top-down and weaker bottom-up effects with warming regardless of nutrient availability. However, the mechanism behind this shift is not known. Therefore, future warming could result in stronger consumer control in systems where nutrients are plentiful (i.e., upwelling or well-mixed aquatic systems) that could lead to short- and /or long-term changes in community structure and function.

Table 1.1 Natural variation in algal cover, temperature and urchin density in shallow subtial habitats in the Galapagos Islands.

Sites were surveyed in June 2010 and July 2012. Site codes: LL = La Loberia (San Cristobal, SC), LT = Las Tijeretas (SC), PP = Punta Pitt (SC), CD = Cabo Douglas (Fernandina, FE), PE = Punta Espinosa (FE). Values represent means ± SE (n = 25 quadrats for urchin density and algal cover). Any other urchin species (e.g., *Tripneustes*) were present at densities less than 0.3m^{-2} in all quadrats. Temperature was estimated with both *in situ* temperature loggers and satellite data (AQUA Modis) for the 30-day period prior to sampling, SE < 0.07 for all sampling points. Light intensity was measured using HOBO Light/Temperature Pendants before and during the experimental duration.

Site	2010 LL	2010 LT	2010 PP	2010 CD	2012 LL	2012 LT	2012 PE
Ulva cover (%)	9.7 ± 3.3	58.4 ± 3.5	2.9 ± 0.4	36.3 ± 5.1	7.8 ± 2.1	28.9 ± 2.7	23.4 ± 1.5
Eucidaris density (m^{-2})	4.8 ± 1.3	1.6 ± 0.7	1.6 ± 0.2	8.4 ± 2.4	6 ± 1.9	2.1 ± 0.4	3.2 ± 1.3
Lytechinus density (m^{-2})	10.2 ± 2.6	11.8 ± 1.8	11.2 ± 1.9	1.2 ± 0.7	14.9 ± 2	13.2 ± 1.6	17.6 ± 4.5
Temperature (°C)	24.8	23.7	20.8	11.4	25.3	23.2	17.8
Light Intensity Range (lumens ft^{-2})	N/A	N/A	N/A	N/A	0-3102	0-2968	N/A

Figure 1.1 Map of Galapagos Archipelago and the surrounding currents.
Colored triangles relate to curves in Figure 2.
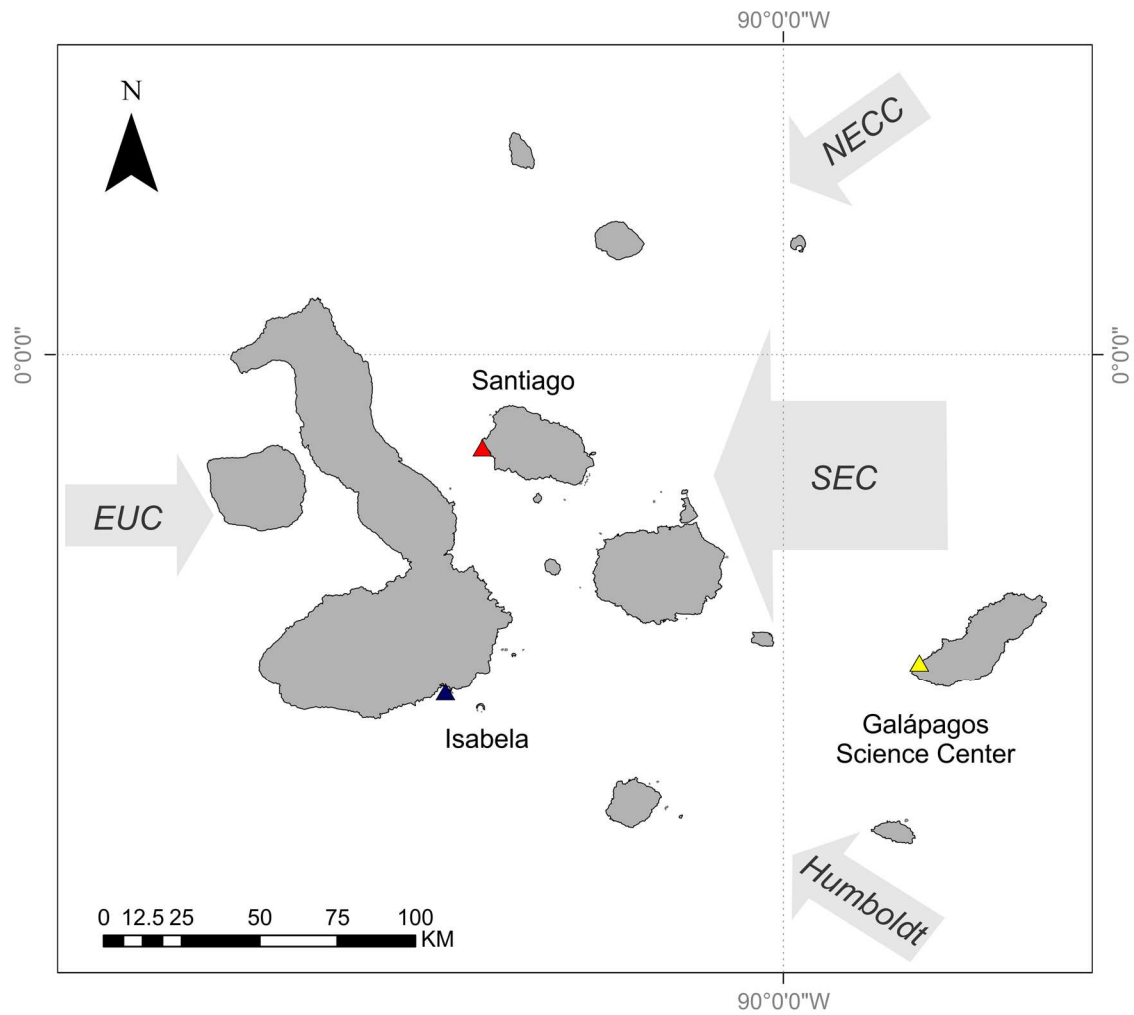
Figure 1.2 Daily water temperature (mean) measured in the shallow subtidal (< 5m) at Santiago, Isabela and San Cristobal
The Galapagos Science Center is on San Cristobal. Water temperature measurements were recorded every 30 mins with a HOBO temp logger. The smoothing curve was done in Kaleidagraph (v. 4.1). A Stineman function was applied to the data. The output of this function has a geometric weight that is applied to the data points and ± 10% of the data range to generate the smoothed curve.
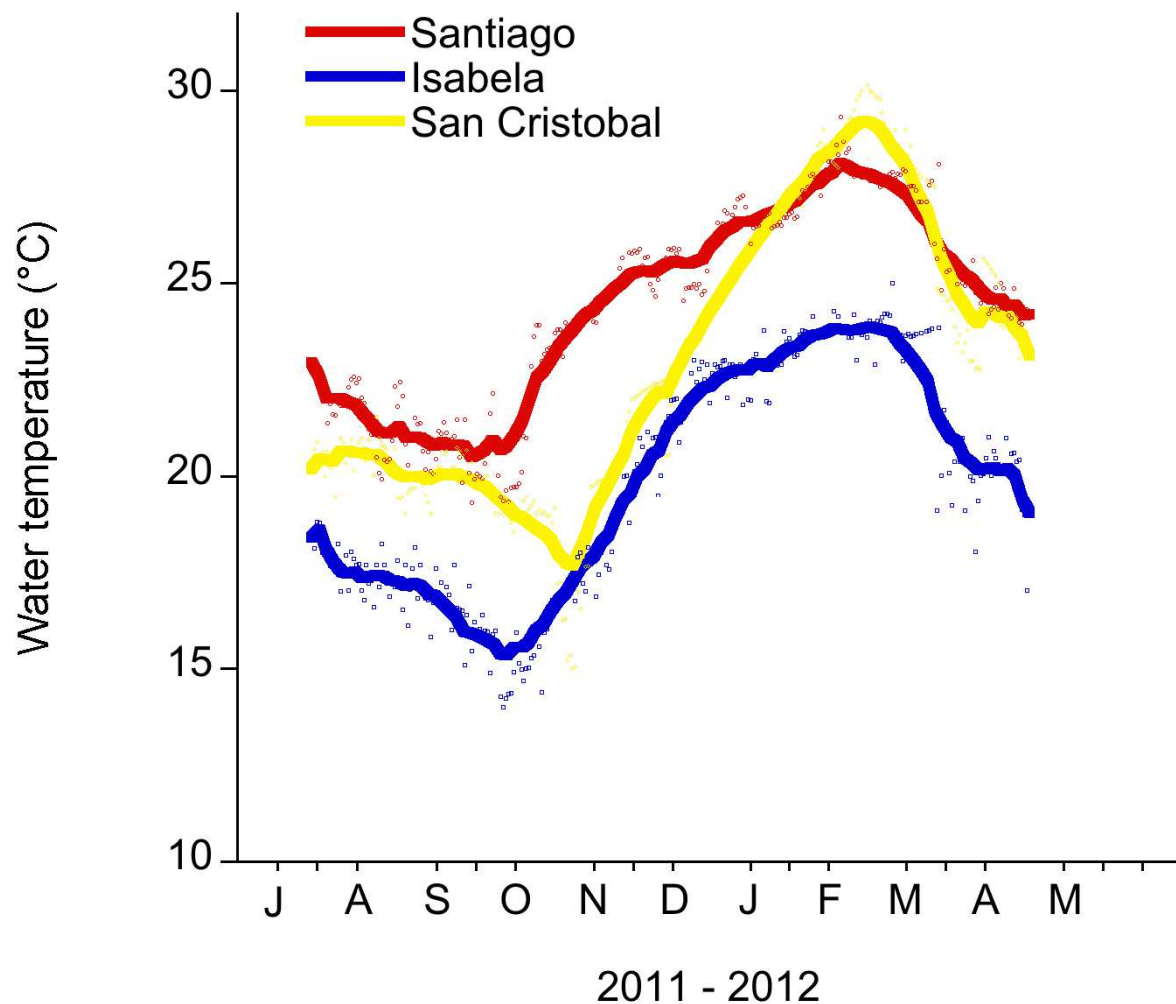
Figure 1.3 Mesocosm temperature values during both experiments.
Temperature in each mesocosm ($n = 20$ per temperature) was recorded every 5 mins. with an iButton Thermochron datalogger (Dallas semiconductor, Dallas, Texas, USA). The box corresponds to the 25th and 75th percentiles and the dark line inside the box represents the median consumption value. Error bars are the minimum and maximum.
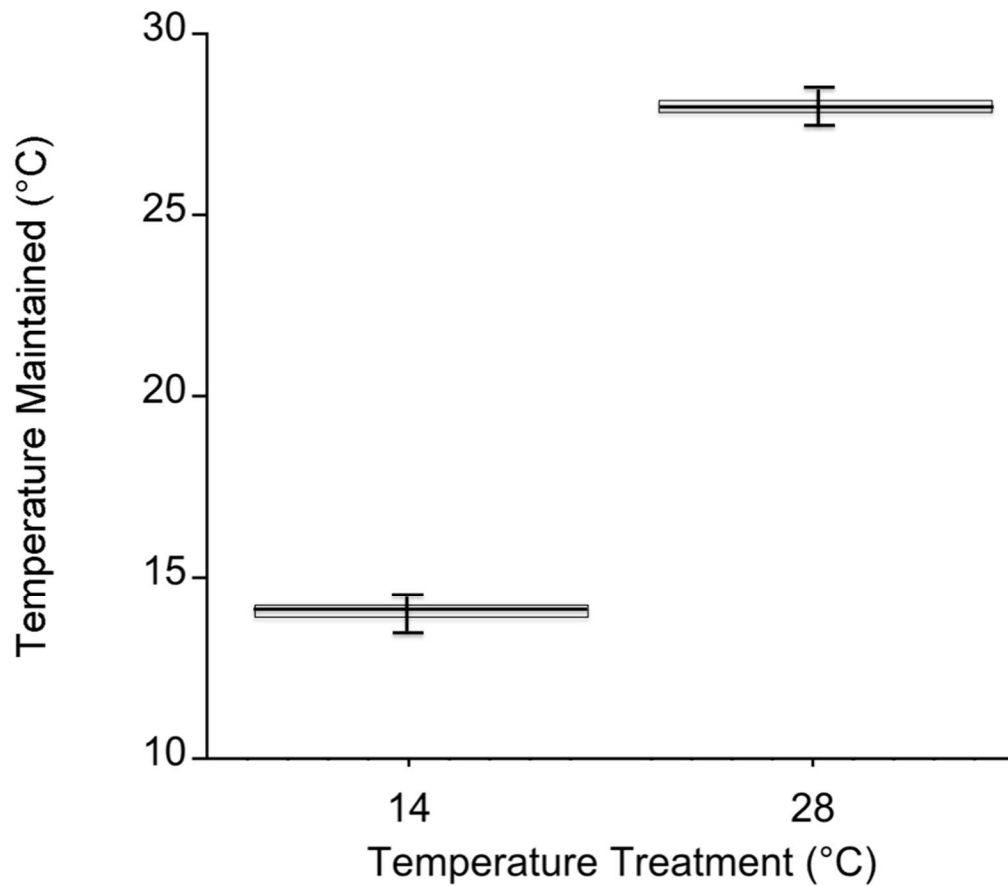
Figure 1.4 Temperature effects on urchin grazing rates, metabolism and algal photosynthesis.
Temperature effects on A) urchin consumption of *Ulva*, B) urchin oxygen consumption, and C) on *Ulva* net photosynthesis. Values are means ± SE; *n* = 10.
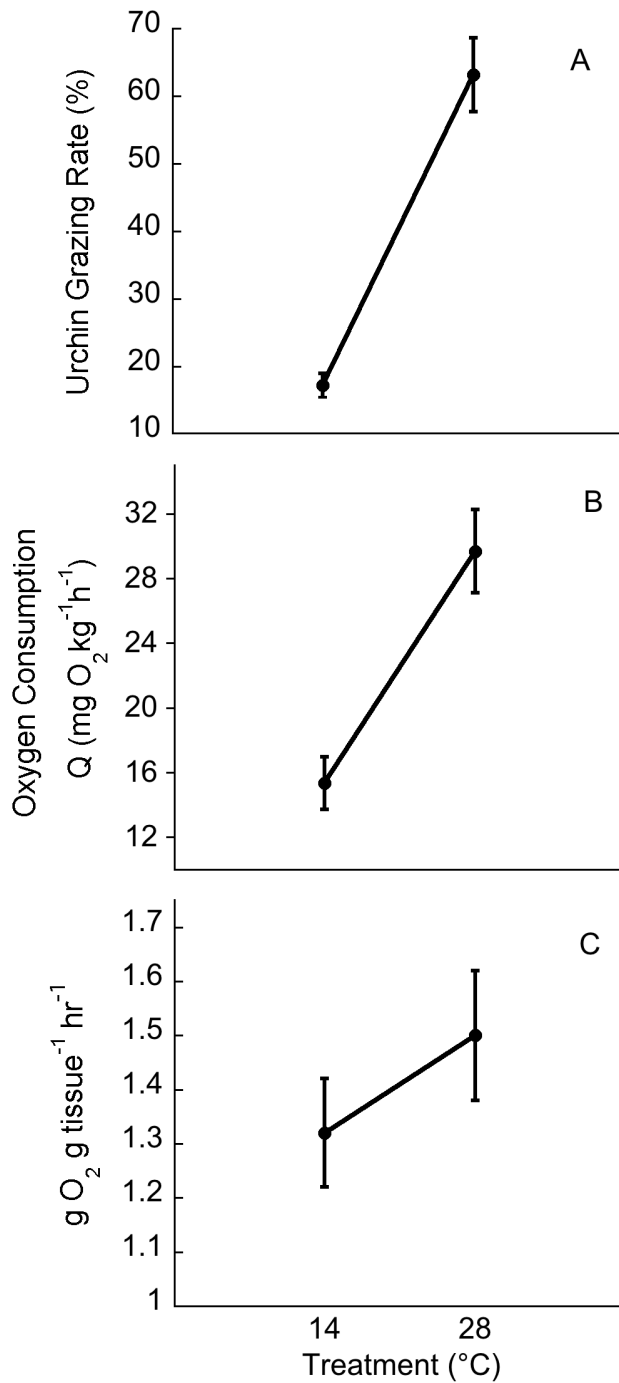
CHAPTER 2: TEMPERATURE INFLUENCES HERBIVORY ACROSS A REGIONAL-SCALE TEMPERATURE GRADIENT IN THE GALAPAGOS ISLANDS, ECUADOR

Introduction

Understanding how the abiotic environment influences species interactions has long been a fundamental goal of ecological research (e.g., Park 1954, Dunson & Travis 1991, Brown et al. 2004). For example, environmental temperature can influence the direction and magnitude of species interactions (Davison 1987, O'Connor 2009). Stressful temperatures can modify the physiological ecology of organisms, resulting in changes to the outcomes of species interactions and initiating changes that propagate to community-level patterns (Menge & Sutherland 1987). Recently, ecological theory and empirical studies have examined how non-stressful (non-lethal) temperatures influence species interactions via predictable effects on individual metabolic function (Davison 1987, Brown et al. 2004).

The metabolic theory of ecology (MTE) relates individual metabolic rate to temperature (Gillooly et al. 2001, Brown et al. 2004) using fundamental biochemical constraints on enzyme kinetics. MTE predicts that metabolic rate scales with temperature in specific and predictable ways across taxonomic groups (Gillooly et al. 2001), providing testable mechanistic predictions regarding the outcome and strength of trophic interactions. For example, while increased metabolic rate at moderate warming (sublethal temperatures) can increase both resource uptake by primary producers (Enquist et al. 2003, Brown et al. 2004) and consumption by organisms at higher trophic levels (Brown et al. 2004); consumption scales more directly with temperature

relative to photosynthesis and thus, consumption might be stronger at warmer (sublethal) temperature compared to production (Allen et al. 2005).

A growing body of empirical work does demonstrate consumption increases relative to production with (non-stressful) warmer temperatures (e.g., O'Connor 2009, O'Connor et al. 2009, Hoekman 2010, Kratina et al. 2012, Shurin et al. 2012, Carr & Bruno 2013). A wide range of lab-based experiments (i.e., environmental chambers) and mesocosm studies conducted in freshwater, marine and terrestrial systems found sublethal warming can increase *per capita* grazing rate and the effect of herbivores on plant biomass, ultimately, resulting in less standing plant biomass at higher temperatures (e.g., O'Connor 2009, Hoekman 2010, Kratina et al. 2012, Sentis et al. 2012, Carr & Bruno 2013). As the strength of herbivore-plant interactions can determine primary producer abundance in a community (Lubchenco & Gaines 1981, Paine 1992, Burkepile & Hay 2006), the temperature dependence of herbivore-plant interactions could translate to alterations in larger-scale ecological patterns, such as primary producer biomass, composition, and distribution.

Several recent studies manipulating temperature in lab and field mesocosms found temperature effects on herbivore consumption rates are context-dependent and influenced by factors such as evolutionary history, local acclimatization, diet, temporal environmental complexity, e.g., heat waves, and predator response to temperature (Shurin et al. 2012, Sentis, Hemptinne & Brodeur 2012, Dell et al. 2013). However, the thermal dependence of herbivore-plant interactions across natural, *in situ*, environmental conditions remains largely unexplored, in part because experimentally manipulating temperature in the field is challenging. Although, a few studies have examined how herbivore bite rates change across latitudinal temperature gradients (Floeter et al. 2005, Freestone et al. 2011). However, other factors co-vary with

latitude (e.g., phenotypic variation, physical oceanographic features, species composition, etc.) and could influence *in situ* feeding rates.

We employed a comparative-experimental design (Menge 1991) along the same latitude across a natural gradient in temperature (via upwelling and oceanographic currents) to quantify its influence on the effects of subtidal benthic and mobile herbivores on algal biomass in the Galápagos Islands. Specifically, we utilized two aspects of thermal variability across the Archipelago: inter-annual (warm and cold season) and spatial (warm and cold areas). Further, to examine whether the temperature-dependence of grazing rates could affect community-level patterns (i.e., standing algal biomass in this system), we also conducted a longer-term field exclusion experiment at one upwelling region.

This system is ideal for examining the effects of temperature on species interactions because the Archipelago is centered at the convergence of several different oceanographic currents (tropical, subtropical and upwelled water), resulting in enormous spatiotemporal variation in water temperature (11°C - 31°C) (Houvenaghel 1984, Schaeffer et al. 2008, Witman et al. 2010). Further, while community composition differs across the Archipelago due to upwelling intensity, there is a suite of organisms that are present at all the sites throughout the year. Thus, this system is a subtidal analogue of the rocky intertidal zone; a continental scale thermal gradient compressed into tens of kilometers and relatively short time scales.

Methods

The Galápagos Islands are located in the Eastern Tropical Pacific Ocean ~ 950 km off the coast of Ecuador. We selected four sites semi-protected from wave action on four islands that vary in temperature and nutrient availability due to variation in upwelling intensity and other oceanographic features (Fig. 2.1). Fernandina is located in the western region of the

Archipelago. The Equatorial Undercurrent (EUC) drives major upwelling as it collides with the western islands, resulting in cold and nutrient-rich waters around Fernandina (Houvenaghel 1984). The study site was located at Punta Espinosa, on the northeastern point of the island (Fig. 2.1), (0°16'06.88"S, 91°26'50.49"W). Isabela is also located in the western region; and assays were conducted on the southern edge of the island, at Túnel del Estero (0°57'39.46"S, 90°59'26.28"W). This region is influenced by the EUC and the cool (and nutrient-rich) Humboldt Current from the south, therefore, this region is also considered an upwelling zone (Houvenaghel 1984, Schaeffer et al. 2008) (Fig. 2.1). Santiago is a northern island, located in the central region of the Archipelago. The study site, Puerto Egas (0°15'13.58"S, 90°52'05.18"W), is located on the northwest side of the island. And influenced by the South Equatorial Current (SEC; a westward flowing current that strongly influences the central region of the Archipelago), the North Equatorial Countercurrent (NECC, a warm and nutrient-poor current) and EUC meanderings, resulting in high productivity, yet warmer waters (Houvenaghel 1984, Schaeffer et al. 2008) (Fig. 2.1). San Cristobal is the easternmost island in the Archipelago. Grazing assays were conducted at Punta Pitt (0°42'38.93"S, 89°15'02.87"W), located on the northeastern point of the island, and influenced by the SEC, Humboldt Current, and the NECC (Houvenaghel 1984, Wellington et al. 2001, Schaeffer et al. 2008). In general, this site has depressed nutrient loads and warmer waters relative to the other sites, as it is north of the upwelling region off San Cristobal (Schaeffer et al. 2008).

Both the NECC and the Humboldt Current contribute to the SEC, and the dominant influence of the SEC changes seasonally (Houvenaghel 1984). During the cool season (May – December), the Humboldt Current is the major contributor to the SEC; with the minimum

average SST usually occurring in August or September. The maximum average SST usually occurs in February and March, when the dominant influence to the SEC is the NECC.

In the Galápagos shallow subtidal, macroalgae are generally the dominant sessile group and sea urchins are the most significant invertebrate grazer guild (Irving & Witman 2009, Brandt, Witman & Chiriboga 2012). At high densities, sea urchins can convert macroalgal assemblages to urchin barrens or pavements of encrusting algae (Edgar et al. 2010). The two most common sea urchins in rocky subtidal habitats at depths between 1 and 5 m are *Lytechinus semituberculatus* (green sea urchin) and *Eucidaris galapagensis* (slate pencil sea urchin). *Lytechinus* is capable of converting algal turfs to urchin barrens in relatively short time periods, while *Eucidaris* does not have any detectable effect on algal turf abundance (Irving & Witman 2009). Other important grazers include fishes (razor surgeonfishes; *Prionurus laticlavius*, blue chin parrotfish; *Scarus ghobban*), sea turtles and marine iguanas.

Natural herbivore densities and benthic community composition were assessed at each site and during both time periods (Table 2.1). We quantified benthic community composition, fish community composition, biomass and density, and urchin identity and abundance along five 30m transects placed parallel to shore at ~3-4m depth.

Along each transect, five photoquadrats were placed adjacent to the transect line at fixed intervals, totaling 25 photquadrats per site. Each photograph captured an area of 0.42 m^2. One hundred points were placed over each photograph in a stratified random design. Image analysis was conducted with ImageJ v1.48. Percent cover of each algal species was classified to genus and filamentous algae was distinguished as red (*Centroceras* spp., *Ceramium* spp., *Polysiphonia* spp.), green (*Bryposis* spp., *Chaetomorpha antennina*) or brown (*Ectocarpus* spp.).

Divers conducted visual fish censuses along 30 x 2m belt transects by recording the species-level identity and length of each fish. Fish length estimates were converted to fish biomass estimates using published length-biomass relationships (Froese & Pauly 2013). Urchin identity and abundance was determined by counting all urchins along 30 x 1m belt transects.

To examine the effect of temperature on grazing rates of *Ulva* (chosen as a food item because it is one of the most abundant macroalgal species in nearshore habitats (Vinueza et al. 2006, Table 2.1) and is highly palatable (Carpenter 1986), we repeated the same grazing rate assay *in situ* at four sites and two time periods (warm and cold season) in 2013. The total temperature range was 19.7 – 29.5°C, with the warm (Feb/Mar 2013) and cold season (Sept/Oct 2013) temperatures ranging from 24.4 – 29.5°C and 19.7 – 24.7°C, respectively.

Three different cage types were deployed: closed cages with *Lytechinus* absent (control), closed cages with *Lytechinus* present, and open cages (no sides or top) ($n = 10$ for each cage type). Open cages were used to assess the temperature effect on natural grazing conditions at each site and time period. *Lytechinus* and *Ulva* were haphazardly collected at each site from a depth of ~2m. The average test size for the urchins placed in cages across all sites and both time periods was 3.82 ± 0.09 cm, which is representative of the green sea urchin populations across the Archipelago (see Table 1 for urchin test sizes in cages for each site and time period). Urchins were then placed in cylindrical vexar cages at a depth of ~3 – 5m and starved for ~ 30 h. Cages were constructed using plastic vexar looped in cylinders with a diameter of 30cm, 15cm height, and a mesh size of 2.5cm. Chain was placed on the substrate at ~3 – 5m depth and cages were attached to the chain via metal fasteners. Treatments were randomly assigned along the chain. Water temperature was measured and recorded every 5 minutes with a HOBO temperature logger (Onset, Bourne Massachusetts, USA) attached to the chain.

Initially, each cage contained 5.00 ± 0.06 g of wet mass *Ulva* tissue and either three

urchins or no urchins (control to test for autogenic loss). *Ulva* was strung onto bead wire and

then was attached to the vexar. The urchin densities used in the cages are representative of

natural urchin densities at these sites (Table 2.1). Scaled for comparison, we used 21 green

urchins per $0.5m^2$, and the range of green urchin densities found at the sites was between 11 and

39 per $0.5m^2$. Assays were terminated and final algal biomass was measured after 24 h, as over

~50% of algal tissue was consumed (Tomas et al. 2011). Biomass consumption was estimated as

$([H_i \times C_f/C_i] - H_f) = F_B$, where H_i and H_f were the initial and final wet weights of algal tissue in

the presence of herbivores, and C_i and C_f were initial and final wet weights of the controls.

Percent consumed (or grazing rate) was determined from F_B/C_f.

To examine the effect of herbivores on algal biomass, we conducted a 12-week field

exclusion experiment at Isabela (Fig. 2.1; upwelling site) during the cold season (September –

December 2013). Isabela was selected as: 1) there is high nutrient availability, 2) relatively cold

ocean temperatures, and 3) accessible for a long-term study. By selecting a relatively cold and

nutrient-rich site, we tested the effects of herbivore grazing in the presence of high nutrient

availability and low metabolic rates. Therefore, if herbivores affect macroalgal biomass at this

site, herbivory is an important process in this system, regardless of nutrient concentration. Forty

boulders (~35cm x 25cm x 15cm; l x w x h) at a depth of ~5m were collected, brought to the

surface and completely cleared of macroalgae and invertebrates. Each boulder was randomly

assigned one of the following treatments ($n = 10$): 1) open plot, completely open to all herbivores

and marked with four nails, 2) complete exclusion cage, 3) cage with sides but no top, accessible

to mobile herbivores, 4) cage with top and cut-out sides, accessible to benthic and small mobile

herbivores. Cages were constructed using plastic vexar looped in cylinders with a diameter of

25cm, 12cm height, and a mesh size of 2.5cm. After construction, boulders were haphazardly placed at a depth of ~5m. Boulders were sampled 12 weeks later, and all macroalgae was collected from the cages/plots. Macroalgae collected from each cage was recorded to genus, spun in a salad spinner for 60 revolutions, and then weighed.

For the grazing assays, we conducted 1) a two-factor analysis of variance (ANOVA) on urchin grazing rate, with site and temperature as fixed factors, and 2) a two-factor analysis (ANCOVA) on the open plot grazing rate, with site and temperature as fixed factors, and green urchin density as a covariate. A logistic (logit) transformation was applied to the grazing rates (Lesaffre et al. 2006). For the field exclusion experiment, we compared treatment effects on final algal biomass using a one-way analysis of variance (ANOVA). The field exclusion analysis was followed with Tukey's HSD post-hoc tests. All analyses were run in R v. 3.0.3 (R Development Core Team 2014).

Results

In the cold season, *Ulva* spp. dominated the benthic community at all sites (19%, 39%, 44%, 49%, San Cristobal, Santiago, Isabela, and Fernandina, respectively). However, algae covered only 50% of the benthos at San Cristobal (Table 2.1). In contrast, during the warm season, there was high percent cover of crustose coralline and turf (filamentous) algae; although overall algal cover was approximately 10% (San Cristobal) to 30% (Fernandina) lower than the algal cover in the warm season (Table 2.1). *Lytechinus* and *Eucidaris* densities varied among the sites, with *Lytechinus* being the more abundant urchin species (Table 2.1). Herbivorous fish biomass also varied among the sites, with the highest biomass at San Cristobal driven by schools of razor surgeonfish. Furthermore, this site had the highest abundances of blue-chin parrotfish relative to the other sites (Table 2.1).

In the urchin-only treatment, urchins consumed 40% more *Ulva* at warmer temperatures than cooler temperatures (Table 2.2, Fig. 2.2A). There was not a significant site effect on grazing rates. However, there was a significant site x temperature interaction (Table 2.2, Fig. 2.2A), as grazing rates at San Cristobal and Fernandina were different at the same temperature (Fig. 2.2A).

In the open plots, temperature and site were significant factors influencing grazing rates (Table 2.2, Fig. 2.2B). Green urchin density was not a significant covariate (Table 2.2). And there was not a significant site x temperature interaction. In the open plots, grazers (including urchins and fishes) consumed 21% more *Ulva* at in the warm season relative to the cold season.

Final algal biomass differed significantly between treatments (Table 2.3, Fig. 2.3, post-hoc Tukey HSD tests). Overall, there was 90% more algal biomass in the full exclusion plots relative to the open plots. There was 48% and 54% less algal biomass in the mobile and benthic herbivore treatments, respectively, relative to the full exclusion plots (Fig. 2.3). Although, the final algal biomass in the mobile herbivore treatments compared to the benthic herbivore treatments were not different from each other (post-hoc Tukey HSD tests). The dominant algal functional group present in the treatments was green sheet-like algae (*Ulva* spp.), and the percent composition of *Ulva* spp. were similar across treatments: 83.3%, 81.7%, 77.1%, and 79.2%, open plots, benthic herbivores, mobile herbivores, and full exclusions respectively. Red filamentous algae (*Ceramium* spp., *Centroceras* spp. and *Polysiphonia* spp.) were present with the following percent composition: 16.9%, 13.5%, 22.9%, and 18.3%, open plots, benthic herbivores, mobile herbivores, and full exclusions respectively. The least common algal functional group present was red corticated algae (*Hypnea* spp.): 0%, 4.8%, 0%, and 2.5%, open plots, benthic herbivores, mobile herbivores, and full exclusions respectively.

Discussion

Consistent with predictions based on metabolic theory and a growing body of evidence from empirical studies conducted in environmental chambers, our results indicated that sublethal warming significantly increases the strength of herbivory across a natural, *in situ*, mesoscale temperature gradient. Overall, we found that a ~10°C change in temperature resulted in 40% and 21% increases in grazing rate for urchin-only and open plots in our grazing assays, respectively. These results are consistent with a similar study conducted in mesocosms on San Cristobal Island that found a 14°C temperature increase resulted in a 46% increase in *L. semituberculatus* grazing rates (Carr & Bruno 2013). Further, results from our field exclusion experiment found in the absence of herbivores, algal biomass increased by almost 90%. Also, a recent meta-analysis on herbivore grazing rates found increasing ambient temperature resulted in higher per capita and community level grazing rates. Therefore, our results coupled with findings from meta-analyses, such as Hillebrand et al. (2009), suggest herbivores could have a strong effect on algal biomass even in nearshore upwelling systems.

Further, in support of several recent studies (Shurin et al. 2012; Sentis et al. 2012; Dell et al. 2013), we found the temperature effect on grazers was context-dependent. Specifically, our results are consistent with local acclimatization, in the urchin-only treatment; urchins consumed different amounts of *Ulva* at the same temperature at different sites (significant site x temperature interaction, Fig. 2.2A). The water temperature at Fernandina during the warm season (Feb 2013) was 24.5°C and urchins consumed 66% of *Ulva*, while the temperature at San Cristobal during the cold season (Nov 2013) was 24.7°C and the urchin grazing rate was 39% (Fig. 2.2A). The shallow subtidal around Fernandina and San Cristobal exhibit different temperature regimes; generally the water is colder around Fernandina relative to San Cristobal (Houvenaghel 1984, Schaeffer et al. 2008, Carr & Bruno 2013). Thus, while the absolute

temperature during the warm season at Fernandina was low relative to the rest of the
Archipelago, it was warm relative to the average water temperature in this region (21.6°C from
Feb – Dec 2013, Carr *unpublished data*; and 22.1°C from Jan 2006 – Jan 2009, Vinueza et al.
2014).

That thermal history influences acclimatization is well documented (Roberts 1957,
Hutchison 1976, Helmuth 2002). For example, a recent study (Marshall & McQuaid 2010)
found that the relationship between metabolic rate and temperature depends on the temperature
range experienced by the organism. However, less is known about other biological responses of
organisms in response to thermal history, and our findings suggest this mechanism may be
important for consumption rates. However, there could be other alternative explanations for the
discrepancy in grazing rates at different sites at the same temperature due to site-specific
differences. For example, current characteristics, wave exposure, and other physical attributes
could vary among sites and influence plant growth, biomass, and even grazing (Dayton 1985,
Irving & Witman 2009). Therefore, future studies should focus on isolating the direct
mechanism of variation in biological responses (such as consumption rates) at similar
temperatures at regional scales.

In contrast to the urchin-only treatment, *Ulva* consumption in the open plots was very
similar between these two temperatures (24.5°C and 24.7°C, during the warm and cold seasons,
respectively); *Ulva* consumption was 79% ± 5 at Fernandina and at San Cristobal, 77% ± 6 (Fig.
2.2B). The open plots allowed unrestricted grazer access, thus, all herbivore guilds (urchins, fish,
sea turtles, marine iguanas) were able to graze on the available algae, although due to the amount
of algae in each plot (5g) only a few individuals could be feeding at any given time. We found
no relationship between green urchin density and grazing rates, suggesting while green urchin

density did differ between sites and time periods (Table 2.1), this was not a significant factor influencing grazing rates. Therefore, an increase in grazing rates with temperature was not a function of changes in green urchin density. These open plots tested the generality of temperature effects on herbivore-algal interactions under more natural conditions. We expected to see higher variance in these assay plots, given the among-plot and -site variance in grazer communities (composition and density, Table 2.1). Nonetheless, more *Ulva* was consumed in the open plots at warmer temperatures even when we did not control for variance in the grazer community (Fig. 2.2B), suggesting the observed effects are general and relatively strong.

At the upper range of species' thermal tolerances, metabolism and consumption are predicted to scale differently and metabolic demands should outpace increased grazing intensity (Rall et al. 2009), leading to decreased strength of top-down effects (Lemoine & Burkepile 2012). However, at the sites with the two warmest temperatures (28°C and 29.5°C), the shallow subtidal temperatures often reach 30°C during the warm season (Carr & Bruno 2013); therefore, the temperatures in these assays were representative of the natural temperature regime.

The utilization of a macroecological approach, such as a comparative-experimental design, to examine the tempesrature dependence of herbivore-algal interactions across relatively large spatial and temporal scales, can provide insight into the possible effects on larger-scale ecological patterns (i.e., primary producer composition and biomass). For example, photosynthesis and cellular respiration scale differently with temperature; as animal metabolism and metabolic demands are more sensitive to warming than plant production (Davison 1987, Allen et al. 2005). Therefore, warmer temperatures should increase primary productivity, yet paradoxically, reduce standing plant biomass due to higher consumer pressure (Enquist et al. 2003, Brown et al. 2004, O'Connor et al. 2009, O'Connor et al. 2011). Thus, in areas where

Lytechinus is locally abundant, the higher grazing rates at warm sites and during warmer seasons and years (e.g., El Niño) may increase the prevalence of urchin barrens or alter algal community composition due to the increased relative strength of herbivory, despite an increase in primary productivity.

Because this study focused on *Ulva* spp., we cannot extrapolate to how temperature would affect other algal-urchin interactions. Nonetheless, *Ulva* spp. is by far the most abundant macroalgal species in intertidal and shallow subtidal habitats (Vinueza et al. 2006, Carr & Bruno 2013, Vinueza et al. 2014, Table 2.1). And further, *Ulva* spp. was the most abundant algal species present in the field exclusion experiment (Fig. 2.3). Notably, this experiment lasted for 12 weeks, however; herbivore exclusion experiments in the Galápagos intertidal conducted over months and years have found ephemeral species (e.g., *Ulva* spp.) are one of the dominant macroalgal species, along with competitively dominant species, like coralline algae (Vinueza et al. 2006, 2014). Therefore, results from both our (and others) field exclusion experiment(s) and field surveys are consistent: *Ulva* spp. is a dominant benthic space occupier in the Galápagos shallow subtidal and thus, changes in herbivore-*Ulva* interactions could strongly influence algal community biomass and composition across the Archipelago.

Our results are also consistent with other studies conducted in the intertidal across varying upwelling conditions that suggest herbivore effects on algal community structure can also be driven by changes in the responses of less palatable, corticated algae (Nielsen & Navarette 2004, Vinueza et al. 2006, 2014). Yet, while Nielsen & Navarette (2004) and Vinueza et al. (2006, 2014) found corticated algae was resistant to herbivory, we found *Hypnea* spp. biomass was strongly influenced by herbivores, as *Hypnea* spp. was not found in either the open plots or the mobile herbivore cages. This difference could be attributed to different grazer guilds

between the intertidal and subtidal. For example, some species of parrotfish exhibit a strong

preference for *Hypnea* spp. and *Gracilaria* spp. (Mantyka & Bellwood 2007).   Our results

support this finding as *Hypnea* spp. were absent from the plots most likely to be visited by

parrotfishes, (i.e., open plots and mobile herbivore treatments).

Although Vinueza et al. (2006, 2014), working in intertidal habitats in the Galápagos (our

study was conducted in the shallow subtidal) attributed greater algal biomass among sites to local

nutrient concentration via spatiotemporal variation upwelling intensity, nutrient concentration

was not quantified or manipulated. And further, Schaeffer et al. (2008) measured nitrate

availability and temperature across the Archipelago at four different times and at 70 stations,

generating 280 sampling points, and did not find the expected negative relationship between

nutrient availability and temperature ($R^2 = 0.002$), unlike other studies in temperate upwelling

systems (e.g., Nielsen & Navarrete 2004). Therefore, it is unlikely that the relationship between

temperature and standing algal biomass and growth in the Galápagos can be solely attributed to

nitrate availability.

Moreover, the results from Vinueza et al. (2006, 2014) were also consistent with

temperature-dependent grazing as temperature was positively related to grazing rate (and

generally declined during upwelling). However, the potential role of temperature was not

explicitly tested. Favoring a bottom-up explanation over the possibility of temperature-mediated

top-down effects is a nearly universal phenomenon in studies of the role of algal-herbivore

interactions in upwelling systems (e.g., Menge & Branch 2001, Nielsen & Navarette 2004).

Furthermore, like Vinueza et al. (2006, 2014), the norm is to not measure or even manipulate

nutrient availability, but rather to use upwelling (and chlorophyll *a*) as a natural (nutrient

availability) treatment even though upwelled water is not just nutrient rich, but also much cooler.

These mensurative studies have led to the paradigm that upwelling systems are largely bottom-up controlled. Yet our field exclusion experiment clearly demonstrates the very large role of grazers in controlling standing algal biomass during the upwelling season in an upwelling region, suggesting top-down effects are also important in this system, even with temperature induced changes in herbivory (i.e., upwelling and cold periods can dampen the strength of grazing).

Recent evidence from microcosms and ecological theory suggests herbivore-plant interactions in upwelling systems could be disproportionately affected with warming temperatures (Smith 2008, O'Connor et al. 2009). For example, O'Connor et al. (2009) found that in nutrient-limited regions, food webs may be more resilient to warming because consumer production and biomass is limited by resource availability. In contrast, in upwelling or well-mixed systems, where nutrient availability is high, small levels of warming can lead to stronger consumer control of primary producer biomass and ultimately, alter food web structure (O'Connor et al. 2009). In further support, results from a global meta-analysis found that even with the expectation of more intense grazing in the tropics and a positive relationship between herbivore feeding rates and temperature, the exclusion of herbivores did not result in higher standing algal biomass relative to temperate regions (Poore et al. 2012). Thus, these results suggest stratification of the water column in tropical waters maintains lower nutrient availability (Poore et al. 2012) and therefore, tropical systems are more constrained by limited nutrient availability relative to temperate regions, where nutrient availability is high, and thus, temperature-mediated herbivory could play a larger role in regulating benthic algal community dynamics. Our grazing assays coupled with the field exclusion experiment provide empirical *in situ* evidence that herbivore-algal plant interactions in upwelling systems are influenced by temperature. Therefore, our experiments and metabolic theory suggest that warmer water

strengthens herbivore effects via an increase in consumer metabolism, and that ultimately, this could result in reduced algal biomass at higher temperatures in upwelling systems.

Table 2.1. Natural variation in site attributes.
Site codes: SC = San Cristobal, ST = Santiago, IS = Isabela, FE = Fernandina. Values represent means ($n = 25$ quadrats for algal cover). Urchin density and fish biomass was determined as described in *Methods* section.

	WARM				COOL			
Site	SC	ST	IS	FE	SC	ST	IS	FE
Temperature (°C)	29.5	28	26	24.5	24.67	20.8	22.5	19.75
Ulva cover (%)	7.4	9.3	29.8	31.3	18.6	39.1	43.6	48.9
Bare cover (%)	39.2	20.5	39.4	35.7	49.4	5.6	19.3	2.3
Crustose coralline algae cover (%)	18.7	30.2	27.6	28.4	5.3	18.2	21.8	21.3
Red filamentous algae cover (%)	0	1.5	1.8	2.3	0	22.4	6.1	6.3
Green filamentous algae cover (%)	0	0	1.4	1.1	0	2.2	5.5	1.2
Brown filamentous algae cover (%)	22.6	29.1	0	1.2	17.9	0	3.7	0
Coralline algae cover (%)	0	0	0	0	0	10.4	0	12.9
Padina cover (%)	12.1	9.4	0	0	8.8	2.1	0	0
Sargassum cover (%)	0	0	0	0	0	0	0	7.1
Eucidaris density (0.5m^{-2})	1.6	6.4	10.9	4.67	3.2	5.53	10.46	5.37
Lytechinus density (0.5m^{-2})	36.4	21.7	14.7	26.1	39.1	11.2	18.7	24.6
Lytechinus test size (cm) (mean ± 1 SE)	3.5 ± 0.03	3.8 ± 0.06	3.9 ± 0.06	4.1 ± 0.04	3.8 ± 0.09	3.9 ± 0.05	3.9 ± 0.06	4.1 ± 0.09
Herbivorous fish biomass (g/m-2)	2000.8	1783.1	551.3	224.3	1109.4	953.2	571.8	184.3
Damselfish biomass (g/m-2)	49.9	69.4	30.1	22.6	76.5	71.7	27.6	30.9

Table 2.2 Two-factor ANOVA and ANCOVA on control-corrected grazing rates.

Grazing Assay Treatment	Factor	SS	d.f.	*F*	*P*
Urchin Enclosures	Temperature	150.46	1	56.35	<0.0001
	Site	20.65	3	2.58	0.060
	Temperature*Site	36.02	3	4.49	0.006
	Error	192.25	72		
Open Plots	Temperature	43.26	1	30.12	<0.0001
	Site	12.49	3	8.69	<0.0001
	Green Urchin Density	0.21	1	0.15	0.704
	Temperature*Site	1.01	2	0.35	0.705
	Error	103.41	72		

Table 2.3. One-factor ANOVA on final algal biomass.

Factor	SS	d.f.	*F*	*P*
Treatment	723.5	3	32.1	<0.0001
Error	270.3	36		

Figure 2.1. Map of the Galápagos Islands and the surrounding currents.
Black triangles indicate site locations. Modified from Schaeffer et al. 2008. EUC = Equatorial Undercurrent, SEC = South Equatorial Current, NECC = North Equatorial Counter Current, Humboldt = Humboldt Current
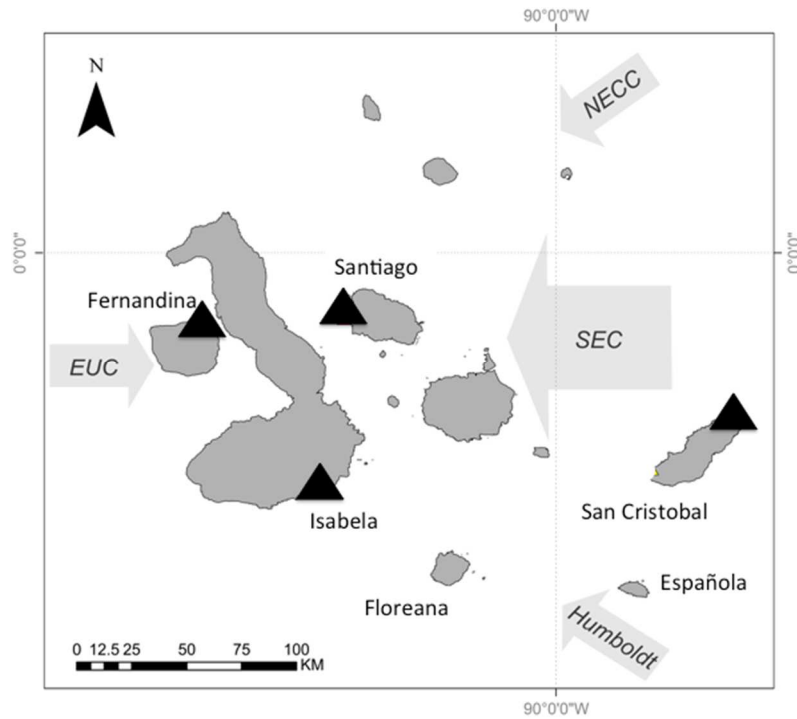
Figure 2.2. Temperature effects on A) urchin and B) mobile and benthic herbivore consumption of *Ulva*.

Biomass consumption was estimated as $([H_i \times C_f/C_i] - H_f) = F_B$, where H_i and H_f were the initial and final wet weights of algal tissue in the presence of herbivores, and C_i and C_f were initial and final wet weights of the controls, F_B = amount consumed. Percent consumed was determined from F_B/C_f. Letters above error bars correspond to island (site) name. FE = Fernandina, ST = Santiago, IS = Isabela, SC = San Cristóbal. Site locations can be found in Figure 1. Red and blue circles denote warm and cold season sampling, respectively. Values are means ± 1 SE; *n* = 10.
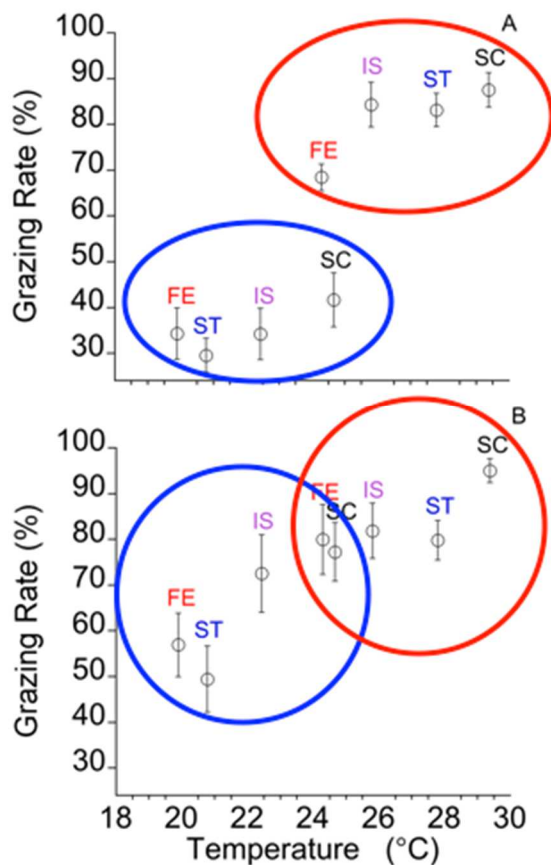
Figure 2.3. Herbivore effects on algal biomass.
Schematic diagram of treatments is shown below treatment names. Values are means; $n = 10$.
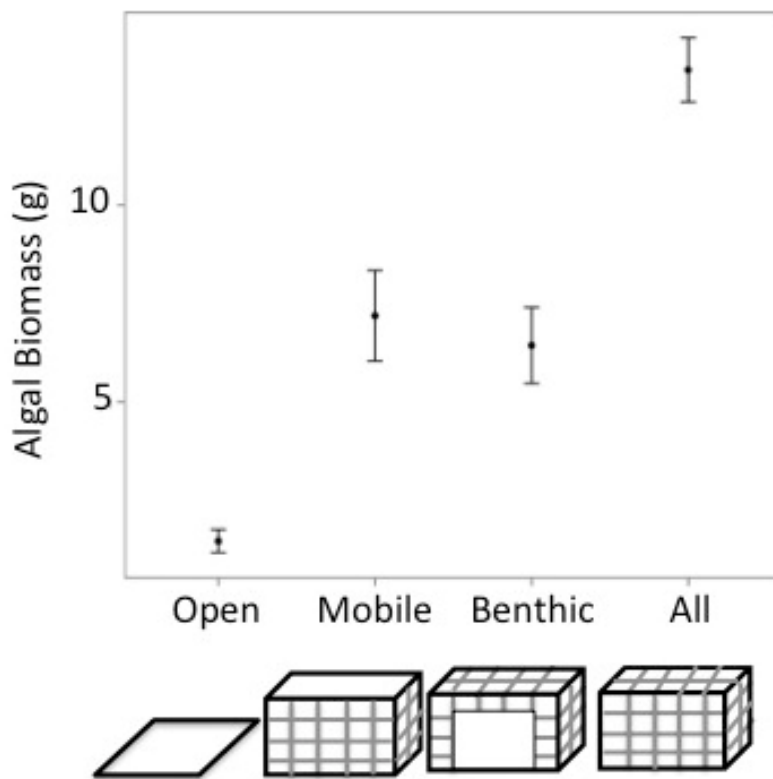
CHAPTER 3: SPATIOTEMPORAL VARIATION IN THERMAL REGIMES AND CONSUMER ASSEMBLAGES INFLUENCES SUBTIDAL BENTHIC COMMUNITIES ACROSS THE GALAPAGOS ISLANDS

Introduction

At the interface of marine ecology and oceanography, a substantial body of work has identified some of the main physical oceanographic processes that can regulate nearshore benthic communities (e.g., Menge 1976, Menge and Lubchenco 1981, Bustamante et al. 1995, Connolly and Roughgarden 1998, Dayton et al. 1999, Roughgarden 2006). There are three major benthic-pelagic pathways, nutrient transport and deposition, larval recruitment and temperature mediated metabolism (Witman and Dayton 2001). These processes can drive benthic-pelagic coupling via physical linkages between these two environments. All three pathways can be modulated by changes in the frequency, duration, and magnitude of upwelling, or the wind-driven oceanographic process of cool, nutrient-rich subsurface currents replacing warmer, nutrient-poor surface currents.

First, the arrival of nutrients from the water column to the benthic environment is an important process influencing nearshore community composition and persistence (Menge et al. 1997, 2003, Nielsen 2003, Navarrete et al. 2008). Second, delivery and recruitment of species with pelagic larval stages to benthic populations are influenced by larval behavior and physical transport processes (for example, internal waves or tidal bores associated with upwelling dynamics) (Leichter et al. 1996, Pineda and Lopez 2002, Witman et al. 1993, 2003). Third, variation in temperature influences organismal metabolism, and thus, other biological processes,

such as growth, reproduction, and consumption, in predictable ways. Specifically, warmer (cooler) water increases (decreases) metabolic rates (Brown et al. 2004). And while upwelled water is nutrient rich, it is also cooler. Metabolic theory coupled with a growing number of empirical studies suggest temperature can decrease metabolic rates in upwelling systems with consequent effects on community dynamics (Smith 2008, O'Connor et al. 2009, Carr and Bruno 2013).

In upwelling systems, macroalgal assemblages are an important part of the subtidal benthic community. Macroalgae-associated consumers (fishes and other grazers) can drive changes in macroalgal biomass and community composition and distribution (Schiel and Foster 1986, Chapman and Johnson 1990, Sala and Boudouresque 1997). For example, exclusion of an herbivorous fish in a temperate rocky reef system in Chile was consistent with changes in macroalgal community composition (increased abundance of green versus red foliose macroalgae) (Ojeda et al. 1999). At high densities, invertebrate grazers, such as sea urchins, can convert macroalgal assemblages to urchin barrens or pavements with bare space and encrusting algae (Chapman and Johnson 1990, Ruttenberg 2001, Edgar et al. 2010).

Numerous studies have examined the relative strength of physical forcing and plant-herbivore interactions on intertidal benthic community structure across varying oceanographic patterns in upwelling systems (e.g., Bustamante et al. 1995, Bustamante and Branch 1996, Menge et al. 1999, Broitman et al. 2001, Menge et al. 2003, Nielsen and Navarrete 2004, Blanchette et al. 2006, Vinueza et al. 2006, 2014). Yet much less is known about how large-scale physical forcing and local-scale interactions can affect shallow subtidal benthic community structure across environmental gradients in upwelling systems.

Although the Galápagos Islands are situated on the equator, due to the strong upwelling signal across the Archipelago, the biological community is in many ways more temperate than tropical (Edgar et al. 2004, Vinueza et al. 2006, Witman et al. 2010, Brandt et al. 2012, Carr and Bruno 2013, Vinueza et al. 2014). Recent studies of benthic-pelagic coupling in the Galápagos have focused on how upwelling influences 1) propagule transfers within and among subtidal rock-wall habitats (Witman et al. 2010) and 2) how bottom-up forcing of nutrients influences intertidal benthic communities (Vinueza et al. 2006, 2014).

Due to spatial, daily, seasonal, and annual changes in oceanographic currents, the nearshore systems of the Galápagos Islands experience tremendous variation in ocean temperature (11 – 31°C) (Houvenaghel 1984, Schaeffer et al. 2008, Witman et al. 2010). The main foundation species in the shallow nearshore (< 3m) benthic community is macroalgae (e.g., *Ulva* spp., *Sargassum* spp.) (Vinueza et al. 2006, Carr and Bruno 2013, Carr et al. *in review*). And similar to many other temperate systems, sea urchins are the most important invertebrate grazer guild in the Galápagos (Irving and Witman 2009, Brandt et al. 2012), although other important grazers include fishes (razor surgeonfish, blue chin parrotfish), sea turtles and marine iguanas.

Previous work in the Galápagos on spatial and temporal variation in macroalgal assemblages has focused on intertidal sites (e.g., Vinueza et al. 2006, 2014). And specifically, how macroalgal communities vary at a couple of sites over time across gradients in oceanographic conditions and grazing pressure. In the shallow subtidal, past experimental work demonstrated that identity (and not diversity) of sea urchins drives changes in benthic community structure (Brandt et al. 2012). Moreover, sea urchin consumption rates are influenced by temperature, via temperature-mediated metabolism, and thus, grazing rates are

higher at warmer relative to cooler temperatures (Carr & Bruno 2013, Carr et al. *in review*).

However, little is known about the spatiotemporal dynamics of macroalgal communities of the

shallow subtidal habitats across the Galápagos Archipelago. Such information is important

because it lays the foundation for exploring the relationship between benthic community

structure and biotic and abiotic processes that generate these patterns (Underwood et al. 2000).

Our objectives were 1) to provide a comprehensive description of the shallow subtidal

benthic community patterns across sites, seasons and years in the Galápagos Archipelago, 2) to

examine how large-scale physical forcing, via natural temperature gradients, changes benthic

community dynamics, and 3) to investigate the relative effects of local scale interactions and

large-scale processes on benthic community organization.

Methods

The Galápagos Islands straddle the equator 965 km off the coast of Ecuador in the

Eastern Pacific Ocean at the center of several different oceanographic currents. The Equatorial

Undercurrent (EUC) is an eastward flowing subsurface current that drives major upwelling as it

collides with underwater seamounts near the western islands resulting in cold and nutrient-rich

water around these islands (Houvenaghel 1978, 1984). The southern region of the archipelago is

strongly influenced by the cool, and nutrient-rich waters of the Humboldt (or Peru) Current

(Kessler 2006). The North Equatorial Countercurrent (NECC, or the Panama current) delivers

warm, and nutrient-poor water to the northeast region (Kessler 2006). Both the Humboldt

Current and the NECC contribute to the westward flowing South Equatorial Current (SEC),

which strongly influences the central area of the archipelago (Houvenaghel 1984) (Fig 3.1).

The dominant influence to the SEC changes seasonally (Houvenaghel 1984). During the

warm season (December – May), the NECC is the major contributor to the SEC; and the

maximum average sea surface temperature (SST) usually occurs in February and March. In

contrast, the minimum average SST usually occurs in August or September, when the dominant

influence to the SEC is the Humboldt Current. However, ENSO events can disrupt the seasonal

cycle (Barber and Chavez 1983, Chavez et al. 1999).

The easterly trade winds weaken during El Niño events (or the warm ENSO phase

defined by the NOAA Climate Prediction Center as a SST anomaly of +0.5°C on the Oceanic

Niño index for a minimum of five consecutive seasons), resulting in a deeper EUC thermocline,

warmer waters, and ultimately, decreased upwelling throughout the Archipelago. Generally, this

results in low primary producer standing stock in the euphotic zone (Pennington et al. 2006). In

contrast, during La Niña, (the cold ENSO phase, a SST anomaly of -0.5°C for a minimum of five

consecutive seasons), the easterly trade winds strengthen, upwelling intensifies, resulting in

higher primary producer standing stock and sea surface temperature decreases (Izumo 2002).

Between 2010-14, nine sites, that are semi-protected from wave action, were surveyed on

six islands that differ in nutrient availability and temperature due to variation in upwelling

intensity and other oceanographic factors (Carr et al. *in review*, Schaeffer et al. 2008, Vinueza et

al. 2006, 2014, Fig. 3.1). All sites were surveyed at least once, and most sites were surveyed

multiple times. At each site, five 30m transects were placed parallel to shore at ~2-3m depth.

Along each transect, five photoquadrats were placed adjacent to the transect line at fixed

intervals, totaling 25 photquadrats per site. Each photograph captured an area of 625 cm^2 (25 x

25 cm). One hundred points were placed over each photograph in a stratified random design.

Image analysis was conducted with ImageJ v1.48.

Percent cover of each algal species was classified into functional groups consistent with

the classification scheme of Steneck and Dethier (1994) and applied in the Galápagos intertidal

by Vinueza et al. (2006, 2014). Algal groups included crustose coralline algae (CCA), other crustose algae (*Hildenbrandia* spp., *Gymnogongrus* spp.), foliose or sheet-like algae (mainly *Ulva* spp.), articulated corallines (*Corallina* spp., *Jania* spp., *Amphiroa* spp.), corticated algae (*Padina* spp., *Sargassum* spp., *Spatoglossum* spp., *Gelidium* spp., *Hypnea* spp.), and filamentous algae distinguished as red (*Centroceras* spp., *Ceramium* spp., *Polysiphonia* spp.), green (*Bryposis* spp., *Chaetomorpha antennina*, *Cladophora* spp.) or brown (*Ectocarpus* spp.).

Consumer identity and abundance

Urchin identity and abundance was determined by counting and identifying all urchins along five 30 x 1m belt transects per site.

Divers conducted visual fish censuses along five 30 x 2m belt transects by identifying, counting and estimating total length of each fish species to the nearest 1 cm. Fish length estimates were converted to fish biomass using published length-biomass relationships (Froese and Pauly 2013). Fish biomass per unit area was calculated using the allometric conversion relationship $W=aL^b$ (Froese and Pauly 2013), where W is the weight of each fish in grams, L is the total length in cm, and a and b are species-specific parameters. When the allometric parameters (a and b) were not available we used values from congeneric species of similar size and in the same geographic range (Froese and Pauly 2013).

We used generalized linear mixed-effects models to examine the relationship between environmental parameters and 1) total macroalgal and 2) *Ulva* spp. biomass across the archipelago. Fixed factors included: herbivorous fish biomass, green and pencil urchin densities, temperature (measured for 30 days prior to sampling date, with either HOBO temperature loggers or AHVRR Pathfinder Version 5.2, PFV5.2, satellite data obtained from the US National Oceanographic Data Center and GHRSST, NOAA 2013), ENSO cycle (obtained from the

Multivariate ENSO Index, maintained by NOAA, and based on the Oceanic Niño Index, ONI, or the running 3-month mean SST anomaly), and distance to and area of closest upwelling region to each site measured from Schaeffer et al. (2008). Because of repeated measurements at the same sites over multiple years (2010-2014), we nested sites within years. This random effect of the model structure accounts for the statistical non-independence of these observations. The best model that explained the observed data was determined through an Information Theoretic approach (Anderson and Burnham 2002). We calculated differences between the Akaike Information Criterion (AICc, for small sample sizes) of each model and the minimum AICc (Bolker 2008).

All numerical explanatory covariates were standardized (divided by two standard deviations) and centered to compare relative effect sizes (Zuur et al. 2009). We evaluated multi-collinearity between all explanatory covariates with a Spearman rank (r_s) correlation matrix and pairs plot based on the mean values. Spearman rank correlation coefficient was used because this technique does not make assumptions about linearity in the relationship between the two variables (Zar 1996). A logistic (logit) transformation was applied to the percent cover data (Lesaffre et al. 2006). Normality was determined by plotting the theoretical quantiles versus the standardized residuals (Q-Q plots). Homogeneity of variance was evaluated by plotting the residuals versus the fitted values for the final model and for each of the covariates.

We examined benthic community composition across environmental gradients using nonmetric multidimensional scaling analysis (NMS), a robust ordination technique for community data that compares differences in functional group composition among sites (Minchin 1987). NMS can examine potential drivers influencing the final structure of the ordination by exploring correlations between the main dataset (i.e., macroalgal community

composition) and variables in a second matrix (environmental gradient matrix) composed of the same variables described above. The dissimilarity matrix was constructed on a Bray-Curtis distance index.

All analyses were performed in the statistical software R v.3.1.2 (R Core Team 2014). Generalized linear mixed-effects models were performed with the *nlme* package (Pinheiro et al. 2015). NMS analysis was created with the *vegan* package (Oksanen et al. 2015).

Results

We sampled a total of nine sites across the Galápagos Archipelago multiple times between 2010-2014, and generated 37 sampling points. Across all sites and time periods, mean foliose (*Ulva* spp.) algal cover was 23%, crustose coralline algae (CCA) was 17%, other encrusting macroalgae was 2%, red filamentous algae was 12%, brown filamentous algae was 11%, coralline macroalgae was 7%, green filamentous algae was 5%, corticated algae was 5%, and bare space was 17%.

Cold sampling periods were defined as <24°C and warm sampling periods were defined as >24°C. The threshold of 24°C was based on the signature of the EUC, adjusted to account for shallow water heating and mixing with the other tropical surface currents (Schaeffer et al. 2008). Overall, macroalgal percent cover was higher at the cold (48%, $n = 21$) compared to the warm (18%, $n = 17$) sampling periods. There was a higher percent cover of foliose (*Ulva* spp.) algae (32% ± 3.9%) during cold relative to warm (10% ± 3.0%) sampling periods, as well as coralline algae (10% ± 1.8% compared to 4% ± 2.0%) and filamentous (34% ± 4.2% compared to 25% ± 8.0%) algae (Fig. 3.2). Conversely, the percentage of bare space was higher at warm (25% ± 2.9%) compared to cold (11% ± 2.1%) sampling periods, as well as crustose algae (24% ± 0.6%

compared to 15% ± 0.8%) (Fig. 3.2). Corticated algae percent cover was similar between sampling periods (4% ± 1.0% during the warm relative to 6% ± 1.0% during the cold) (Fig. 3.2).

Ulva spp. biomass was negatively related to herbivorous fish biomass, green urchin density, and temperature (Tables 3.1 and 3.2, Fig. 3.3A, Fig. 3.4A and 3.4C). However, spatial and temporal variability for macroalgal biomass (not including *Ulva* spp.) was only negatively related to temperature (Tables 3.1 and 3.2, Fig. 3.3B, Fig. 3.4B and 3.4D). Or in other words, at higher temperatures, macroalgal biomass decreased, independent of grazing biomass and density (Tables 3.1 and 3.2, Fig. 3.3B, Fig. 3.4B and 3.4D).

The non-metric multidimensional scaling (NMS) ordination converged on a stable, 2-dimensional solution (final stress = 0.10, iterations = 14) (Fig. 3.5). Colder sampling periods were characterized by foliose and corticated algae (upper left) and coralline algae (lower left) (Fig. 3.5), while warmer sampling periods were characterized by bare space and filamentous algae (Fig. 3.5). Bare space was ordinated along a gradient of green urchin density (Fig. 3.5). Crustose coralline algae, along with other crustose algal species, were ordinated along a gradient of herbivorous fish biomass (Fig. 3.5).

Temperature, green urchin density, and herbivorous fish biomass were significantly correlated with the ordination axes (Table 3.3). Temperature and green urchin density were positively correlated with axis one (Table 3.3). Upwelling area, ENSO, and pencil urchin density were positively correlated with axis two, while distance to upwelling region, herbivorous fish biomass and temperature were negatively correlated with axis two (Table 3.3). Overall, temperature was the predominant gradient structuring the macroalgal assemblages ($r^2 = 0.58$, Table 3.3). Green urchin density ($r^2 = 0.24$, Table 3.3) and herbivorous fish biomass ($r^2 = 0.27$, Table 3.3) were the other major factors structuring macroalgal communities.

59

Discussion

Foliose macroalgae (mainly *Ulva*) and filamentous (or turf) algae are the dominant

components in shallow subtidal benthic communities across the Galápagos Archipelago (Fig. 2).

These results are consistent with manipulative studies conducted in the Galápagos in the low

intertidal (Vinueza et al. 2006, 2014) and shallow subtidal zones (Carr and Bruno 2013, Carr et

al. *in review*) where foliose and coralline macroalgae and filamentous algae were the main

benthic space occupiers, particularly after consumer exclusion.

Consistent with observations from other studies conducted in the Galápagos (Vinueza et

al. 2006, 2014, Carr et al. *in review*), these results demonstrate macroalgal biomass is higher

during cold (<24°C) than warm (>24°C) periods (Fig. 3.2). Temperature was negatively

associated with spatial and temporal variation in both *Ulva* and macroalgal biomass. Macroalgal

biomass refers to all other species except for *Ulva*, those include corticated species, such as

Padina, *Sargassum*, and *Spatoglossum* and coralline species, such as *Corallina*, *Jania*, and

Amphiroa. Percent cover of *Ulva* was 32% during the cold compared to 10% during the warm

sampling periods. All other macroalgal cover abundance was 30% higher at cold relative to

warm temperatures (Fig. 3.2).

While grazer biomass and density (herbivorous fish biomass and green urchin density)

were negatively associated with variation in *Ulva* biomass (Fig. 3.4A and 3.4C), there was no

relationship between grazers and all other macroalgal biomass (Fig. 3.4B and 3.4D).

Manipulative studies conducted in intertidal zones in upwelling systems have found similar

results. Ephemeral species, such as *Ulva*, are early colonizers and readily consumed by grazers,

while corticated and coralline species are late successional species and are more resistant to

grazers (Nielsen and Navarrete 2004, Vinueza et al. 2006, 2014). Further, these results support

other studies that found evidence for strong top-down control in the Galápagos subtidal (Irving and Witman 2009, Witman et al. 2010, Brandt et al. 2012, Carr et al. *in review*). Specifically, Irving and Witman (2009) and Carr et al. (*in review*) demonstrated green sea urchins to be voracious consumers of algae relative to other sea urchin species in the Galápagos.

Consistent with the results from the GLMM, temperature, herbivorous fish biomass and green urchin density were significant predictor variables describing the spatial and temporal variation in benthic community composition and abundance. Warmer temperatures were negatively associated with foliose and corticated macroalgae, and positively associated with filamentous algae and crustose coralline algae. Herbivorous fish biomass was positively correlated with crustose coralline algae, and negatively correlated with foliose and corticated macroalgae. Green urchin density was positively correlated with bare space and green filamentous algae, and negatively correlated with coralline algae.

In contrast with other studies (Vinueza et al. 2006, 2014), ENSO cycle was not correlated with benthic community dynamics. This result is likely due to the absence of a strong El Niño/La Niña during our sampling period. The exception was a fairly strong La Niña in August 2010, but only two sites were sampled during this period. Also, neither of the upwelling variables (distance to and area of closest upwelling region) were correlated with benthic community composition and abundance. Schaeffer et al. (2008) reported that these upwelling or productive regions are highly ephemeral in space and time.

In upwelling systems, temperature and nitrate concentrations are assumed to co-vary, with lower temperatures an indicator of higher nitrate concentration and availability. Often lower temperatures are used as a proxy for nitrate/nutrient availability. However, the temperature-nitrate relationship in the Galápagos appears to be more complicated. For example,

while Nielsen and Navarrette (2004) found an expected negative relationship between nitrate concentration and temperature in the Chilean upwelling system, other *in situ* and satellite-derived studies conducted across the Galápagos Archipelago did not find any relationship between nitrate concentration and temperature (Palacios 2002, 2004; Schaeffer et al. 2008) (Fig. 6A).

Chlorophyll concentrations, a measure of phytoplankton biomass, are often used as a proxy for nutrient availability because the uptake of nitrate by algae could deplete nitrate availability in colder waters, resulting in a non-significant relationship between nitrate concentration and temperature. In other words, standing phytoplankton biomass is used as a proxy for primary production. Yet production is the rate that a photosynthetic organism photosynthesizes and adds to its biomass while accounting for other metabolic needs (e.g., cellular respiration). In other words, primary production can vary widely while phytoplankton biomass remains relatively constant (Dugdale 1989, Kudela and Dugdale 1996). Disentangling the rate of primary production from standing biomass requires sophisticated models that incorporate ocean color, sea surface temperature, estimation of nitrogen uptake rates and the phytoplankton community size structure (e.g., Silio-Cazada et al. 2008). Therefore, it could be difficult to infer nutrient availability based on chlorophyll concentrations alone.

In the Galápagos Archipelago, Schaeffer et al. (2008) reported a negative relationship between chlorophyll concentration and temperature at 70 stations sampled four times across the Galápagos Archipelago (Fig. 3.6B). An alternative explanation to a resource availability bottom-up mechanism could be temperature-mediated variation in consumptive pressure. For example, colder waters could result in decreased grazing rates, via temperature-mediated metabolism, and result in higher primary producer standing biomass. Differential temperature scaling of primary and secondary production, specifically photosynthesis and respiration, leads to decreased

consumption relative to primary production at cooler temperatures (Davison 1987, Allen et al. 2005, Padilla-Gamiño and Carptenter 2007). The end result would be lower rates of both primary and secondary production with cooler temperatures, but higher standing biomass due to less intense grazing (Bruno et al. 2015). Conversely, laboratory and *in situ* experiments suggest that predation intensifies at warmer temperatures, resulting in lower standing algal biomass (O'Connor 2009, Carr and Bruno 2013).

In the Galápagos Islands, temperature variation in the Galápagos can influence sea urchin metabolism and grazing rates (Carr and Bruno 2013, Carr et al. *in review*). Ultimately, warmer temperatures result in higher green sea urchin metabolic demands (Carr and Bruno 2013) and thus, increased consumption of *Ulva* (Carr and Bruno 2013, Carr et al. *in review*). Further, empirical and meta-analysis results suggest temperature can influence the prevalence of sea urchin barrens (Carr and Bruno 2013, Byrnes et al. 2013, Carr et al *in review*). For example, in systems with high temperature variation, and given the concomitant mismatch in metabolic responses between producers and herbivores (O'Connor 2009, O'Connor et al. 2009, 2011), warmer temperatures could result in either the 1) formation (Byrnes et al. 2013), or 2) increased size or persistence (Carr and Bruno 2013, Carr et al. *in review*) of sea urchin barrens. The negative correlation between percent cover of *Ulva* and sea urchin density, demonstrated by empirical studies (Carr and Bruno 2013, Carr et al. *in review*), indicates top-down effects are important drivers of macroalgal dynamics in the Galápagos, and further, these effects can be mediated by changes in temperature. Therefore, a negative correlation between temperature and *Ulva* could be due in part to temperature-mediated effects of grazing pressure.

In summary, macroalgal cover was negatively correlated with ocean temperature. However, there is still a lack of understanding regarding the mechanistic underpinnings of this

relationship. The links between nutrients, temperature and algal biomass appear to be more complicated, perhaps due to the predictable effects of temperature on trophic interactions, and/or possibly some other factor(s). However, this study coupled with recent empirical work (Carr and Bruno 2013, Carr et al. *in review*) suggest temperature could be an additional physical driver of benthic community dynamics via predictable temperature-mediated effects on organismal metabolism. Due to the importance of macroalgae in the Galápagos, a better mechanistic understanding of how the interplay among temperature, nutrient availability and consumers maintain benthic community patterns will provide insight into how they will change in the face of climate change, and other anthropogenic stressors.

Table 3.1 Ranking of the 10 best generalized linear mixed models (GLMM) plus the null model for each response variable.
AICc = Akaike Information Criterion for small sample sizes. All models included the random effect = (1|Year/Site), site nested in year. Other covariates: green = green urchin density, Temp = ocean temperature, HFish = herbivorous fish biomass, Upwelling Area = area of nearest upwelling or productive region, Pencil = pencil urchin density, ENSO = El Niño Southern Oscillation. Bold indicates best model. ΔAICc = difference between the AICc of a particular model compared to the lowest AICc observed.

Response variable	Model	d.f.	ΔAICc
Ulva spp. biomass	NULL: Biomass ~ Intercept	21	36.9
	Biomass ~ Intercept + Green	32	32.8
	Biomass ~ Intercept + Green + Temp	41	2.9
	Biomass ~ Intercept + Temp	32	11.9
	Biomass ~ Intercept + HFish		33.3
	Biomass ~ Intercept + HFish + Temp		12.3
	Biomass ~ Intercept + HFish + Green		23.0
	Biomass ~ Intercept + HFish + Green + Temp		**0.0**
	Biomass ~ Intercept + HFish + Green + Temp + Upwelling Area		1.4
	Biomass ~ Intercept + HFish + Green + Temp + Pencil		1.5
	Biomass ~ Intercept + HFish + Green + Temp + Pencil + Upwelling Area		2.6
Macroalgal Biomass (without *Ulva* spp.)	NULL: Biomass ~ Intercept		14.9
	Biomass ~ Intercept + Temp		**0.0**
	Biomass ~ Intercept + ENSO		3.0
	Biomass ~ Intercept + Green		3.0
	Biomass ~ Intercept + Temp + Pencil		1.9
	Biomass ~ Intercept + Temp + Green		1.8
	Biomass ~ Intercept + Temp + ENSO		2.0
	Biomass ~ Intercept + Temp + Upwelling Area		5.1
	Biomass ~ Intercept + Temp + Green + Upwelling Area		2.0
	Biomass ~ Intercept + Temp + Green + Upwelling Area + Pencil		4.5
	Biomass ~ Intercept + Temp + Green + Upwelling Area + ENSO		3.1

Table 3.2 Model results for best-fit GLMM model based on AICc rankings.

Response variable	Covariate	β± SE	*t* – statistic	*P*
Ulva. spp. biomass	(Intercept)	-1.499 ± 0.171	-8.75	<0.001
	Temperature	-0.529 ± 0.085	-6.24	<0.001
	Green Urchin Density	-0.458 ± 0.110	-4.17	0.002
	Herbivorous Fish Density	-0.179 ± 0.078	-2.32	0.031
Random effects				
Site nested in year estimated variance ± SE: 0.697 ± 0.235				
Macroalgal Biomass (without *Ulva* spp.)	(Intercept)	-2.726 ± 0.128	-21.23	<0.001
	Temperature	-0.164 ± 0.095	-1.723	0.003
Random effects				
Site nested in year estimated variance ± SE: 0.513 ± 0.410				

Table 3.3 Correlation coefficients of environmental variables of each study site with each of the nonmetric multidimensional scaling ordination axes.

	NMDS1	NMDS2	*P*-values
Temperature	**0.7992**	**-0.6010**	**0.001**
Green Urchin Density	**0.8675**	**0.4974**	**0.024**
Pencil Urchin Density	0.0160	0.9999	0.085
ENSO	-0.3857	0.9226	0.876
Herbivorous Fish Biomass	**0.2594**	**-0.9658**	**0.017**
Distance to Upwelling Region	0.3514	-0.9362	0.993
Upwelling Area	-0.1045	0.9945	0.724

Figure 3.1 Map of the Galápagos Islands and the surrounding currents.
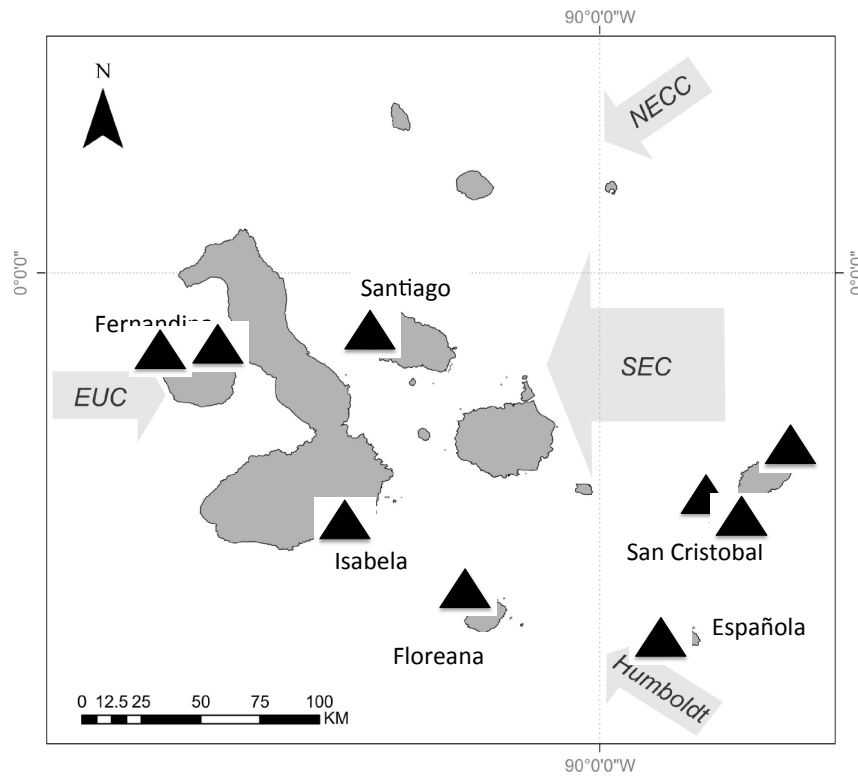Black triangles indicate site locations. Modified from Schaeffer et al. 2008.

Figure 3.2 Benthic community composition at cold and warm sampling periods.
Benthic community composition (% cover) at cold (<24°C, $n = 21$) and warm (>24°C, $n = 17$) sites.
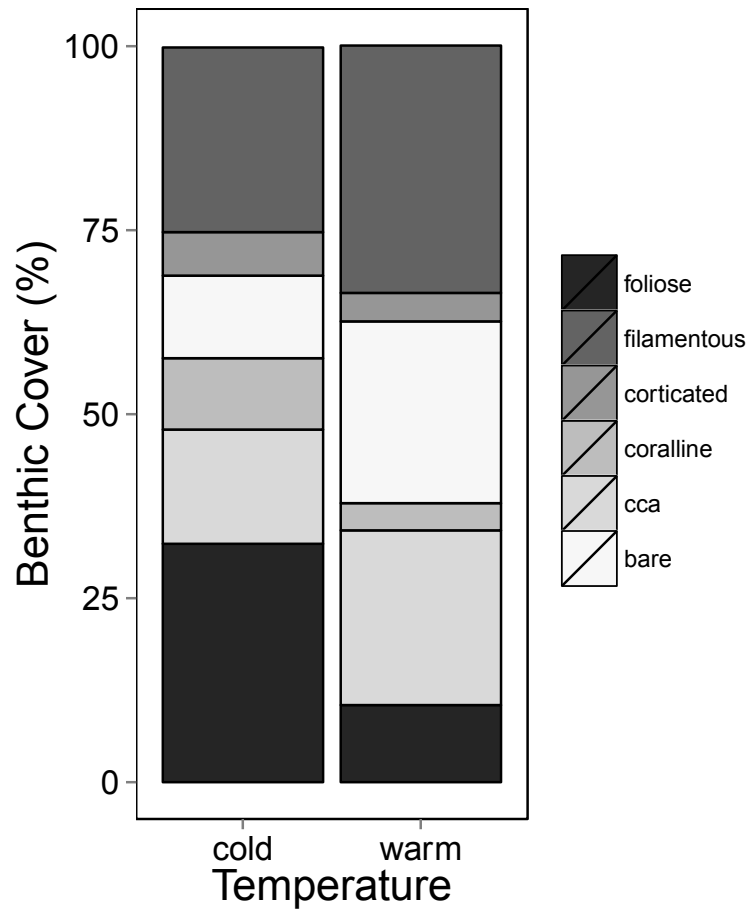
Figure 3.3 Relationship between temperature (°C) and macroalgal percent cover.
Relationship between temperature (°C) and A) foliose macroalgal cover (%) ($p < 0.00001$, $R^2 = 21.8$, $y = -4.9x + 138.6$), and B) all other macroalgal species cover (%) ($p = 0.01$, $R^2 = 14.4$, $y = -1.9x + 56.6$).
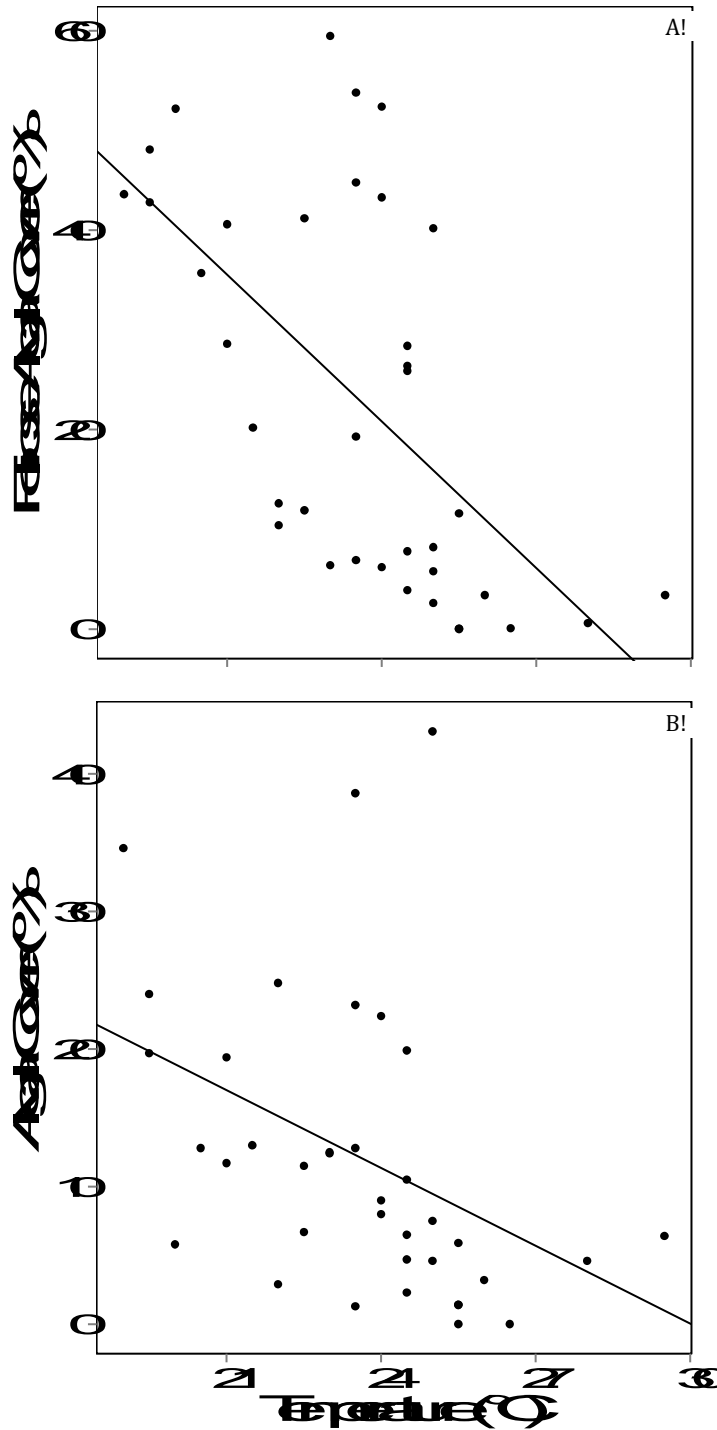
Figure 3.4 Relationship between green urchin density and macroalgal percent cover.
Relationship between green urchin density (No./m^2) and a) foliose macroalgal cover (%) and c) all other macroalgal species cover (%), and between herbivorous fish biomass (g/m^2), and b) foliose macroalgal cover (%) and d) all other macroalgal species cover (%).
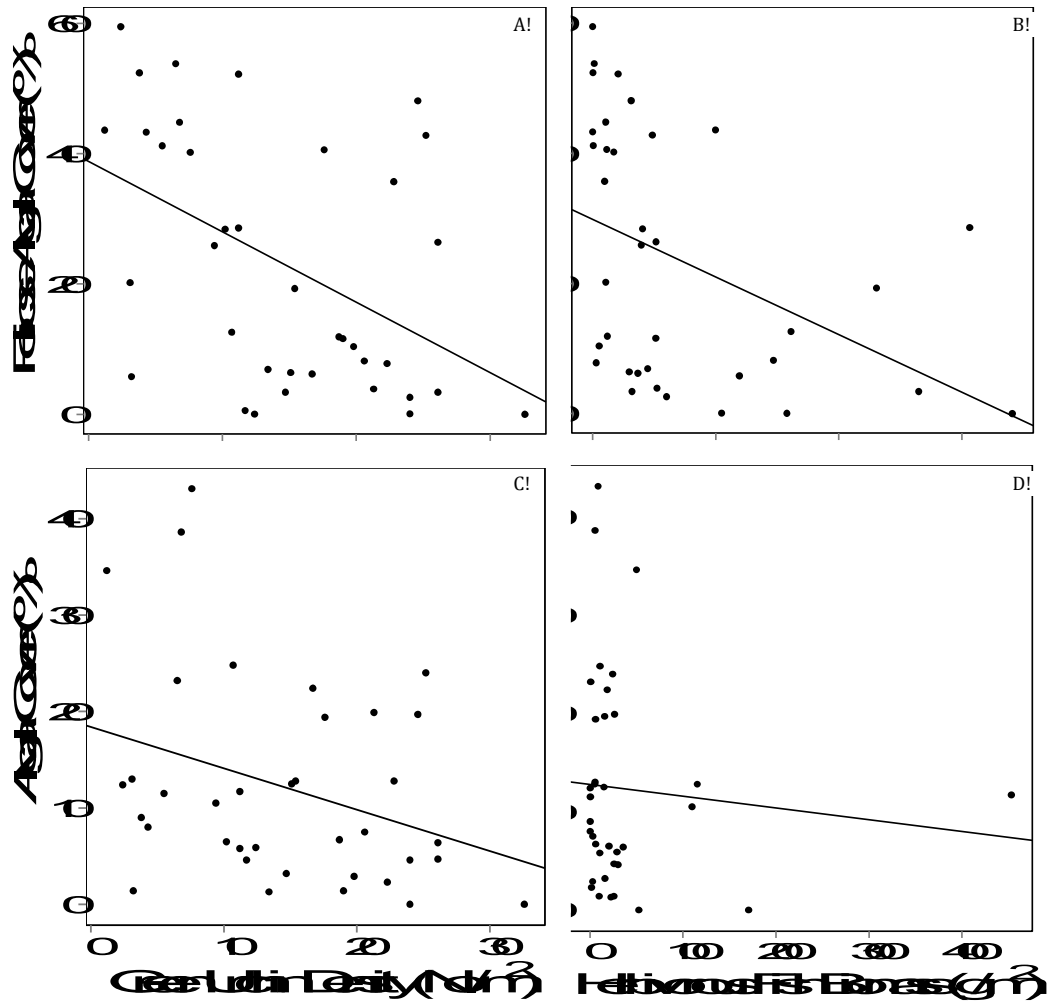
Figure 3.5 Results of nonmetric multidimensional scaling (NMS) ordination.
Results of nonmetric multidimensional scaling (NMS) ordination for each sampling point (number) in relation to macroalgal functional group (red words) and environmental variables (vectors). The length of each vector is proportional to the strength of the correlation.

Figure 3.6 Relationship between temperature (°C) and environmental parameters.
Relationship between temperature (°C) and a) nitrate concentration (µM) and b) chlorophyll a concentration (mg/m^3). Data from Schaeffer et al. (2008).

CHAPTER 4: VARIATION IN THERMAL REGIMES AND HERBIVORE-ALGAL INTERACTIONS ACROSS UPWELLING SYSTEMS
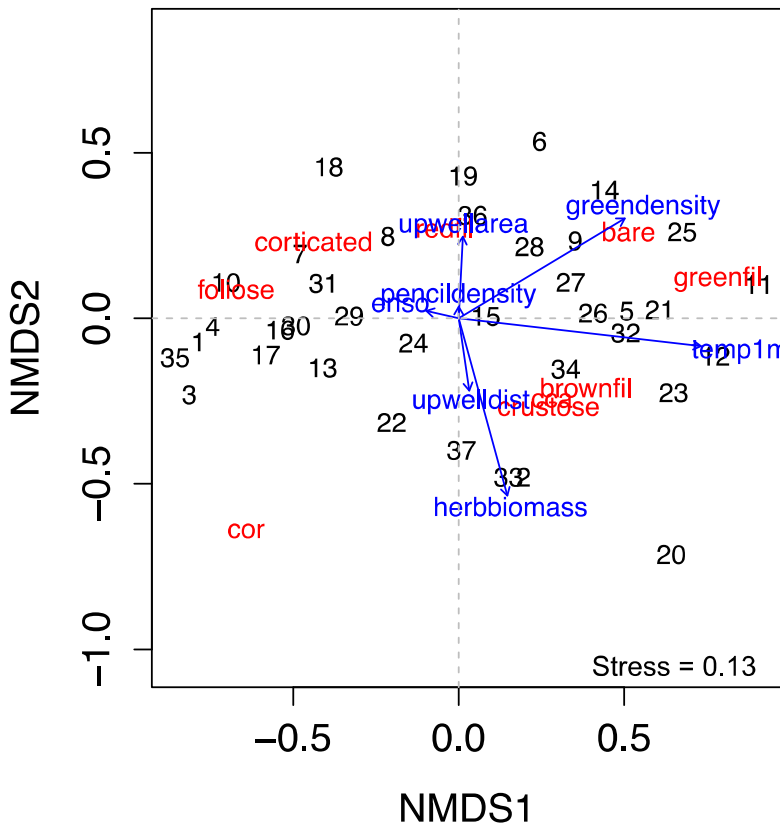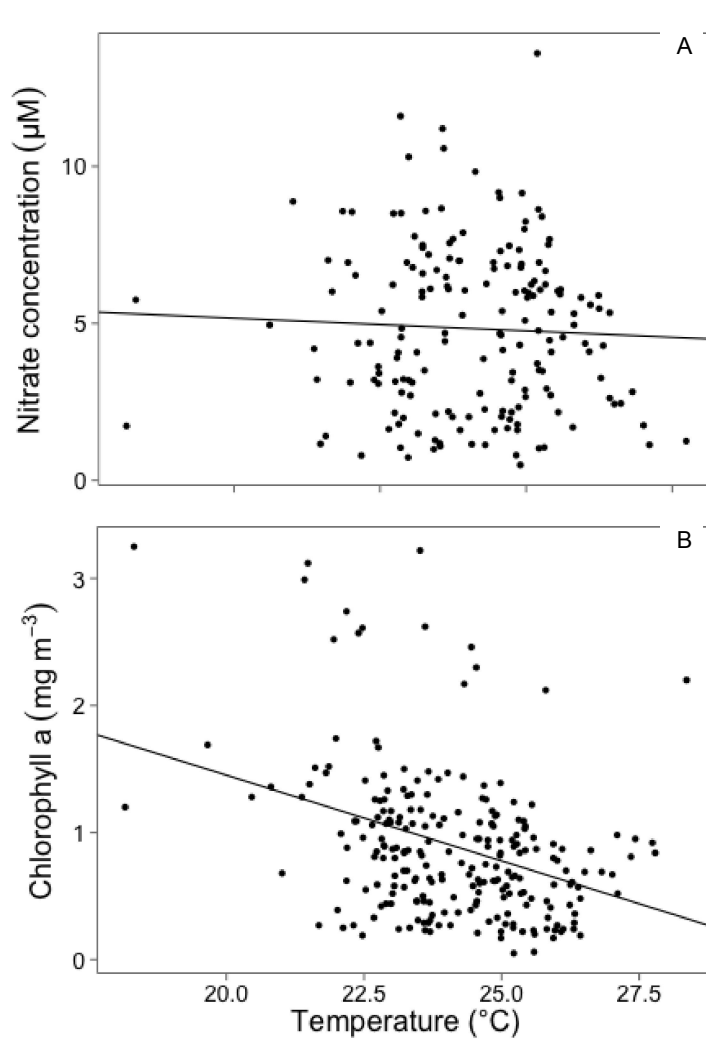
Introduction

Metabolic Scaling Theory (MST) describes how temperature constraints on individual biological rates scale with temperature across taxonomic groups, providing mechanistic predictions on how variation in temperature will drive ecological pattern and process (Gillooly et al. 2001, Brown et al. 2004). For example, temperature mediated metabolism can influence population level processes such as population growth rates. Specifically, maximum and equilibrium population sizes are predicted to increase with warmer temperatures (Sibly et al. 2012). Temperature can also affect community and ecosystem level processes as the outcome and strength of species interactions as well as food web properties like biomass distribution across trophic levels, scale predictably with changes in temperature. For example, the temperature dependence of herbivore-algal interactions can result in changes to larger-scale ecological patterns (i.e., primary producer composition and biomass) because photosynthesis and cellular respiration scale differently with temperature (Gillooly e al. 2001, Brown et al. 2004). Animal metabolism is more sensitive to warming relative to plant production (Davison 1987, Allen et al. 2005). Therefore, warmer temperatures should increase primary production yet result in a reduction of standing plant biomass due to higher consumption by herbivores (Brown et al. 2004, O'Connor et al. 2009).

A growing body of research has tested these predictions in lab and mesocosm settings (e.g., O'Connor 2009, O'Connor et al. 2009, Hoekman 2010, Kratina et al. 2012, Shurin et al.

2012, Carr and Bruno 2013), as well as in the field across natural temperature gradients (Carr et al. *in review*). However, the application of MST across similar ecosystems at global scales remains a significant research gap. Much research has been conducted on how spatiotemporal variation in the tempo, mode and frequency of upwelling, modulates ecological patterns at local, regional and global scales (e.g., Connell 1970, Haury et al. 1978, Harrold et al. 1988, Barry and Dayton 1991, Dayton et al. 1999, Menge 2000, Witman et al. 2010). Yet while many studies have been conducted on how upwelling can regulate benthic community dynamics in upwelling systems via nutrient delivery and larval transport (e.g., Menge et al. 1979, Menge et al. 2008, Bustamante et al. 2008), much less is known about how variation in temperature across upwelling systems can drive changes in benthic community dynamics via metabolic scaling.

Upwelling can occur along the coastlines (Eastern Boundary Current Ecosystems, EBCEs) and the equator (equatorial upwelling), and around islands, or other similar biogeographic features (localized upwelling). There are four major EBCEs: Benguela, Canary, Humboldt and California current systems. All systems are characterized by comparatively narrow continental shelves, equator-ward surface flow over a pole-ward undercurrent, prevailing equator-ward wind stress and coastal wind-driven nearshore upwelling. Equatorial upwelling occurs along the equatorial Pacific due to the easterly trade winds that result in a perpendicular and divergent flow of warm, surface water away from the equator. Localized upwelling occurs along island coastlines and other similar biogeographic features as island wakes (Houvenaghel 1978, Feldman 1986) and internal waves (Witman and Smith 2003).

Upwelled water is generally cold, nutrient-rich, high-salinity, and oxygen poor (*see* Hill et al. 1998 for a review). Therefore, on a global scale, these similar physical characteristics appear to translate to similar ecosystem structure and function across upwelling regions, like disproportionately high primary and secondary production (Chavez and Toggweiler 1995, Pauly

and Christensen 1995) and comparable plankton and fish assemblages (Parrish et al. 1983). Yet it is well documented that changes in the frequency, intensity and duration of upwelling events can influence ecological processes in both rocky intertidal and subtidal systems (e.g., Bustamante et al. 1995, Vinueza et al. 2006, Witman et al. 2010).   However, most of our current knowledge generates from studies conducted in single systems or regions, and there is a lack of quantitative information about spatiotemporal variation in environmental conditions across different upwelling systems, and further, how this variation could influence ecological processes, such as species interactions or benthic community structure via metabolic scaling.

Wieters et al. (2009) compared spatiotemporal variation in nearshore SST fluctuations between two EBCEs, the Benguela system in South Africa and the Humboldt system in Chile. While long-term mean SSTs were generally similar between the two regions they identified striking differences in SST regimes. The Chilean coast is characterized by warmer temperatures, and more stable thermal dynamics, with fluctuations in temperature occurring over relatively longer time-scales. Whereas the South African coast has greater thermal extremes that occur over shorter time scales. Their results also suggest that these different patterns of temporal variability in temperature (beyond average conditions) could drive major changes in nearshore benthic community structure.

MST and empirical studies suggest herbivore-plant interactions in upwelling systems could be disproportionately affected by increasing temperatures relative to tropical or other low-nutrient aquatic systems (O'Connor et al. 2009). Food webs in nutrient-limited systems might be more resilient to warming because consumer production and biomass is constrained by resource availability. In contrast, in systems with high nutrient availability, such as upwelling or well-mixed systems, warmer temperatures can result in stronger consumer effects on primary producer biomass, and thus, alter food web structure (O'Connor et al. 2009).

In upwelling systems, sea urchins are major drivers of benthic ecosystem structure and function, as they can control foundation species biomass and distribution by denuding kelp and other macroalgal species and creating urchin barrens or pavements of encrusting algae (Chapman 1981). For example, in the Galápagos Islands, sea urchins are the most significant invertebrate grazer guild (Irving & Witman 2009, Brandt et al. 2012), and at high densities can convert macroalgal assemblages to urchin barrens (Edgar et al. 2010). Further, recent studies conducted at local scales demonstrate sea urchin metabolism and grazing rates are temperature dependent, resulting in higher oxygen respiration and grazing rates at warmer temperatures (e.g., Carr and Bruno 2013). Yet temperature dependence of herbivore-plant interactions are highly context dependent (Lemoine et al. 2013). Therefore, it is important to examine the temperature dependence of sea urchin-algal interactions across upwelling systems to generate testable and specific hypotheses that predict how sea urchin-algal interactions at local scales will translate to changes at community and ecosystem level patterns.

Here we synthesized available *in situ* temperature data from five upwelling regions, and 1) described and compared thermal regimes at each region, 2) utilized MST to examine how this temperature variation could influence population and community properties in each region.

Methods

We examined spatial and temporal variation in temperature in three Eastern Boundary Current Systems (Chile, South Africa and the Oregon/California coast, broken into two regions: Oregon/Northern California and Central/Southern California). And across the Galápagos Islands, a system where upwelling is driven by different physical mechanisms, including equatorial upwelling. We utilized temperature data collected at a depth of ~1 – 1.5m. In general, temperature data was collected daily from ~ 1999-2010. All regions experience upwelling that is

neither temporally continuous nor spatially uniform, and a brief description of variability in each region is described below.

To examine variation along a weekly timescale, we performed autocorrelation analyses of time series, after the annual and semiannual trends were removed. Autocorrelation functions were obtained by aggregating autocorrelation estimates at a 7 d time lag. Autocorrelation functions describe dissimilarity between observations at time lags and the 7 d time lag is an indicator of linear dependence between successive observations in a time series. We used this function to test for differences in biweekly *in situ* temperature dynamics (Buishand and Beersma 1993). Autocorrelation functions were performed in R v. 3.2.3 (R Development Core Team 2015) using the acf package.

For each upwelling region we selected the sea urchin species that was 1) abundant, and 2) the strongest interactor in the system. To examine the relationship between temperature and urchin consumption rates of algae, we searched ISI Web of Science using the sea urchin species name for each region and "temperature*," "feed*," "consumpt*," "metaboli*," and "rate*."

Galápagos Islands

The Galápagos Islands straddle the equator 965 km off the coast of Ecuador in the Eastern Pacific Ocean at the center of several different oceanographic currents. The Equatorial Undercurrent (EUC) is an eastward flowing subsurface current that drives major upwelling as it collides with underwater seamounts near the western islands (Fernandina and Isabela) resulting in cold and nutrient-rich water around these islands (Houvenaghel 1978, 1984). On smaller spatial scales, topographically induced upwelling occurs in the form of island wakes (Houvenaghel 1978, Feldman 1986), internal waves (Witman and Smith 2003) and other flow-topography interactions along island coasts (Houvenaghel 1978, Feldman 1986). The Humboldt (or Peru) Current (an Eastern Boundary Current) also plays a major role in influencing upwelling

dynamics across the Archipelago. Specifically, the westward advection of the cool and nutrient-rich waters, of the Humboldt Current, result in upwelling across the eastern region of the Archipelago (Houvenaghel 1984). The North Equatorial Countercurrent (NECC, or the Panama current) delivers warm, and nutrient-poor water to the northeast region (Houvenaghel 1984). Both the Humboldt Current and the NECC contribute to the westward flowing surface current, the South Equatorial Current (SEC), which strongly influences the central area of the archipelago (Houvenaghel 1984).

Temperature data was semi-continuously collected between 1998-2013 from 26 nearshore sites across an ~36000 km^2 region between 89-91°W and 0-1°S (Fig. 4.1) with *Onset Hobo®* U22-001 water temperature loggers (Carr and Bruno 2013, Vinueza et al. 2006, 2014, Carr et al. *in review*), and SBE 19*plus* CTD system (Sea-Bird Electronics Inc., Bellevue, WA, USA) casts (Schaeffer et al. 2008).

In rocky subtidal habitats throughout the Galápagos archipelago at depths between 1-5m, *Lytechinus semituberculatus* and *Eucidaris galapagensis* are the two most common urchins (Carr and Bruno 2013). *Lytechinus* was chosen as the study organism, as it is a strong interactor and capable of converting algal turfs (brown filamentous turf, order Ectocarpales: *Giffordia* sp., *Ectocarpus* sp.) to urchin barrens in relatively short time periods, while *Eucidaris* does not have any detectable effect on the abundance of algal turfs (Irving & Witman 2009).

Central-Northern Chilean Coast

Coastal upwelling along the central-northern coast of Chile (eastern Pacific) is driven by the Humboldt Current (an Eastern Boundary Current). The Humboldt Current flows north along the west coast of South America from the southern tip of Chile to northern Peru, and then veers west along the equator, across the Galapagos.

Two coastal zones have been identified due to the seasonality of the alongshore winds. The northern region (18-30°S) is characterized by relatively weaker, but more persistent winds, resulting in year-round favorable upwelling winds. While the central region (30-41°S) has strong seasonality in upwelling (during the austral spring and summer) due to stronger, but more temporally variable winds (Pizarro et al. 1994). Spatial variation in upwelling occurs in the central region due to increases in upwelling intensity around prominent topographic features, like a few large headlands, Punta Lengua de Vaca (30°S) and Punta Curaumilla (33°S) (Gan and Allen 2002).

For this study, we used temperature data collected with StowAway TidbiT temperature loggers (Onset Computer Corporation) from 22 sites across an ~ 30,000 km^2 region encompassing both the northern and central regions (between 29-34°S) (Nielsen and Navarrete 2004, Lagos et al. 2005, Aravena 2013, Tapia et al. 2014)(Fig. 4.1).

Loxechinus albus, or the red sea urchin, is one of the most economically important species in shallow benthic habitats along the Peru and Chilean coast (Stotz 2004). Along the Chilean coast, *L. albus* is a major benthic grazer in both intertidal and subtidal rocky environments and is closely associated with *Macrocystis* beds and overgrazing can result in urchin barrens (Dayton 1985, Vasquez and Buschmann 1997). *L. albus* consumes both *Ulva* and *Macrocystis* (Vasquez and Buschmann 1997).

West Coast of South Africa

Along the western coast of South Africa (western Atlantic), the Benguela Current drives coastal upwelling. The Benguela Current is an Eastern Boundary Current that flows equator-ward from the southern extreme tip of Africa (34°S) to the Angola-Benguela Front (15°S) then flows offshore and to the west (Shannon 1985). The cool Benguela Current (~ 12°C) is bounded

by warm water both at the North (Angola Current, ~18°C) and at the South (South Atlantic Current and the Agulhas Current, ~24°C) (Strub et al. 1998).

The Benguela Current System is ultimately two different subsystems, north and south of 26°S, separated by the permanent upwelling cell off Luderitz (Strub et al. 1998). For our analysis, we focused on the region south of 26°S. This region encompasses both perennial and seasonal upwelling cells (Silio et al. 2008). Although, the seasonal signal is strongest in the south, and upwelling intensifies during the spring and summer (Strub et al. 1998).

We utilized temperature data collected from 44 stations across an ~ 40,000 km^2 region between 26-35°S, from Luderitz, Namibia to Cape Point (Wieters 2006, Roualt et al. 2007, Silio et al. 2008, Smit et al. 2013) (Fig. 4.1). Smit et al. (2013) collates all available *in situ* data for the South African coast, and the majority of the data is available at http://www.cfoo.co.za and was collected with *Onset Hobo*® U22-001 water temperature loggers. Silio et al. (2008) used the "World Ocean Database 2005" (WOD05) of the NOAA-NESDIS-National Oceanographic Data Center for *in situ* temperature data and is available at:

http://www.nodc.noaa.gov/OC5/WOD05/docwod05.html.

The California Current System

The California Current System (CCS) is forced by large-scale winds influenced by the North Pacific High, the Aleutian Low, and the thermal low-pressure system extending from central California to northern Mexico. Currents associated with the California Current System include: the southward flowing California Current and the coastal jet, the northward flowing California Undercurrent and Davidson Current, and the Southern California Eddy (Checkley and Barth 2009). The California Current (CC) flows equatorward within about 1000 km off the west

coast of North America. The CC is present year-round, and is fed in the north by the bifurcating North Pacific Current and is part of the North Pacific Gyre (Sverdrup et al. 1942).

Oregon and Northern California

We used temperature data collected from 18 sites across an ~32000 km^2 region between 38-45°N, south of Cape Mendocino to north of Cape Blanco (Fig. 4.1). Temperature was collected with StowAway TidbiT temperature loggers (Onset Computer Corporation, TBI32-05 + 37) (Tapia et al. 2009, Iles et al. 2011, http://www.piscoweb.org), and from a depth of ~0.6m from the National Data Buoy Center (http://www.ndbc.noaa.gov).

Central and Southern California

Temperature data was collected from 24 sites across an ~24000 km^2 region between 32-38°N, ~ Point Conception to Cape Mendocino (Fig. 4.1). Temperature data was recorded with StowAway TidbiT temperature loggers (Onset Computer Corporation, MA), Pendant temperature loggers (Onset Computer Corporation, MA) and from a depth of ~0.6m from the National Data Buoy Center (Tapia et al. 2009, Seo et al. 2012, http://www.ndbc.noaa.gov, http://cce.lternet.edu, http://www.piscoweb.org).

Strongylocentrotus purpuratus are capable of converting kelp forests to urchin barrens (Paine and Vadas 1969, Tegner and Dayton 2000) in nearshore rocky intertidal and subtidal habitats along the west coast of North America and range from Isla Cedros in Baja California, Mexico to Cook Inlet, Alaska (Tegner and Dayton 2000).

Results

Ocean temperature along the Chilean coast ranged from 8.4°C - 23°C (Fig. 4.2, Fig. 4.3, Fig. 4.4A). The mean temperature along the Chilean coast was 14.8°C ± 0.25°C (Fig. 4.2, Fig. 4.3, Fig. 4.4A).

Temperature data was recorded from five sites along the Chilean coast (Fig. 4.5B). The northernmost site, Arrayan, was the warmest site and also the site with the greatest temperature variability (Fig. 4.5B). The temperature range was 12.5°C to 23.6°C, with a mean temperature of 16.3°C ± 0.18°C (Fig. 4.5B). Mantanzas, the southernmost site, was the coldest site as well as the site with the least temperature variability (Fig. 4.5B). The mean temperature was 14.1°C ± 0.14°C, with a temperature range of 11.1°C to 18.2°C (Fig. 4.5B).

The coldest month was September with a mean of 13.3°C ± 0.07°C, and mean temperatures ranged from 13.3°C to 14.2°C (Fig. 4.6A). February was the warmest month, with a mean temperature of 18.1°C, and a range of 15.2°C to 19.4°C (Fig. 4.6A). February was also the month with the largest mean temperature range (Fig. 4.6A). The month with the smallest temperature range was October with a temperature range of 13.4°C to 14.3°C, and a mean temperature of 13.9°C ± 0.05°C (Fig. 4.6A)

In situ feeding rates and water temperature were measured for two years (1968-69) for *Loxechinus* (Buckle 1978). The total temperature range was 4.5°C. The dominant algae consumed were *Macrocystis* and *Ulva*. There was no relationship between temperature and *Loxechinus* grazing rates (Figure 4.7A, $R^2 = 0.04$, $p = 0.23$).

Temperature ranged from 13.4 °C – 20.6°C along the west coast of South Africa (Fig. 4.2, Fig. 4.3, Fig. 4.4B). Mean temperature over whole region was 16.5°C ± 0.2°C (Fig. 4.2, Fig. 4.3, Fig. 4.4B).

Temperature data was recorded from five sites along the South African coast (Fig. 4.5C). The northernmost site, Hanglip, was the warmest site and also the site with the smallest temperature variability (Fig. 4.5C). The temperature range was 15°C to 22.7°C, with a mean temperature of 18.8°C ± 0.21°C (Fig. 4.5C). McDougall, the southernmost site, was the coldest

83

site as well as the site with the largest temperature variability (Fig. 4.5C). The mean temperature was 13.8°C ± 0.16°C, with a temperature range of 8.3°C to 18.7°C (Fig. 4.5C).

March was the warmest month with a mean temperature of 19.0°C ± 0.12°C, and a range of 17.1°C to 20.6°C (Fig. 4.6B). August was the coldest month with a mean of 14.1°C ± 0.09°C, and mean temperatures ranged from 13.3°C to 14.9°C (Fig. 4.6B). June had the least temperature variability with mean temperatures ranging from 14.5°C to 15.4°C. March and November had the largest mean temperature range (Fig. 4.6B). Mean temperatures ranged from 14.7°C to 18.3°C for November (Fig. 4.6B).

The Galápagos Islands had the greatest temperature variation across all regions with ocean temperatures recorded between 11-31°C; as well as, the highest ocean temperature relative to the other regions (Fig. 4.2, Fig. 4.3, Fig. 4.4C). The mean temperature across the Galápagos Islands was 22.9°C ± 2.1°C (Fig. 4.2, Fig. 4.3, Fig. 4.4C).

Temperature data was recorded from seven sites across the Galapagos (Fig. 4.5A). Punta Espinosa, a site located on the northeastern side of the westernmost island, Fernandina, had the greatest temperature variability. The temperature range was 11.5°C to 27.8°C, with a mean temperature of 22.6°C ± 0.17 (Fig. 4.5A). The coldest site was Cabo Douglas, located on the northwestern point of Fernadina. Mean temperature was 21.9°C ± 0.19, with a range of 15.3°C to 27.8°C (Fig. 4.5A). Punta Pitt, a site located on the northeastern side of the easternmost island, San Cristobal, was the warmest site. The temperature range was 18.5°C to 31°C, with a mean temperature of 24.6°C ± 0.37 (Fig. 4.5A). Las Tijeretas is located on the southwestern side of San Cristobal. Mean temperature at this site was 22.9°C ± 0.18, with a range of 18.1°C to 28.3°C (Fig. 4.5A). Española is a southern island, temperature was recorded at Gardner Bay, a

northern location. Mean temperature was 23.1°C ± 0.19, with a range of 17.9°C to 27.5°C (Fig. 4.5A).   Temperature was recorded at Tunel del Estero, a southern site on the island Isabela. Temperature ranged from 18.2°C to 28.3°C, with a mean temperature of 23.1°C ± 0.19 (Fig. 4.5A). Puerto Egas, located on the northwestern side of Santiago, a central northern island, had a mean temperature of 23.5°C ± 0.18 (Fig. 5A). Temperature ranged from 17.6°C to 29.4°C (Fig. 4.5A).

The warmest month was March with a mean of 26.3°C ± 0.15, and a range of 24.4°C to 27.2°C (Fig. 4.6C). The coldest month was September with a mean of 20.7°C ± 0.09, and a range of 19.5°C to 22.6°C (Fig. 4.6C).   October and November had the largest mean temperature range relative to the other months (Fig. 4.6C).   Mean temperatures ranged from 19.6°C to 23.8°C and 19.9°C to 24.1°C for October and November, respectively (Fig. 4.6C). February had the smallest mean temperature range, 24.3°C to 26.2°C (Fig. 4.6C).

The effect of temperature on *Lytechinus* consumption rates of *Ulva* was measured *in situ* and in laboratory experiments across a 16°C temperature range (Carr and Bruno 2013, Carr et al. *in review*). *Lytechinus* grazing rates significantly increased with warmer temperatures (Figure 4.7B, $R^2 = 0.58$, $p = 0.002$).

Mean temperature ranged along the Central/Southern California coast from 8.2°C to 22.6°C (Fig. 4.2, Fig. 4.3, Fig. 4.4D). Mean temperature across the whole region was 14.8°C ± 0.1°C (Fig. 4.2, Fig. 4.3, Fig. 4.4D).

The warmest site was Point Conception, the southernmost site. Mean temperature was 17.6°C ± 0.2°C, with a range of 14.0°C to 22.6°C (Fig. 4.5D). Bodega Bay, the northernmost site was the coldest with a mean temperature of 11.7°C ± 0.1°C, and a range of 8.2°C to 17.0°C (Fig. 4.5D). Half Moon Bay had the largest variability in temperature with a range of 10.2°C to

20.9°C (Fig. 4.5D). Cambria had the smallest variability in temperature with a range of 14.0°C to 22.4°C (Fig. 4.5D).

The warmest month was September with a mean temperature of 16.9°C ± 0.9°C, and a range of 15.9°C to 18.1°C (Fig. 4.6D). March was the coldest month with a mean temperature of 13.1°C ± 0.6°C (Fig. 6D). The month with the smallest temperature variability was also March, with a range of 12.3°C to 13.8°C (Fig. 4.6D). The month with the largest temperature variability was July, with a range of 14.7°C to 19.9°C (Fig. 4.6D).

Various laboratory experiments were performed examining the effect of temperature on the feeding rate of *S. purpuratus* on *Macrocystis* (Azad et al. 2011, Brown et al. 2014). These experiments were conducted over an 8°C temperature range. The relationship between temperature and *S. purpuratus* grazing rates was positive (Figure 4.7C, $R^2 = 0.71$, $p = 0.005$).

Temperature ranged from 8°C to 19.5°C along the Northern CA/ Oregon coast (Fig. 4.2, Fig. 4.3, Fig. 4.4E). The mean temperature over the whole region was 12.1°C ± 0.15°C (Fig. 4.2, Fig. 4.3, Fig. 4.4E).

Temperature data was recorded from five sites along the Northern California/Oregon coast (Fig. 4.5E). Cape Mendocino North, one of the southern sites, located on the Northern California coast was the coldest site (Fig. 4.5E). The temperature range was 8.1°C to 19.5°C, with a mean temperature of 11.7°C ± 0.14°C (Fig. 4.5E). Cape Blanco, the northernmost site was the warmest, with a mean temperature of 12.2°C ± 0.21°C. This site also had the lowest temperature variability with a range of 8.2°C to 17.5°C (Fig. 4.5E). Rocky Point and Cape Mendocino had the largest temperature variability with ranges of 8.0°C to 19.5°C and 8.2°C to 19.7°C, respectively (Fig. 4.5E).

August was the warmest month with a mean temperature of 14.8°C ± 0.1°C, and a range of 12.2°C to 16.1°C (Fig. 4.6E). January and February were the coldest months with a mean temperature of 10.3°C (Fig. 4.6E). Temperature ranged from 9.5°C to 11.9°C in January and 9.6°C to 11.7°C in February (Fig. 4.6E). The month with the largest temperature variability was July, with a range of 12.8°C to 16.4°C (Fig. 4.6E). October had the smallest temperature variability with a range of 11.6°C to 12.3°C (Fig. 4.6E).

The autocorrelation functions were different between the five regions (slope comparison in Fig. 4.8). The decorrelation scales are approximately 19 d in the Galápagos, 37 d in South Africa, 92 d in Chile, 101 d in Northern California/Oregon and 115 d in Southern California (Fig. 4.8). These results suggest that the variation *in situ* temperature dynamics across the Galápagos and South Africa is "high-frequency" or occurs on shorter time scales (days to weeks) relative to the other regions. While *in situ* temperature variation along the Chilean and California/Oregon coast occurs over longer time scales (order of several months).

Discussion

Our results demonstrate that there is striking variation in thermal regimes between upwelling regions around the world. For example, over a ten-year time period, ocean temperature around the Galápagos Islands can vary by 20°C, while temperature along the S. African coast varied by only 6°C. Mean ocean temperatures were similar along the South African coast (16.5°C ± 0.2°C), central and southern California coast (14.8°C ± 0.1°C) and the Chilean coast (14.8°C ± 0.3°C). The Galápagos Islands had the highest (22.9°C ± 2.1°C), and the northern California and Oregon coast had the lowest (12.1°C ± 0.2°C) mean ocean temperature. Punta Pitt, in the Galápagos Islands, was the site that had the greatest temperature variability, with water temperatures varying over 12°C between the warm and cool

season.

There was less spatial variation in temperature across the Galapagos Islands and along the Chilean and Central/Southern California coast. There was higher spatial variation along the S. African and Northern California/Oregon coast. Seasonally, temperature trends across the Galapagos Islands and along the Chilean and South African coast align with the Southern Hemisphere, with warmer temperatures in February/March and cooler temperatures in August/September/October. While the California/Oregon coast seasonal trends follow the Northern Hemisphere seasons, with warmer temperatures in August/September and cooler temperatures in February/March.

Thermal regimes were different between the regions, with *in situ* temperature fluctuations occurring along the California/Oregon coast over longer time scales relative to the Galápagos, Chile and South Africa. The California/Oregon coast and the Chilean coast are both characterized by relatively more stable dynamics, with temperature fluctuations occurring over longer timescales (order of several months). This suggests that large-scale oceanic or atmospheric forcing that produces low-frequency variability is important in these regions (Hormazabal et al. 2001, Wieters et al. 2009). In contrast, both the Galapagos and South Africa experience greater extremes in thermal conditions with pulses occurring over much shorter time scales (days to weeks). Therefore, local forcing, which results in high-frequency variability, likely plays a dominant role influencing the thermal regimes of South Africa and the Galapagos. This variation in average conditions as well as temporal variance could drive differences in local scale ecological patterns.

Understanding how biological responses change with temperature variation is key to conserving ecological structure and function in the face of global climate change, especially in vulnerable and important systems like upwelling zones. And while non lethal responses, such as changes in the phenology and distribution of species, and stress-induced, lethal reactions (e.g.,

coral bleaching) to climate change are well studied and the ecological consequences are relatively intuitive (e.g., Walther et al. 2002, Parmesan 2006, Hoegh-Guldberg et al. 2007), less is known about how variation in individual metabolic responses with temperature will drive changes in ecological patterns and processes in the future (Bruno et al. 2015).

Recent *in situ* grazing assays demonstrated that herbivore-algal interactions in upwelling systems are influenced by temperature, with stronger top-down effects on algal biomass in warmer waters (Carr et al. *in review*). Therefore, in upwelling regions and when herbivores, specifically sea urchins, are locally abundant, higher grazing rates at warmer seasons and years (e.g., El Niño) may alter algal community composition or result in localized barrens. In upwelling systems, a decrease in the dominant foundation species, macroalgal standing biomass, can propagate up the food web affecting consumers, and possibly ecosystem function (e.g., Tegner and Dayton 1991).

Although, results from several recent studies have found temperature effects on herbivory are context-dependent and influenced by other factors such as evolutionary history, local acclimatization, diet, predator and competitor response to temperature and heterogeneity in thermal regimes (e.g., heat waves, cold shocks) (Shurin et al. 2012, Sentis et al. 2012, Dell et al. 2013). Therefore, given the complexity of herbivore-algal temperature dependence, the important role sea urchins play in benthic community structure and how critically economically and ecologically important upwelling regions are it is surprising that we found a lack of studies that directly examined how temperature affected sea urchin grazing rates in these regions.

The grazing rates of the three sea urchin species differed in response to sublethal temperature variation. *Lytechinus* and *Strongylocentrotus* grazing rates increased with warming temperatures, while *Loxechinus* grazing rates were not correlated with temperature. The

temperature range studied with *Loxechinus* grazing rates was only 4.5°C, relative to 16°C and 8°C for *Lytechinus* and *Strongylocentrotus*, respectively. Therefore, it is possible that with a larger temperature range, a positive relationship between temperature and grazing rates would be observed. While a non-significant relationship was observed in this study, as temperature dependent metabolism is prominent in invertebrates (Sibly et al. 2012), it is unlikely that temperature does not influence grazing rates or other biological rates in *Loxechinus*. Results from the above studies demonstrate that an increase in temperature of 7°C could increase sea urchin grazing rate by as much as 30%, possibly resulting in increased urchin barren size, persistence and prevalence with warmer temperatures (Carr and Bruno 2013, Byrnes et al. 2014, Carr et al. *in review*).

While there is a growing body of evidence demonstrating variation in temperature can directly influence individual metabolism, and consequently other biological rates like consumption and respiration, much less is known about the effect on community and ecosystem structure and function. One exception is Barneche et al. (2014); they estimated respiratory fluxes of reef-fish communities at 22°C and 28°C, and found an ~2-fold increase from cooler to warmer temperatures. Thus, under similar reef conditions, a warmer reef can support less fish biomass relative to cooler reefs. In our study, *Macrocystis* and *Ulva* are two of the dominant benthic foundation species at each of the upwelling zones (Buckle 1978, Vinueza et al. 2006, Azad et al. 2011, Carr and Bruno 2013), and changes in herbivore-*Ulva* or herbivore-*Macrocystis* interactions could strongly influence algal community biomass and composition, resulting in changes to community and ecosystem structure and possibly, function.

In the five regions examined here, the effects of temperature variability on population dynamics, could influence community structure via metabolic scaling. For example, across the

Galapagos Islands, temperature ranges by 20°C, various studies indicate this degree of variation would profoundly affect population growth (reviewed in Sibly et al. 2012). Specifically, Savage et al. (2004) estimated a 20°C increase in temperature would triple the population growth rate of zooplankton. As the growth rate of herbivores is unlikely to be matched by the growth rate of primary production, higher herbivore population growth rates, and the subsequent increased metabolic demand, are possibly unsustainable at warmer temperatures (Kordas et al. 2014). Therefore, in upwelling systems, while warmer temperatures could result in lower herbivore population levels, due to increased metabolic demand, higher incidences of sea urchin barrens (and other types of denuded areas) are possible.

Due to the importance of upwelling ecosystems worldwide coupled with global climate change, a better understanding of how MST will influence benthic community patterns across regions is important for developing more comprehensive and sensitive models that predict the effects of climate change on upwelling systems worldwide.

Figure 4.1. Map of study regions and sites.

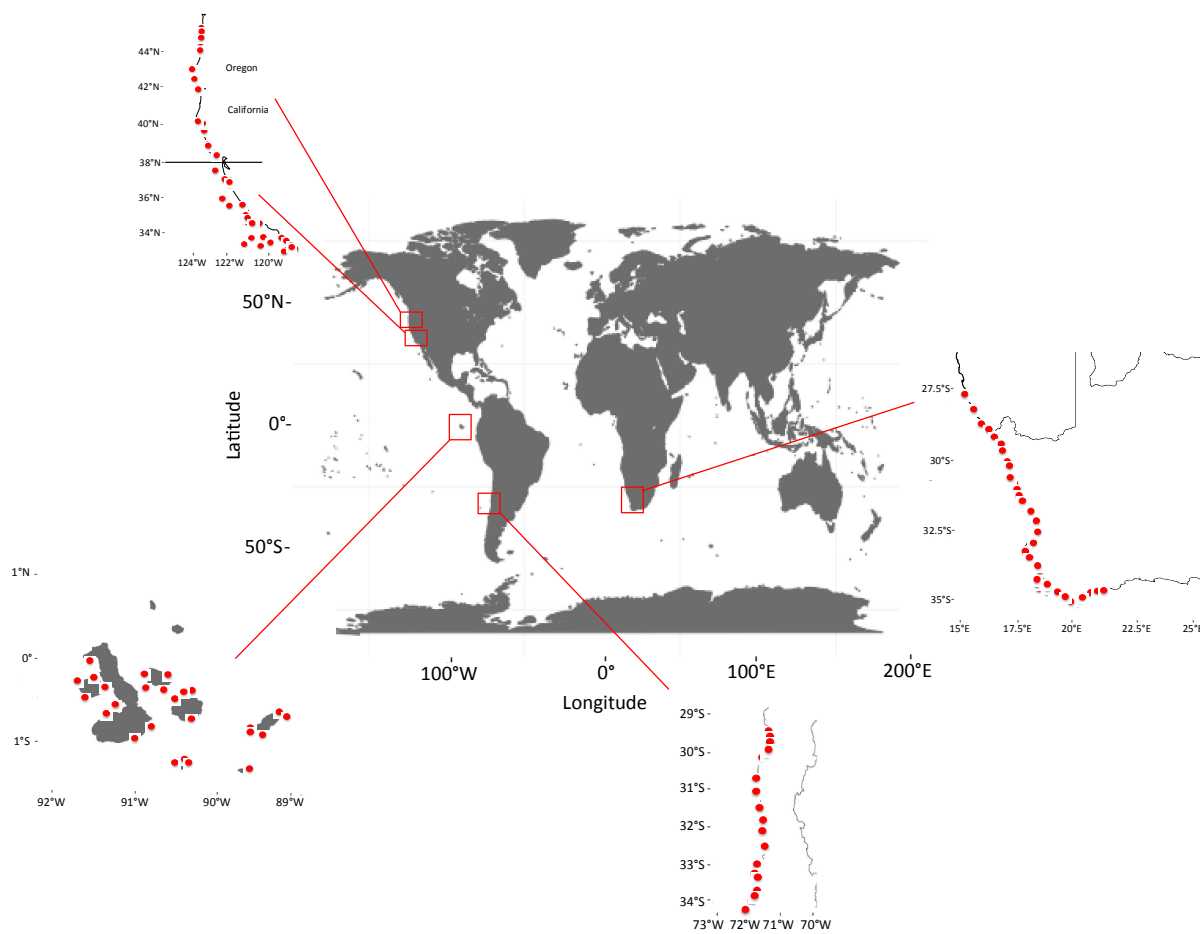Individual sites are denoted by red circles.

Figure 4.2. Variation in A) minimum, B) maximum and C) mean ocean temperature.
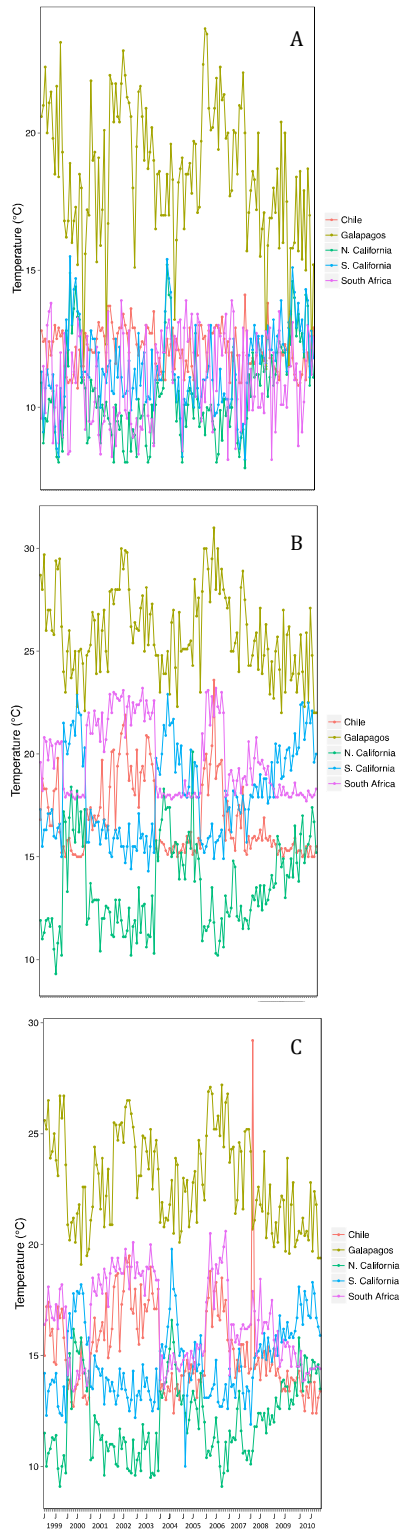Values are daily averaged monthly values.

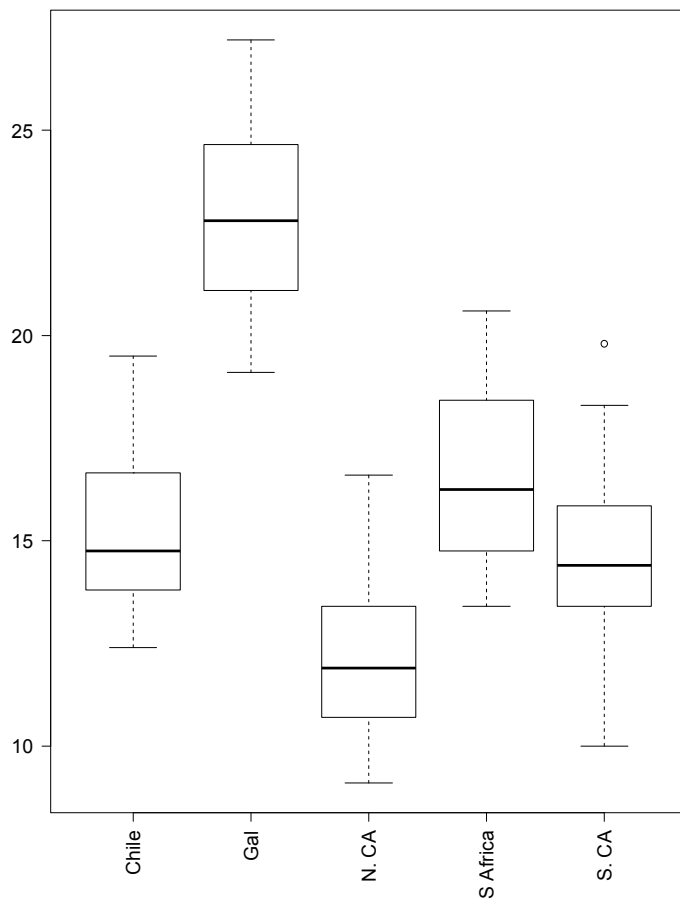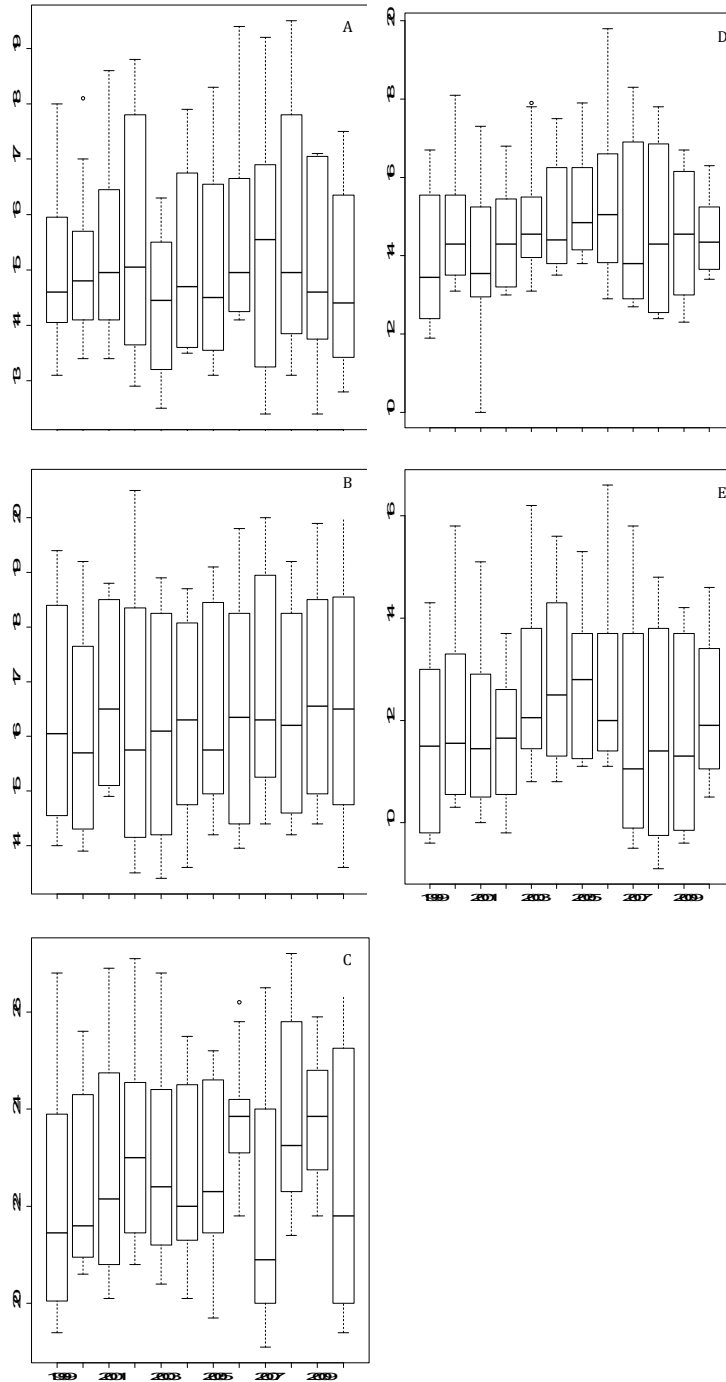**Figure 4.3. Boxplot of weekly averaged mean temperature for 1999 – 2010.**

Figure 4.4. Boxplot of weekly averaged mean temperature between years between 1999-2010.
Weekly averaged mean temperature for the A) Chilean coast, B) S. African coast, C) Galapagos Islands, D) Central and Southern California coast, and E) Northern California and Oregon coast.

Figure 4.5. Variation in spatial mean ocean temperature.
Variation in spatial mean ocean temperature along the A) Chilean coast, B) S. African coast, C) Galapagos Islands, D) Central and Southern California coast, and E) Northern California and Oregon coast.
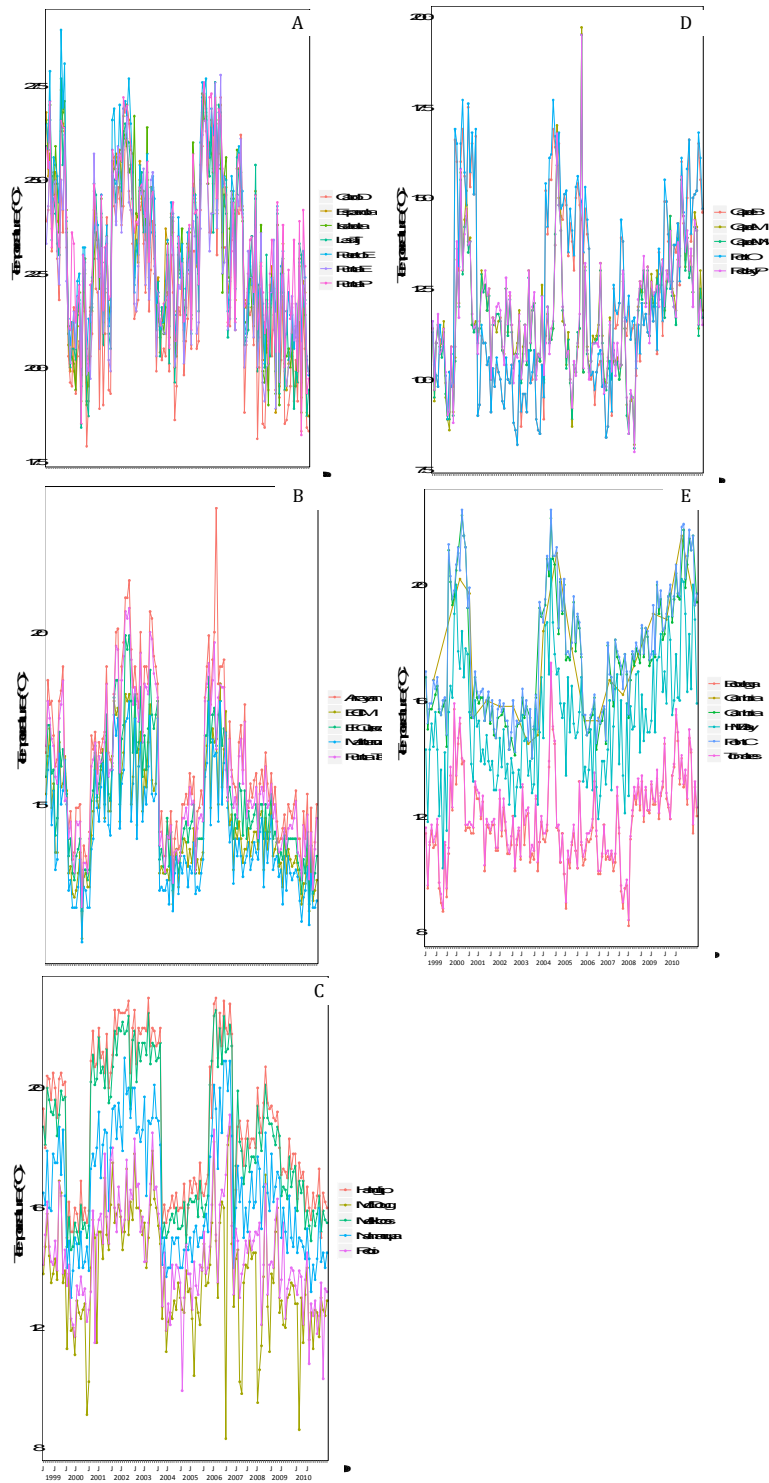
Figure 4.6. Boxplot of averaged monthly mean temperatures between months between 1999-2010.
Boxplot of averaged monthly mean temperatures between months between 1999-2010 for the A) Chilean coast, B) S. African coast, 3) Galapagos Islands, 4) Central and Southern California coast, and 5) Northern California and Oregon coast.
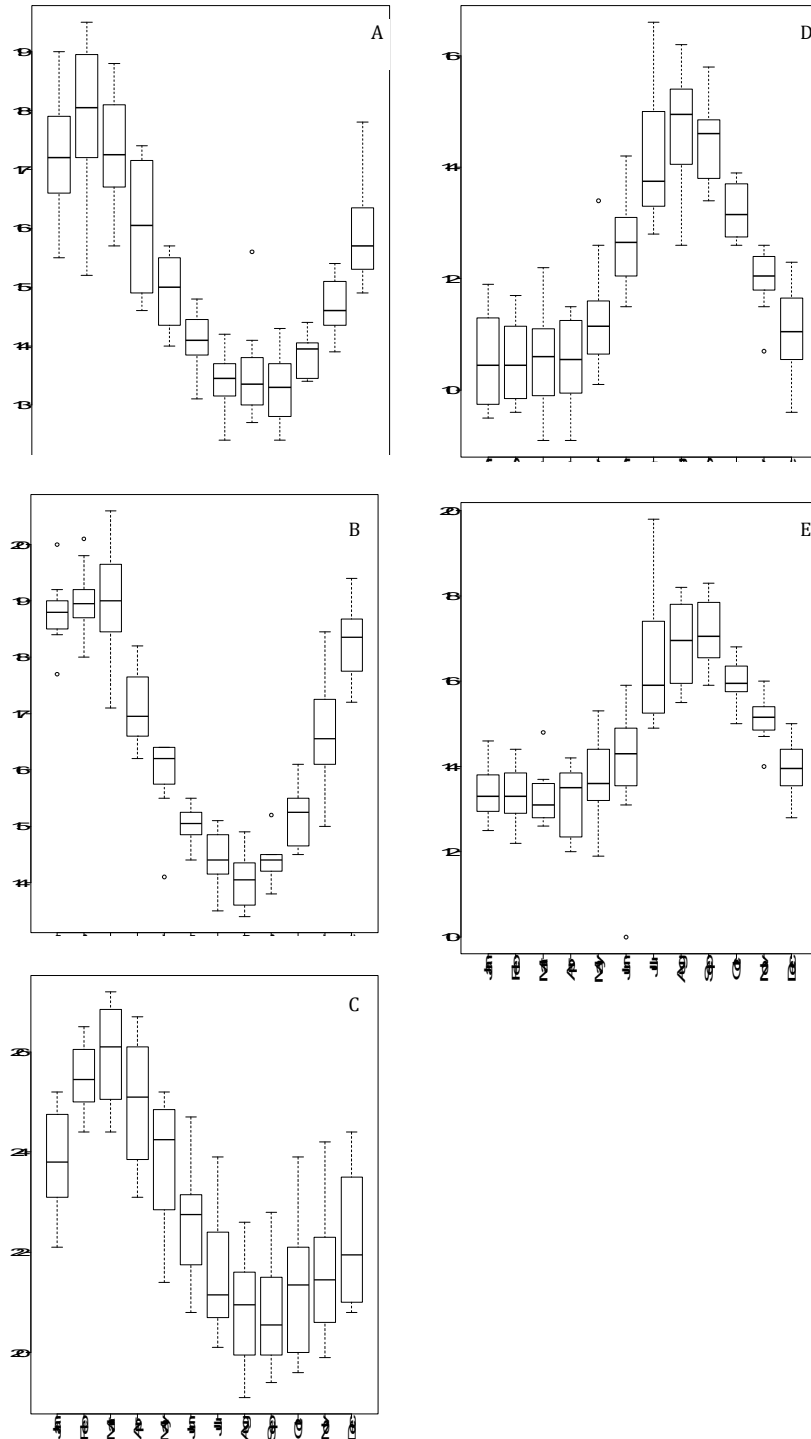
Figure 4.7. Relationship between temperature and urchin grazing rates
A) *Loxechinus albus*, (results from Buckle et al. 1978) B) *Lytechinus semituberculatus* (results from Carr and Bruno 2013, Carr et al. *in review*), C) *Strongylocentrotus purpuratus* (results from Azad et al. 2011, Brown et al. 2014). Amount of algae consumed is measured in wet weight (g).
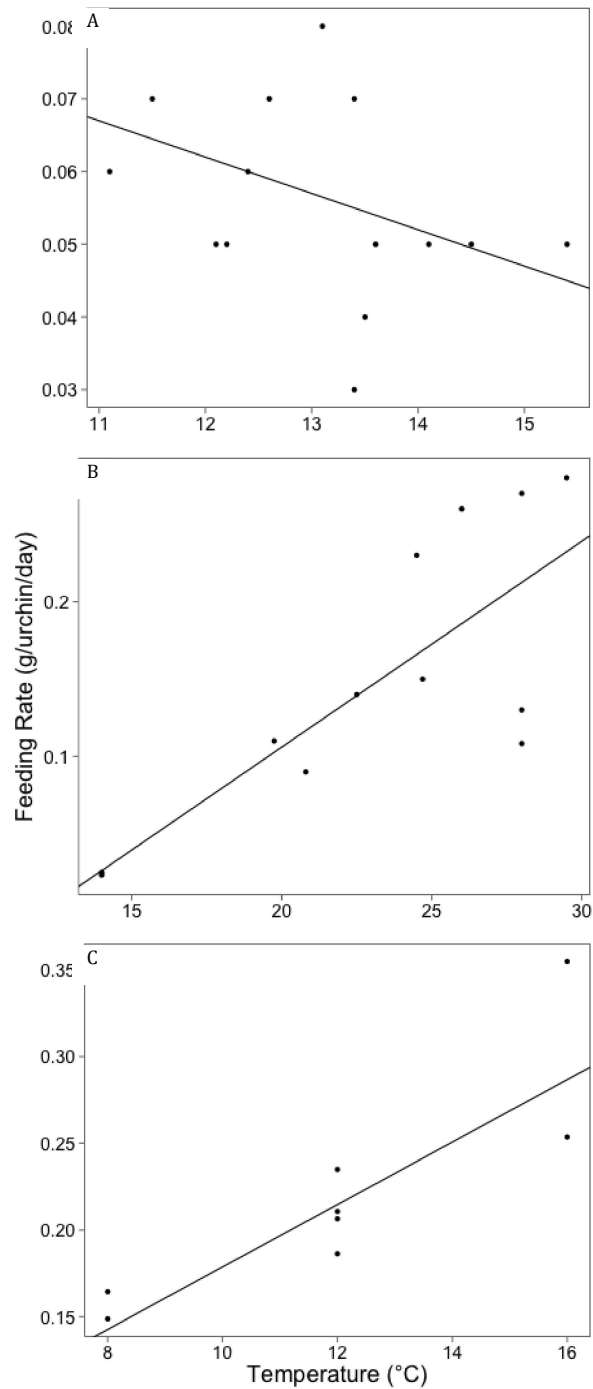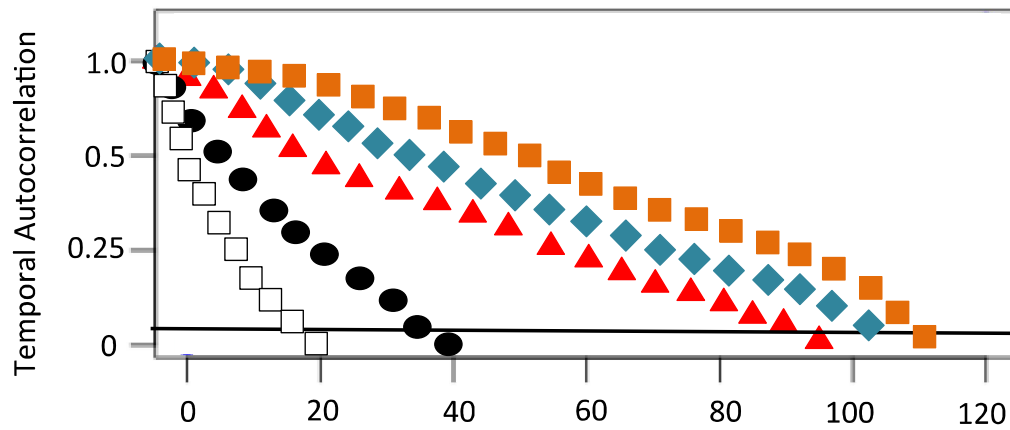
Figure 4.8. Temporal autocorrelation functions of weekly averaged *in situ* temperature. At ~1.0m depth at Galapagos (squares), South Africa (circles), Chile (triangles), Northern California (diamonds), and Southern California (orange squares). The solid black line is Bonferroni-corrected ($\alpha = 0.05$) confidence interval for significant autocorrelation.

REFERENCES

Allen, A. P., J. F. Gillooly, and J. H. Brown. 2005. Linking the global carbon cycle to individual metabolism. Functional Ecology 19:202–213.

Anderson, D. R., and K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. The Journal of Wildlife Management 66:912–918.

Aravena, G., B. Broitman, and N. C. Stenseth. 2013. Twelve years of change in coastal upwelling along the Central-Northern Coast of Chile: spatially heterogeneous responses to climatic variability. PLoS One 9:e90276.

Azad, A. K., C. M. Pearce, and R. S. Kinley. 2011. Effects of diet and temperature on ingestion, absorption, assimilation, gonad yield and gonad quality of the purple sea urchin (*Strongylocentrotus purpuratus*). Aquaculture 317:187-196.

Barber, R. T., and F. P. Chavez. 1983. Biological consequences of El Niño. Science 222:1203–1210.

Barneche, D. R., M. Kulbicki, S. R. Floeter, A. M. Friedlander, J. Maina, and A. P. Allen. 2014. Scaling metabolism from individuals to reef-fish communities at broad spatial scales. Ecology Letters 17:1067-1076.

Barry, J. P., and P. K. Dayton. 1991. Physical heterogeneity and the organization of marine communities. Pages 269-320 *in* J. Kolasa and S. T. A. Pickett, eds. Ecological heterogeneity. Springer, New York, New York, USA.

Barton, B. T., A. P. Beckerman, and O. J. Schmitz. 2009. Climate warming strengthens interactions in an old-field food web. Ecology 90:2346–2351.

Blanchette, C. A., B. R. Broitman, and S. D. Gaines. 2006. Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA. Marine Biology 149:689–701.

Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton.

Brandt M., and P. Guarderas. 2002. Erizos de mar (E Danulat and GJ Edgar, Eds.). Servicio Parque Nacional Galápagos, Santa Cruz, Galápagos.

Brandt, M., J. D. Witman, and A. I. Chiriboga. 2012. Influence of a dominant consumer species reverses at increased diversity. Ecology 93:868–878.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of southeastern Pacific intertidal communities. Marine Ecology Progress Series 224:21–34.

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

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Bruno, J. F., L. A. Carr, and M. I. O'Connor. 2015. Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96:3126-3140.

Buckle, L. F., K. Alveal, E. Tarifeño, C. Guisado, L. Córdoba, C. Serrano, and J. Valenzuela. 1978. Biological studies on the Chilean sea urchin *Loxechinus albus.* Food analysis and seasonal feeding rate. Anales Centro Ciencias Mar Limnologia 5:21-36.

Burkepile, D. E., and M. E. Hay. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128-3139.

Bustamante, R. H., and G. M. Branch. 1996. Large scale patterns and trophic structure of Southern African rocky shores: the roles of geographic variation and wave exposure. Journal of Biogeography 23:339–351.

Bustamante, R. H., G. M. Branch, S. Eekhout, B. Robertson, P. Zoutendyk, M. Schleyer, A. Dye, N. Hanekom, D. Keats, M. Jurd, and C. McQuaid. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102:189–201.

Byrnes, J. E. K., L. E. Johnson, S. D. Connell, N. T. Shears, S. McMillan, A. D. Irving, A. H. Buschmann, M. Graham, and B. P. Kinlan. 2013. The sea urchin - the ultimate herbivore and biogeographic variability in its ability to deforest kelp ecosystems. PeerJ Preprints 1:e174v1.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 56:345-364

Carr, L. A., and J. F. Bruno. 2013. Warming increases the top-down effects and metabolism of a subtidal herbivore. PeerJ 1:e109.

Carr, L. A., R. Gittman, and J. F. Bruno. *In review*. Temperature influences herbivory across a regional-scale temperature gradient in the Galápagos Islands, Ecuador. Journal of Animal Ecology

Chapman, A. R. O. 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. Marine Biology 62:307-311

Chapman, A. R. O., and C. R. Johnson. 1990. Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. Hydrobiologia 192:77–121.

Chavez, F. P., and J. R. Toggweiler. 1995. Physical estimates of global new production: the upwelling contribution. Pages 313-320 *in* Dahlem Workshop on Upwelling in the Ocean: modern processes and ancient records. Wiley and Sons, Chichester, UK

Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. F. Foley, and M. J. McPhaden. 1999. Biological and chemical response of the Equatorial Pacific ocean to the 1997-1998 El Niño. Science 286:2126–2131.

Checkley, D. M., and J. A. Barth. Patterns and processes in the California Current System. Progress in Oceanography 83:49-64.

Choat, J. H., and A. M. Ayling. 1987. The relationship between habitat structure and fish faunas on New Zealand reefs. Journal of Experimental Marine Biology and Ecology 110:257–284.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40:49-78.

Davison, I. R. 1987. Adaptation of photosynthesis in *Laminaria saccharina* (Phaeophyta) to changes in growth temperature. Journal of Phycology 23:273–283.

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

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecological Monographs 69:219 250.

Dell, A. I., S. Pawar, and V. M. Savage. 2013. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70–84.

Development Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Duffy, J. E., and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. Ecological Monographs 70:237–263.

Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. American Naturalist 138:1067-1091.

Ebeling, A. W., and D. R. Laur. 1985. The influence of plant cover on surfperch abundance at an offshore temperate reef. Environmental Biology of Fishes 12:169–179.

Edgar, G. J., S. Banks, J. M. Fariña, M. Calvopiña, and C. Martínez. 2004. Regional biogeography of shallow reef fish and macro-invertebratecommunities in the Galapagos archipelago. Journal of Biogeography 31:1107–1124.

Edgar, G. J., S. Banks, M. Brandt, R. H. Bustamante, A. I. Chiriboga, S. A. Earle, L. E. Garske, P. W. Glynn, J. S. Grove, S. Henderson, C. P. Hickman, K. A. Miller, F. Rivera, and G. M. Wellington. 2010. El Niño, grazers and fisheries interact to greatly elevate extinction risk for Galapagos marine species. Global Change Biology 16:2876–2890.

Enquist, B. J., E. P. Economo, T. E. Huxman, A. P. Allen, D. D. Ignace, and J. F. Gillooly. 2003. Scaling metabolism from organisms to ecosystems. Nature 423:63–67.

Feldman, G. C. 1986. Patterns of phytoplankton production around the Galápagos Islands. Pages 77–106 *in* M. J. Bowman, C. M. Yentsch, and W. T. Peterson, editors. Tidal mixing and plankton dynamics. Springer-Verlag.

Floeter, S. R., M. D. Behrens, C. E. L. Ferreira, M. J. Paddack, and M. H. Horn. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. Marine Biology 147:1435-1447.

Freestone, A. L., R. W. Osman, G. M. Ruiz, and M. E. Torchin. 2011. Stronger predation in the tropics shapes species richness patterns in marine communities. Ecology 92:983-993.

Froese, R., and D. Pauly. 2013. FishBase. http://www.fishbase.org.

Gaines, S., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67:267-272.

Gan, J., and J. Allen. 2002. A modeling study of shelf circulation off northern California in the region of the Coastal Ocean Dynamics Experiment. Simulations and comparisons with observations. Journal of Geophysical Research 107:3184-3204.

Gordon, R. M., K. S. Johnson, and K. H. Coale. 1998. The behaviour of iron and other trace elements during the IronEx-I and PlumEx experiments in the Equatorial Pacific. Deep Sea Research Part II: Topical Studies in Oceanography 45:995–1041.

Harris, M. P. 1969. Breeding seasons of sea-birds in the Galapagos Islands. Journal of Zoology in London 159:145–165.

Harrold, C. J., J. Watanabe, and S. Lisin. 1988. Spatial variation in the structure of kelp forest communities along a wave exposure gradient. PSZN I: Marine Ecology 9:131-156.

Haury, L. R., J. A. McGowan, and P. H. Wiebe. 1978. Patterns and processes in the time-space scales of plankton distributions. Pages 277-327 *in* J. H. Steele, editor. Spatial pattern in plankton communities. Plenum, New York, New York, USA.

Hawkins, S. J., and R. G. Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. Oceanography and Marine Biology: An Annual Review:195–282.

Helmuth, B. 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. Integrative and Comparative Biology 42:837-845.

Hereu, B., M. Zabala, C. Linares, and E. Sala. 2005. The effects of predator abundance and

habitat structural complexity on survival of juvenile sea urchins. Mar Biol 146:293–29.

Hill, A., B. M. Hickey, F. A. Shillington, P. T. Strub, K. H. Brink, E. D. Barton, and A. C. Thomas. 1998. Eastern ocean boundaries coastal segment. Pages 29-67 *in* A. R. Robinson and K. H. Brink, eds. The sea. Wiley, Hoboken, New Jersey, USA.

Hillebrand, H., E. T. Borer, M. E. S. Bracken, B. J. Cardinale, J. Cebrian, E. E. Cleland, J. J. Elser, D. S. Gruner, W. S. Harpole, J. T. Ngai, S. Sandin, E. W. Seabloom, J. B. Shurin, J. E. Smith, and M. D. Smith. 2009. Herbivore metabolism and stoichiometry each constrain herbivory at different organizational scales across ecosystems. Ecology Letters 12:516-527.

Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldiera, N. Knowlton, C. M. Eakin, R. Iglesias Preito, N. Muthiga, R. H. Bradbury, A. Dubui, M. E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acification. Science 318:1737-1742.

Hoekman, D. 2010. Turning up the heat: Temperature influences the relative importance of top-down and bottom-up effects. Ecology 91:2819-2825.

Houvenaghel, G. T. 1978. Oceanographic conditions in the Galápagos Archipelago and their relationship with life on the islands. Pages 181–200 *in* R. Boje and M. Tomczak, editors. Upwelling Ecosystems. Springer-Verlag, New York.

Houvenaghel, G. T. 1984. Oceanographic conditions in the Galápagos Archipelago and their relationship with life on the islands. Pages 181–202 *in* R. Boje and M. Tomczak, editors. Upwelling Ecosystems. Springer-Verlag.

Howells, E. J., R. Berkelmans, M J. H. van Oppen, B. L. Willis, and L. K. Bay. 2013. Historical thermal regimes define limits to coral acclimatization. Ecology 94:1078-1088.

Hutchison, V. 1976. Factors influencing thermal tolerance of individual organisms. Pages 10–26 *in* Esch, G.W., and R. McFarlane, editors. Symposium Series of the National Technical Information Service. Springfield, VA.

Irving, A. D., and J. D. Witman. 2009. Positive effects of damselfish override negative effects of urchins to prevent an algal habitat switch. Journal of Ecology 97:337–347.

Izumo, T. 2002. Tropical pathways, equatorial undercurrent variability and the 1998 La Niña. Geophysical Research Letters 29:2080.

Karamushko, L. I., and J. S. Christiansen. 2002. Aerobic scaling and resting metabolism in oviferous and post-spawning Barents Sea capelin *Mallotus villosus* (Muller, 1776). Journal of Experimental Marine Biology and Ecology 269:1-8.

Kessler, W. S. 2006. The circulation of the eastern tropical Pacific: A review. Progress in Oceanography 69:181–217.

Kordas, R. L., C. D. G. Harley, and M. I. O'Connor. 2011. The influence of temperature on interspecific interactions in marine systems. Journal of Experimental Marine Biology and Ecology 400:218-226.

Kratina, P., H. S. Greig, P. L. Thompson, T. S. A. Carvalho-Pereira, and J. B. Shurin. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. Ecology 93:1421–1430.

Lagos, N. A., S. A. Navarrete, F. Veliz, A. Masuero, and J. C. Castilla. 2005. Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along the coast of central Chile. Marine Ecology Progress Series 290:165-178.

Laurie, W. A., and D. Brown. 1990. Population biology of marine iguanas (Amblyrhynchus cristatus). II. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. Journal of Animal Ecology 59:529–544.

Leichter, J. J., S. R. Wing, S. L. Miller, and M. W. Denny. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. Limnology and Oceanography 41:1490-1501.

Lemoine, N. P., and D. E. Burkepile. 2012. Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. Ecology 93:2483–2489.

Lemoine, N. P., D. E. Burkepile, and J. D. Parker. 2014. Variable effects of temperature on insect herbivory. PeerJ 2:e376.

Lesaffre, E., D. Rizopoulos, and R. Tsonaka. 2006. The logistic transform for bounded outcome scores. Biostatistics 8:72–85.

Levin, P. S. 1994. Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. Environmental Biology of Fishes 40:271–281.

Lindley, S. T., and R. T. Barber. 1998. Phytoplankton response to natural and experimental iron addition. Deep Sea Research Part II: Topical Studies in Oceanography 45:1135–1150.

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

Marshall, D. J., and C. D. McQuaid. 2010. Warming reduces metabolic rate in marine snails: adaptation to fluctuating high temperatures challenges the metabolic theory of ecology. Proceedings of the Royal Society B: Biological Sciences 278:281–288.

Martin, J. H., K. H. Coale, K. S. Johnson, S. E. Fitzwater, R. M. Gordon, S. J. Tanner, C. N. Hunter, V. A. Elrod, J. L. Nowicki, T. L. Coley, R. T. Barber, S. Lindley, A. J. Watson, K. Van Scoy, C. S. Law, M. I. Liddicoat, R. Ling, T. Stanton, J. Stockel, C. Collins, A. Anderson, R. Bidigare, M. Ondrusek, M. Latasa, F. J. Millero, K. Lee, W. Yao, J. Z. Zhang,

G. E. Friederich, C. Sakamoto, F. P. Chavez, K. Buck, Z. Kolber, R. Greene, P. Falkowski, S. W. Chisholm, F. Hoge, R. Swift, J. Yungel, S. Turner, P. Nightingale, A. Hatton, and P. Liss. 1994. Testing the iron hypothesis in ecosystems of the equatorial Pacific Ocean. Nature 371:123–129.

Menge, B. A. 1991. Generalizing from experiments: is predation strong or weak in the New England rocky intertidal? Oecologia 88:1–8.

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

Menge, B. A., and G. M. Branch. 2001. Rocky intertidal communities. Pages 221-251. *In* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine Community Ecology. Sinauer Associates, Sunderland, MA.

Menge, B. A., C. Blanchette, P. Raimonid, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. Ecological Monographs 74:663-684.

Menge, B. A., B. A. Daley, J. Lubchenco, E. Sanford, E. Dahlhoff, P. M. Halpin, G. Hudson, and J. L. Burnaford. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecological Monographs 69:297–330.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, and E. Sanford. 1997. Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences 94:14530–14535.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences 100:12229–12234.

Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69:89–107.

Navarrete, S. A., B. R. Broitman, and B. A. Menge. 2008. Interhemispheric comparison of recruitment to intertidal communities: pattern persistence and scales of variation. Ecology 89:1308–1322.

Nielsen, K. J., and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecology Letters 7:31–41.

O'Connor, M. I. 2009. Warming strengthens an herbivore–plant interaction. Ecology 90:388–398.

O'Connor, M. I., B. Gilbert, and C. J. Brown. 2011. Theoretical Predictions for How

Temperature Affects the Dynamics of Interacting Herbivores and Plants. The American Naturalist 178:626–638.

O'Connor, M. I., M. F. Piehler, D. M. Leech, A. Anton, and J. F. Bruno. 2009. Warming and resource availability shift food web structure and metabolism. PLoS Biology 7:e1000178.

Ojeda, F. P., and A. A. Muñoz. 1999. Feeding selectivity of the herbivorous fish *Scartichthys viridis*: effects on macroalgal community structure in a temperate rocky intertidal coastal zone. Marine Ecology Progress Series 184:219–229.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G.L., Solymos, P., Stevens, M. H. H., Wagner, H. 2015. vegan: Community Ecology Package. R Package Version 2.2-1., http://CRAN.R-project.org/package=vegan.

Padilla-Gamiño, J. L., and R. C. Carpenter. 2007. Seasonal acclimatization of "*Asparagopsis taxiformis*" (Rhodophyta) from different biogeographic regions. Limnology and Oceanography 52:833–842.

Paine, R. T. 1980. Food webs: Linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:666–685.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature 355:73-75.

Paine, R. T., and R. L. Vadas. 1985. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography 14:710-719.

Palacios, D. M. 2002. Factors influencing the island-mass effect of the Galápagos Archipelago. Geophysical Research Letters 29:2134.

Palacios, D. M. 2004. Seasonal patterns of sea-surface temperature and ocean color around the Galápagos: regional and local influences. Deep Sea Research Part II: Topical Studies in Oceanography 51:43–57.

Park, T. 1954. Experimental studies of interspecies competition II. Temperature, humidity, and competition in two species of *Tribolium*. Physiological Zoology 27:177-238.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology and Evolutionary Systemaics 37:637-669.

Parrish, R. H., A. Bakun, D. M. Husby, and C. S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish production. Pages 731-778 *in* G. D. Sharp and J. Csirke, eds. Proceedings of the expert consultation to examine changes in abundance and species of neritic fish resources, Vol. 291. FAO.

Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature 376:279.

Pennington, J. T., K. L. Mahoney, V. S. Kuwahara, D. D. Kolber, R. Calienes, and F. P. Chavez. 2006. Primary production in the eastern tropical Pacific: A review. Progress in Oceanography 69:285–317.

Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science 253:548-551.

Pineda, J., and M. Lopez. 2002. Temperature, stratification and barnacle larval settlement in two Californian sites. Continental Shelf Research 22:1183-1198.

Pinheiro, J., Bates, D., Debroy, S., Sarkar, D. 2015. nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1-120., http://CRAN.R-project.org/package=nlme

Pizarro, O., S. Hormazabal, A. González, and E. Yañez. 1994. Variabilidad del viento, nivel del mar y temperature en la costa norte de Chile. Investigaciones Mar Chile 22:85-101.

Rall, B. C., O. Vucic-Pestic, R. B. Ehnes, M. Emmerson, and U. Brose. 2009. Temperature, predator-prey interaction strength and population stability. Global Change Biology 16:2145–2157.

Rilov, G., S. E. Dudas, B. A. Menge, B. A. Grantham, J. Lubchenco, and D. R. Schiel. 2008. The surf zone: a semi-permeable barrier to onshore recruitment of invertebrate larvae? Journal of Experimental Marine Biology and Ecology 361:59-74.

Roberts, J. L. 1957. Thermal acclimation of metabolism in the crab, *Pachygrapsus crassipes* Randall. II. Mechanisms and the influence of season and latitude. Physiological Zoology 30:242-255.

Rosseel, Y. 2012. lavaan: Latent Variable Analysis. R Package Version 0.5-1.8., https://cran.r-project.org/web/packages/lavaan

Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. Science 241:1460-1466.

Rouault, M., S. Illig, C. Bartholomae, C. J. C. Reason, A. Bentamy. 2007. Propagation and origin of warm anomalies in the Angola Benguela upwelling system in 2001. Journal of Marine Systems 68:473-488.

Ruttenberg, B. I. 2001. Effects of artisanal fishing on marine communities in the Galápagos Islands. Conservation Biology 15:1691–1699.

Sala, E., and C. F. Boudouresque. 1997. The role of fishes in the organization of a Mediterranean sublittoral community I: algal communities. Journal of Experimental Marine Biology and Ecology 212:25–44.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. Science 283:2095–2098.

Sanford, E. 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. Integrative Computional Biology 42:881-891.

Schaeffer, B. A., J. M. Morrison, D. Kamykowski, G. C. Feldman, L. Xie, Y. Liu, W. Sweet, A. McCulloch, and S. Banks. 2008. Phytoplankton biomass distribution and identification of productive habitats within the Galapagos Marine Reserve by MODIS, a surface acquisition system, and in-situ measurements. Remote Sensing of Environment 112:3044–3054.

Schiel, D. R., J. R. Steinbeck, and M. S. Foster. 2014. Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. Ecology 85:1833–1839.

Sentis, A., J.-L. Hemptinne, and J. Brodeur. 2012. Effects of simulated heat waves on an experimental plant-herbivore-predator food chain. Global Change Biology 19:833–842.

Seo, H., K. H. Brink, C. E. Dorman, D. Koracin, and C. A. Edwards. 2012. What determines the spatial pattern in summer upwelling trends on the U.S. West Coast? Journal of Geophysical Research 117:C08012.

Shanks, A. L., and W. G. Wright. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. Journal of Experimental Marine Biology 114:1-13.

Shannon, L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. Oceanography and Marine Biology Annual Review 23:105-182.

Shurin, J. B., J. L. Clasen, H. S. Greig, P. Kratina, and P. L. Thompson. 2012. Warming shifts top-down and bottom-up control of pond food web structure and function. Philosophical Transactions of the Royal Society B: Biological Sciences 367:3008–3017.

Siiavuopio, I., A. Mortensen, and J. S. Christiansen. 2008. Effects of body weight and temperature on feed intake, gonad growth and oxygen consumption in green sea urchin, *Stronglyocentrotus droebachiensis*. Aquaculture 281:77-82.

Sibly, R. M., J. H. Brown, and A. Kodric-Brown. 2012. Metabolic Ecology: A Scaling Approach. Wiley & Sons. New York, New York, USA. 262p.

Silió-Calzada, A, A. Bricaud, J. Uitz, and B. Gentili. 2008. Estimation of new primary production in the Benguela upwelling area using ENVISAT satellite data and a model dependent on the phytoplankton community size structure. Journal of Geophysical Research 113:C11023.

Smit, A. J., M. Roberts, R. J. Anderson, F. Dufois, S. F. J. Dudley, T. G. Bornman, J. Olbers, J. Bolton. 2013. A coastal seawater temperature dataset for biogeographical studies: large biases between *in situ* and remotely-sensed data sets around the coast of South Africa. PLoS One 8:e81944.

Smith, T. B. 2008. Temperature effects on herbivory for an Indo-Pacific parrotfish in Panamá: implications for coral-algal competition. Coral Reefs 27:397-405.

Stotz, W. B. 2004. Sea-urchin fisheries: a Chilean perspective. Pages 3-17 *in* J. M. Lawrence and O. Guzman, eds. Sea Urchins: fisheries and ecology. DEStech Publications Inc, Lancaster, Pennsylvania, USA.

Strub, P. T., J. M. Mesias, V. Montecinos, J. Rutllant, and S. Salinas. 1998. Coastal ocean circulation off western South America. Pages 273-315 *in* A. R. Robinson and K. H. Brink, eds. The global coastal ocean: regional studies and syntheses. Wiley, Hoboken, New Jersey, USA.

Sverdrup, H. U. 1942. Oceanography for Meterologists. Prentice Hall, New York, New York, USA. 246 pages.

Tapia, F. J., J. L. Largier, M. Castillo, E. A. Wieters, and S. A. Navarrete. 2014. Latitudinal discontinuity in thermal conditions along the nearshore of Central-Northern Chile. PLoS One 9:e110841.

Tapia, F. J., S. A. Navarrete, M. Castillo, B. A. Menge, J. C. Castilla, J. Largier, E. A. Wieters, B. L. Broitman, and J. A. Barth. 2009. Thermalindices of upwelling effects on inner-shelf habitats. Progress in Oceanography 83:278-287.

Tegner, M. J., and P. K. Dayton. 1991. Sea urchins, *El Niños*, and the long term stability of Southern California kelp forest communities. Marine Ecology Progress Series 77:49-63.

Tegner, M. J., and P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. ICES Journal of Marine Science 57:579-589.

Tomas, F., J. M. Abbott, C. Steinberg, M. Balk, S. L. Williams, and J. J. Stachowicz. 2011. Plant genotype and nitrogen loading influence seagrass productivity, biochemistry, and plant–herbivore interactions. Ecology 92:1807–1817.

Tupper, M., and R. G. Boutilier. 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series 151:225–236.

Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology 250:97–115.

Valle, C. A., F. Cruz, J. B. Cruz, G. Merlen, and M. C. Coulter. 1987. The impact of the 1982-1983 El Niño-Southern Oscillation on seabirds in the Galápagos Islands, Ecuador. Journal of Geophysical Research 92:437–444.

Vasquez, J. A., and A. H. Buschmann. 1997. Herbivore-kelp interactions in Chilean subtidal communities: a review. Revista Chilena Historia Natural 70:41-52.

Vinueza, L. R. 2009. The role of herbivores and productivity on community structure of rocky shores of the Galápagos Islands, Ecuador. Oregon State University

Vinueza, L. R., B. A. Menge, D. Ruiz, and D. M. Palacios. 2014. Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem. Ecological Monographs 84:411–434.

Vinueza, L. R., G. M. Branch, M. L. Branch, and R. H. Bustamante. 2006. Top-down herbivory and bottom-up El Niño effects on Galápagos rocky-shore communities. Ecological Monographs 76:111–131.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Wellington, G. M., A. E. Strong, and G. Merlen. 2001. Sea surface temperature variation in the Galápagos Archipelago: a comparison between AVHRR nighttime satellite data and *in situ* instrumentation (1982-1998). Bulletin of Marine Science 69:27-42.

Wieters, E. A. 2006. Benthic-pelagic coupling: rocky intertidal communities and nearshore oceanographic conditions across multiple scales. PhD Dissertation. University of Cape Town. 194 pages.

Wieters, E. A., B. R. Broitman, and G. M. Branch. 2009. Benthic community structure and spatiotemporal thermal regimes in two upwelling ecosystems: comparisons between South Africa and Chile. Limnology and Oceanography 54:1060-1072.

Witman, J. D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. Ecological Monographs 55:421–445.

Witman, J. D., M. Brandt, and F. Smith. 2010. Coupling between subtidal prey and consumers along a mesoscale upwelling gradient in the Galápagos Islands. Ecological Monographs 80:153–177.

Witman, J. D., R. J. Etter, and F. Smith. 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. Proceedings of the National Academy of Sciences USA 101:156644-15669.

Witman, J. D., and F. Smith. 2003. Rapid community change at a tropical upwelling site in the Galápagos Marine Reserve. Biodiversity and Conservation 12:25-45.

Yvon-Durocher, G., J. I. Jones, M. Trimmer, G. Woodward, and J. M. Montoya. 2010. Warming alters the metabolic balance of ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2117-2126.

Zar, J. H. 1996. Biostatistical Analysis. Third edition. Prentice-Hall, Upper Saddle River.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2009. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.