

Abstract

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Abstract approved: _____
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The coastal regions of Chile and Oregon are some of the most productive ecosystems in the world. The intertidal communities of both areas have been well studied, but much remains to be learned about how those communities are structured over large scales. Here, I explore the upwelling regimes and the subsequent bottom-up effects which have been documented for both regions. These effects include differences in metabolic rates of invertebrates, recruitment rates, plankton and algal growth, and top-down interaction strengths. I focus on my study of the common Chilean predatory crab, *Acanthocyclus gayi*, to demonstrate how bottom-up effects can regulate community dynamics via facilitation. I found that feeding rates of *A. gayi* were mediated by algal turf heights directly linked to upwelling regimes. I conclude that understanding the complex ecological links associated with bottom-up effects are increasingly important as we attempt to understand community dynamics at the large scales relevant to conservation and management decisions.

**Intertidal Ecology along the Western Coastlines of the Pacific:
Upwelling and Bottom-up Effects in Chile and Oregon**

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A THESIS
Submitted to
Oregon State University Honors College

In partial fulfillment of
the requirements for the
degrees of

Honors Bachelors of Science in Biology
and in Fisheries & Wildlife

Honors Bachelor of Arts in International Studies in Fisheries & Wildlife

Honors Baccalaureates of Science in Fisheries and Wildlife and Biology and Honors Baccalaureate of Arts in International Studies thesis of Christina Amy Murphy presented on May 16, 2008.

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

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Intertidal Ecology along the Western Coastlines of the Pacific: Upwelling and Bottom-up Effects in Chile and Oregon

Introduction

The coastal regions of Chile and Oregon are some of the most productive ecosystems in the world (Halpin, Strub et al. 2004) due to upwelling along their respective coastlines. Intertidal communities and oceanographic processes have been studied intensively in both areas. Traditionally, ecological studies focused on interactions within small areas, drastically limiting their application (Dayton and Tegner 1984). Today, studies in marine communities focus increasingly on the connections between oceanographic conditions and community structure. These connections aid in the understanding and prediction of community interactions over mesoscales (10s to 100s of thousands of kilometers) relevant to conservation and management efforts (Menge 2000; Nielsen and Navarrete 2004).

In this thesis I first to summarize how oceanographic regimes can be tied to intertidal community structure, and then review and compare the intertidal communities and ecological processes documented for the Oregon and the central Chilean coasts. With this context, I then present my research on the feeding rates of a predatory Chilean crab as they relate to habitat. I show that upwelling processes appear to be ultimately mediating predation rates through their effects on algal turf height. Finally, I relate these results to the larger ecological context referred to above.

Background

What is upwelling?

Upwelling refers to the rise of cool, nutrient rich waters from depth towards the surface (EEA 2008). Rates of upwelling are affected by season, temperature, wind patterns, currents, and land formations. Upwelling is generally caused by the movement of warm surface waters offshore (due to a combination of wind and the Coriolis effect), known as Ekman transport (Nybakken 2001). Upwelling is commonly associated with the west coast of continents because the wind stress is parallel to the coastal boundary (Reddy 2001). This means that as southward coastal winds along the west coast of North America push water towards the equator, the Coriolis effect moves that water offshore, and deep, cool, nutrient-rich water rises up to replace it (Figure 1). Upwelling is important because it brings nutrients from depth to surface waters exposed to light, stimulating bursts of primary productivity upon which entire communities are based. Upwelling events are also tied to currents and water movement and may have important impacts on larval transport and survival (Menge, Daley et al. 1997; Menge 2000; Narvaez, Navarrete et al. 2006). Larval transport is not always entirely passive, however, as documented in studies that show that swimming behavior may compensate for movement of water offshore during upwelling, limiting transport (Shanks and Brink 2005).

What are bottom-up effects?

Bottom-up effects refer to structuring forces on an ecological community which are determined by productivity, nutrients, and horizontal and vertical transport (oceanographic features) (Menge, Daley et al. 1997). The term can be contrasted with top-down effects such as predation or grazing. Historically, top-down effects were

considered to have primacy in structuring marine intertidal communities (Paine 1974) although today it is believed that those communities are shaped by both top-down and bottom-up processes (Menge 1992; Menge 2000).

In the context of intertidal community studies, bottom-up effects are defined as inputs of nutrients or primary production (Menge 2000), although growth and composition of algal species have also been regarded as bottom-up factors (Broitman, Navarrete et al. 2001; Nielsen and Navarrete 2004). Bottom-up influences appear to develop on a slower temporal scale relative to top-down effects in intertidal systems (Nielsen 2003; Nielsen and Navarrete 2004). These processes may be intertwined and difficult to separate as they interact to determine competitive interactions (Xavier, Branch et al. 2007). It may also be difficult to predict the effects of upwelling variability because upwelling may enhance local primary production, but it may in turn carry larvae and particulate matter offshore (Xavier, Branch et al. 2007).

The study of bottom-up processes is relevant in part because it allows ecologists to relate community features to large-scale oceanographic processes, allowing for understanding/predictions over larger scales, ranging from mesoscales (mentioned above; 10's of km) to macroscales (100's to 1000's of km). In this way, they can be used to make broader generalizations than what is possible based on a site-specific ecological study.

What is the El Niño Southern Oscillation?

El Niño Southern Oscillation (ENSO) refers to the relationship between ocean surface temperatures and atmospheric pressure in the tropical west Pacific Ocean, a source of inter-annual variability in marine conditions. ENSO is generally referred to as

a cycle with warm, El Niño, and cool, La Niña, events at the two extremes (Halpin, Strub et al. 2004). The frequency of warm and cool events is variable, but they are generally separated by about 3 to 8 years (Figure 2). Typically, warm phases are associated with stratification and high ocean temperatures along the western South American and North American coastlines, and reducing upwelling of the Humboldt or Peru-Chile (Figure 3) and California Currents. The length of El Niño events is measured in months and is highly variable (approx. 6-22 months) (Trenberth 1997). El Niño most strongly affects the tropical Pacific, but its oceanographic influences can extend poleward as well (including the Oregon coast) (NOAA 2008).

What is the Pacific Decadal Oscillation?

Ocean conditions can show high inter-annual variability. However, we now know that some variation occurs over longer time scales and has some degree of predictability. Effects of the Pacific Decadal Oscillation can be seen in historic fisheries data (Francis and Hare 1994) and are similar to ENSO, except in scale (20 to 30 years instead of 6 to 22 months) and in the origin of its primary signatures. The PDO is most visible in the North Pacific, unlike ENSO which originates in the tropics (Mantua 2000). Both have strong effects in temperate systems. The PDO may be important in the dynamics of intertidal ecosystems, especially in Oregon, as its effects can be similar to those seen during ENSO events (Figure 3; Menge 2008).

Areas of Focus

Chile

The Peru-Chile current is a dominant factor in the climate and environment of the western South American coastline. This current is an Eastern Boundary Current which, like the California current, transports cooler, nutrient-rich waters towards the equator. A poleward undercurrent transports more saline, nutrient rich-water towards the pole. Productivity is driven by upwelling, as described above (Halpin, Strub et al. 2004; Thiel, Macaya et al. 2007).

The Chilean coastline is 6,435 km (CIA 2004) long and ranges from 17° to ~56°S. Although the coastline is relatively straight, local geographic features cause the nearshore region to be highly variable. The coastline is predominantly rocky (volcanic, granitic, or sedimentary), narrow, and very wave exposed. Short sandy beaches are more common in southern Chile (Thiel, Macaya et al. 2007).

Upwelling along the Chilean coast is seasonal in the south, while northern Chile experiences sustained upwelling in some areas throughout the year. Points of major upwelling can be identified using sea surface temperature (Figure 4).

Oregon

The California current is also an Eastern Boundary Current of near-surface flows directed towards the equator. Much like the Peru-Chile current, the California current transports cooler, nutrient rich, and less saline water towards the tropics while a poleward undercurrent of salty, nutrient rich water which flows northward towards the pole (Halpin, Strub et al. 2004).

Oregon's coastline stretches 476km (2) from 41° to 46°N and is characterized by a greater number of broad and gently sloping rocky benches than Chile. Wave exposure depends on the location and local topography of a site and can range from wave protected to highly wave exposed.

Upwelling along the Oregon coast is seasonal. From the Columbia River to ~43°N upwelling alternates on a 3 to 10 day cycle with a relaxation of upwelling. South of ~43°N can be characterized as a persistent upwelling region as summer upwelling is less frequently punctuated by periods of relaxation (Menge, Daley et al. 1997) (Figure 5).

As in Chile, the intertidal community of the Oregon coast is dominated by macroalgae and sessile, filter-feeding invertebrates which inhabit large patches of the landscape (Halpin, Strub et al. 2004). Invertebrate predators, such as sea stars, can have strong impacts on community structure (Paine 1974; Paine 1976). Humans have relatively little direct impact on the intertidal community, especially when compared to the type and extent of human activities in Chile (Halpin, Strub et al. 2004).

Rates of intertidal mussel recruitment are 2-3 orders of magnitude higher in Oregon and northern California than in central Chile. However, the spatial scales are similar in both regions and persistent patterns of recruitment can be seen at meso-scales (tens of kilometers), even while local scales show highly variable recruitment (Navarrete, Broitman et al. 2008).

Intertidal Communities

Chile

The intertidal community of Oregon is dominated by macroalgae and sessile, filter-feeding invertebrates which occupy large patches of the landscape. Large kelps (primarily *Lessonia* sp.) are abundant in the low intertidal, with smaller macroalgae forming dense carpets (turfs) closer to the rock surface (Thiel, Macaya et al. 2007). Humans act as top-predators in the intertidal community, harvesting a diverse array of intertidal organisms from large barnacles (e.g. *Austromegabalanus* sp.) to kelps. The removal of these organisms can shift the dynamics of the intertidal community (Castilla and Duran 1985) (Figure 6).

Oregon

As in Chile, the intertidal community of the Oregon coast is dominated by macroalgae and sessile, filter-feeding invertebrates which inhabit large patches of the landscape (Halpin, Strub et al. 2004). Invertebrate predators, such as sea stars (*Pisaster* sp.), can have strong impacts on community structure (Paine 1974; Paine 1976). Humans have relatively little direct impact on the Oregon intertidal community, especially when compared to the type and extent of human activities in Chile (Halpin, Strub et al. 2004).

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Community Effects

Human Effects on Bottom-Up Processes

Bottom-up processes may be difficult to detect under intense levels of human exploitation. In the Canary Archipelago, bottom-up effects seemed to be correlated to the abundance of topshell snails, which were not heavily harvested, while no large-scale spatial differences were observed in limpets, which were heavily collected (Tuya, Ramirez et al. 2006). This could have important implications along coastlines such as Chile, where human impacts are relatively high (Castilla and Duran 1985; Halpin, Strub et al. 2004).

In Chile, increased nutrients, due to upwelling, are associated with strong positive effects on the growth of corticated algae (herbivore resistant) and negative effects on that of ephemeral algae (thin and palatable). Herbivores also have a negative effect on ephemeral algae. However, they have no discernable effect on corticated algae which may be an indirect consequence of the collection by humans of large keyhole limpets (which feed on corticated algae). It seems that humans may be indirectly changing the dynamics of the community mediated by the effects of upwelling (Nielsen and Navarrete 2004).

Additional evidence for human impacts in Chile relates to the abundance of intertidal filter feeders, herbivores, and carnivores. While algal cover changes significantly in areas strongly influenced by upwelling, no corresponding differences in abundances of filter feeders, herbivores, or carnivores can be detected. Human collections may be determining abundance and composition of these groups (Broitman, Navarrete et al. 2001).

Bottom-Up Effects in Oregon

In Oregon, *Mytilus californianus* mussels are more metabolically active at a site with more upwelling than one with less upwelling, indicating that physiological indices (such as RNA and enzyme production) may be useful in determining the strength of bottom-up effects (Dahlhoff and Menge 1996). Phytoplankton growth has also been found to vary with upwelling and available nutrients (Menge 2000).

Top-down interactions have themselves been found to vary positively with bottom-up processes as high levels of recruitment and phytoplankton may enhance predation impact through “bottom-up” subsidies. Mesoscale variation in coastal geography (e.g. headlands, shelf width, etc.) and the resultant coastal hydrography may therefore be an ultimate cause of the differences between sites because water movement likely determines both recruitment success and phytoplankton concentration (Menge, Daley et al. 1997; Menge, Blanchette et al. 2004).

Bottom-Up Effects in Chile

Sections of the Chilean coast (~15-20km) downstream (equatorward) from upwelling centers may exhibit consistently higher phytoplankton concentrations than sites at upwelling centers, generating a source-sink type of geographic pattern of nearshore nutrients and phytoplankton along the coast (Wieters, Kaplan et al. 2003). This relationship has been documented between sites along the Oregon coast as well (Menge, Daley et al. 1997).

Variability in the intensity of upwelling occurring over mesoscales produces predictable variation in mussel recruitment. While patterns of community structure are

not affected, community dynamics do change abruptly with discontinuities in upwelling regimes. These discontinuities couple benthic and pelagic systems and set bounds to the strength of species interactions (Navarrete, Wieters et al. 2005), consistent with similar findings along the Oregon coast (Menge, Daley et al. 1997).

Upwelling along the Chilean coast has been linked to differences in growth rates of *Gelidium chilense*, a turf-forming alga. These differences cause predictable mesoscale patterns of turf height, with tall turf at upwelling centers where growth rates are high and short turf in areas with less upwelling. A common intertidal mussel, *Perumytilus purpuratus*, is more successful when recruiting to short turf, indicating that upwelling affects community processes such as facilitation (Wieters 2005).

P. purpuratus is a preferred, but not exclusive, prey item of the predatory intertidal crab, *Acanthocyclus gayi* (Navarrete and Castilla 1988). Due to its relatively high consumption rates and abundance, *A. gayi* may exert a top-down influence on intertidal community structure (Navarrete and Castilla 1988; Castilla, Luxoro et al. 1989). Previous laboratory experiments have shown differential responses in refuging behavior by *A. gayi* based on the height of available algal turf (Wieters, unpublished data). For this reason, behavioral studies on *A. gayi* are a logical next step in understanding how bottom-up effects influence relationships between species and how they may ultimately impact the strength of top-down effects.

Case Study: Feeding rates of the predatory crab *Acanthocyclus gayi*

Upwelling-driven habitat modification alters feeding rates of the predatory crab Acanthocyclus gayi along the Chilean coast.

Introduction

Investigating how environmental conditions that vary over large, geographic spatial scales modify dynamics of local populations and communities has become increasingly urgent as concerns over the stability of marine resources rise. Changing habitat qualities across a landscape influence local populations and their relationships.

Along the rocky, wave-exposed shores of central Chile, algal turfs, composed largely of *Gelidium chilense*, are abundant in the low intertidal zone. However, across ~900 km of the central coast, turf height and morphology vary greatly among sites, due largely to persistent variation in growth rates driven by local differences in nearshore oceanographic conditions (e.g. nutrient supply) linked to upwelling focal points (Wieters 2005).

Changes in the seascape have multiple effects on local environmental conditions and thus can have a major influence on associated assemblages. Studies suggest that algal turf (hereafter “turf”) height differentially affects the behavior of the carnivorous crab *Acanthocyclus gayi*. Seeking protection from visual predators (e.g. birds), adult crabs are typically restricted to aggressively-defended refuges (e.g. rock crevices) during daytime low tides, and become active during nocturnal low tides (Navarrete and Castilla 1990). Crab refuge habitat utilization varies greatly among sites along the coast, as adults recognize and prefer to take refuge in turf where the turf is tall, but select rock crevices where the turf is short. Moreover, crab density strongly and positively correlates with

turf height, suggesting that refuge habitat availability limits local population sizes along the coast (Wieters, unpublished data).

A. gayi are carnivorous, feeding primarily on invertebrates in the algal turf (Navarrete and Castilla 1988). Their disproportionate distribution over time in turf vs. crevice in relation to turf height led us to question whether feeding rates would vary between crabs with access to tall vs. short turf. That is, if crabs spend more time in tall turf (where foraging would be expected) then do they have higher feeding rates? The question of whether differential feeding rates were found among habitat types was addressed using both laboratory and field trials. We also examined activity levels and natural mortality in our efforts to better interpret the results of the feeding trials.

Methods

Laboratory

Laboratory trials were conducted at the Estación Costera de Investigaciones Marinas (ECIM) in Las Cruces, Chile. Feeding rates were determined by placing crabs into individual aquaria containing equal covers of artificial turf (either tall, 5cm or short, 1cm) and crevice habitat. Square turf plates (15 x 15 cm) were constructed using a hard plastic base covered with either short (FieldTurf®) or tall (MegaTurf®) artificial turf (generally used for sporting events).

All crabs were collected from the area directly adjacent to the ECIM reserve (Chile, Region V). Twenty-five similar-sized (0.6 to 1.0cm) mussels (*Perumytilus purpuratus*) were collected from the same site and transplanted into each turf plate 3 days prior to the start of the experiment to allow mussels to firmly attach. Two trials were run, wherein mussels were arranged in either a grid pattern (evenly spaced throughout the turf) or spatially clumped (at the center of the turf plate) (Figure 8). Control plates were placed in aquaria without crabs, to account for natural mussel mortality.

Aquaria were supplied by a flow-through sea water system and were drained and filled at 6 hour intervals (approximating field conditions) to account for behavior variation at high and low tides. Water removal occurs directly adjacent to the ECIM site and no additional water treatment or processing occurred.

A wooden insert supported the plates and kept crabs from accessing the drain below. All crabs were food deprived for 3 days prior to the experiments. Individual crabs were used in a single trial and then held until their release. Female crabs carrying eggs were not collected and females who released eggs in the laboratory were excluded

from the trials to avoid possible effects on feeding rate and behavior. An equal number of males and females of comparable sizes were used in each trial type. All crabs used were of moderate size (>14mm to <24mm).

Aquaria were divided into grids to allow for accurate records of location and movement (Figure 7). Crabs were monitored hourly for the first group of feeding experiments (20 tanks, mussels in grid pattern) and detailed movement notes of crab location and activity type within the grid were recorded. Activities were categorized as feeding (handling a mussel), walking (moving around the tank), picking (moving chelae in a search pattern) or immobile (stationary). These activities were mutually exclusive. Subsequent experiments did not include activity levels. The length of trials was 72 hours, comprised of six high tides (full tank) and 6 low tides (empty tank).

Field

Feeding rates were determined in a field setting using a turf plate (either short or tall). Plates were either designated as a control (-crab) or had a crab tethered (using a clear epoxy and string) to the central screw (+crab). All plates were stocked with mussels sized and arranged as in the laboratory grid design. Mussels were allowed at least 24 hours to attach to the turf plate. Plates were anchored in the low intertidal and crabs were tethered to the central screw to prohibit movement off the plate. Plates where crabs disappeared (due to escape or mortality) were not used in final data analyses. All crabs were food deprived for 3 days prior to placement.

Results

Feeding Rates

I analyzed data with JMP Statistical Software. The number of mussels consumed was highly variable among individuals, but we found no correlations between consumption rates and size or sex. In the grid laboratory trials, crabs in short turf consumed more mussels than crabs in tall turf (One-way ANOVA, $p < 0.01$) (Figure 9). No mussel mortality was seen in laboratory control plates. Although rare, females who began carrying eggs during the trial were excluded from the analysis.

Feeding rates in the clumped mussel trials did not differ (One-way ANOVA, $p = 0.15$). This appears to be due to the high levels of individual variation and the small sample size resulting from time constraints. There do appear to be generally higher consumption rates in short turf across both trials (Figure 9).

Field trials using turf plates and a grid mussel pattern were consistent with laboratory trials. Feeding rates on plates with short turf were different from both the control short turf plates and the tall turf plates with crabs ($p < 0.01$). No differences were seen between controls or between tall turf treatment and control plates. Mean number of mussels consumed or missing was 12.3 for short turf treatment plates (short turf +crab), 5.9 for short turf control plates (short turf –crab), 4.6 for tall turf treatment plates (tall turf +crab), and 3.8 for tall turf control plates (tall turf –crab).

Activity Levels

Crabs were more active during the night (18:01-06:00) than the day (06:01-18:00). Activity type or level did not differ between turf types in either day or night trials (Figure 10). However, refuge type did vary between turf types. In short turf trials, crabs

preferred to use the crevice as refuge. In tall turf trials, the turf was the preferred refuge (Figure 11).

Discussion

The reduced feeding rates in tall turf were contrary to our predictions. I predicted that *A. gayi* exposed to a habitat which acts as secure refuge and provides constant access to prey species would take advantage of the protection and resources, feeding more frequently. We saw no evidence of more frequent feeding or of daytime feeding which we had considered a possibility.

The feeding rates could reflect differential energy expenditure. However, the activity levels in the lab were not different and would not appear to support such a conclusion. The benefits of using feeding habitat as a refuge may be offset by search time and possibly mussel abundance (in the field). Interestingly, no differences have been found in the size and weight of crabs at short vs. tall turf sites (Wieters, unpublished data). Mortality rates for crabs tethered in natural turf are higher in short turf than tall turf (Murphy and Wieters, unpublished data).

Additional trials using a clumped design would have been valuable in assessing the impact of search time/encounter rates on feeding behavior. The lack of significant differences between feeding rates for clumped mussels could be due to a small sample size and high levels of variation among individuals.

The data do suggest that feeding rates of the predatory crab *A. gayi* are mediated at least in some instances by turf height. Wieters (2005) found a consistent relationship between *Gelidium* turf height and upwelling patterns. These relationships would indicate that bottom-up processes are at least partly responsible for the feeding rates of *A. gayi*. Interestingly, mussel recruitment into *Gelidium* is facilitated more by short turf than by tall turf. Additional dietary studies would be useful to determine differences between

habitat types as *A. gayi* are known to prey on a range of invertebrate species (Navarrete and Castilla 1988).

This study agrees with previous findings indicating that *A. gayi* prefers tall turf to crevices and crevices to short turf when seeking refuge habitat (primarily during daylight hours). This behavior appears to be directly mediated by the height of available turf.

The roles of bottom-up processes as they travel up the marine intertidal community are still poorly described. This study suggests the possibility that nutrient availability could influence habitat-mediated behaviors in intertidal predators. Understanding these types of relationships will allow us to gain insight into the forces structuring unique marine intertidal communities over mesoscales relevant to conservation and management applications.

Conclusion

Upwelling appears to ultimately influence both the density and the feeding rates of *A. gayi* through the facilitative impacts of *Gelidium* turf on crab behavior. This demonstrates bottom-up effects moving through the system and ultimately influencing top-down trophic effects (Figure 12). The combined effects of increased density and decreased feeding rates on prey species have yet to be quantified. While impacts of bottom-up effects on top-down processes have been previously noted, *A. gayi* in particular may prove an important study species due to the strong impacts of turf height on its behavior in addition to the strong connection between that turf height and the upwelling regimes along the Chilean coast.

General Conclusion

Although the species present on the Oregon and Chilean coasts are different, many of the families and genera are the same. It appears that the coastlines experience similar bottom-up effects driven by variation in coastal features and wind patterns. Both areas continue to contribute to the growing understanding of intertidal ecology and bottom-up processes. Comparing the systems may become especially valuable as the role of humans in the Chilean intertidal community becomes increasingly well documented and understood.

The study I conducted in Chile indicated a link between the feeding rates of *A. gayi* and upwelling due to the effect of upwelling on algal turf height and the impact of that turf height on crab behavior. Interestingly, turf height is itself connected to the recruitment of mussels, upon which *A. gayi* are known to feed. These complex links, although difficult to untangle will allow us to better understand communities over the large scales at which management and conservation decisions are made.

There is a need to study these areas as soon as possible due to alterations over time, such as global warming, or even the implementation of marine reserves. The more we know now, the more we can understand and predict what is and will be happening in the world around us.

Acknowledgements

This project and manuscript would never have been possible without the astounding support of both mentors and friends at home and abroad. It has taken me 5 years to reach this point in my undergraduate career, 4 of which prepared me for this experience. I cannot possibly begin to thank everyone who has helped me to reach this place in my life. I can only hope that those of you who have made a difference in who I am, what I know, and how I see the world, already know that I am deeply grateful for everything that you have done.

Specifically, I would like to allocate many thanks for the support, guidance, tireless editing and incredible international connections provided my thesis mentor, Dr. Bruce Menge. His instruction of Marine Ecology ultimately led to my increasing fascination with the salinated world and a curious obsession with intertidal organisms. My research at ECIM was conducted under the wonderfully knowledgeable and supportive Dr. Evie Weiters, who taught me how to survive both the Chilean intertidal and Chilean Spanish and provided all of the materials required for my field and laboratory experiments. Thank you to Dr. Sergio Navarrete, director of ECIM, who generously provided laboratory access, space, and equipment, and who began studies on *A. gayi* many years ago. I would like to send warm fishes and buckets of thanks to Dr. Selina Heppell and Dr. David Noakes, who are serving on my committee in addition to teaching, researching, and saving the world.

The generous support of the Ford Family Foundation made my adventures in Chile possible. Their commitment to education and community development continues to inspire me.

Finally, I would like to thank my friends and my mother, Pamela. Mom, you will always be a role model of strength and dedication. To all of my friends, especially Chee Sing Lee, I thank you for hours of editing drafts and discussing ideas. Sanity has been your gift to me, and I would not be here without it.

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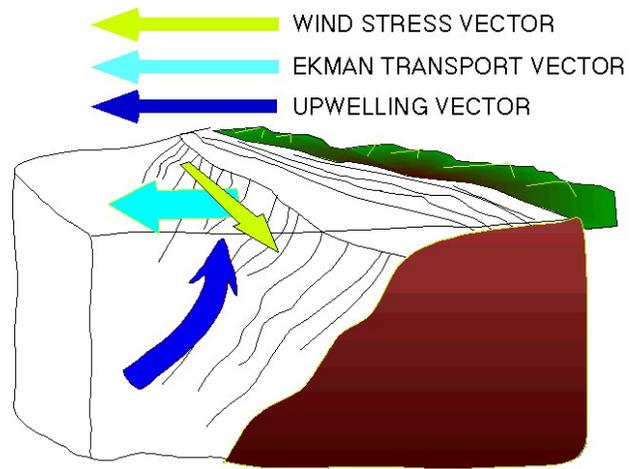


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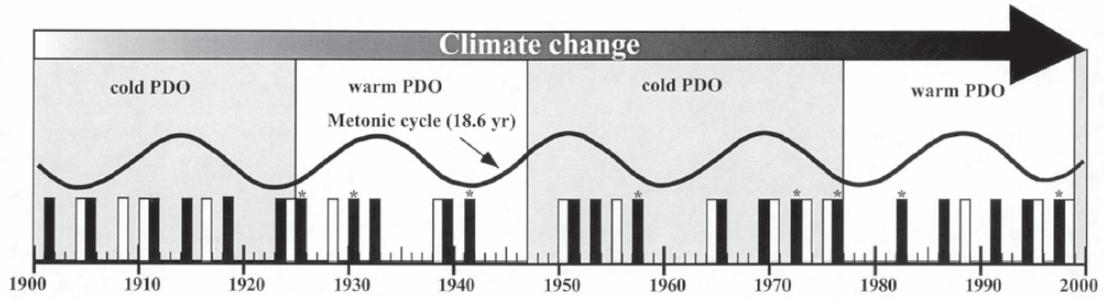


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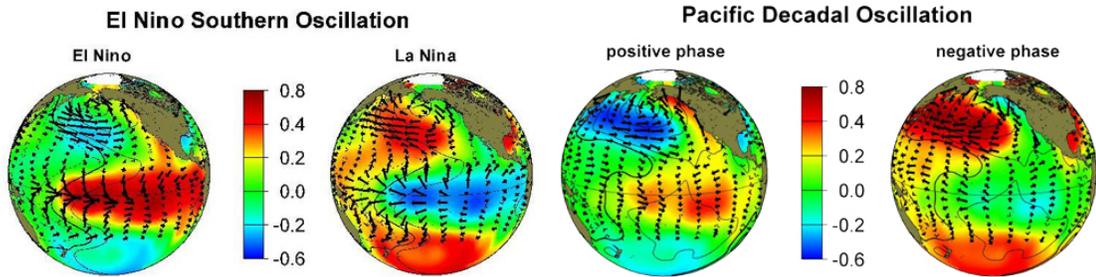


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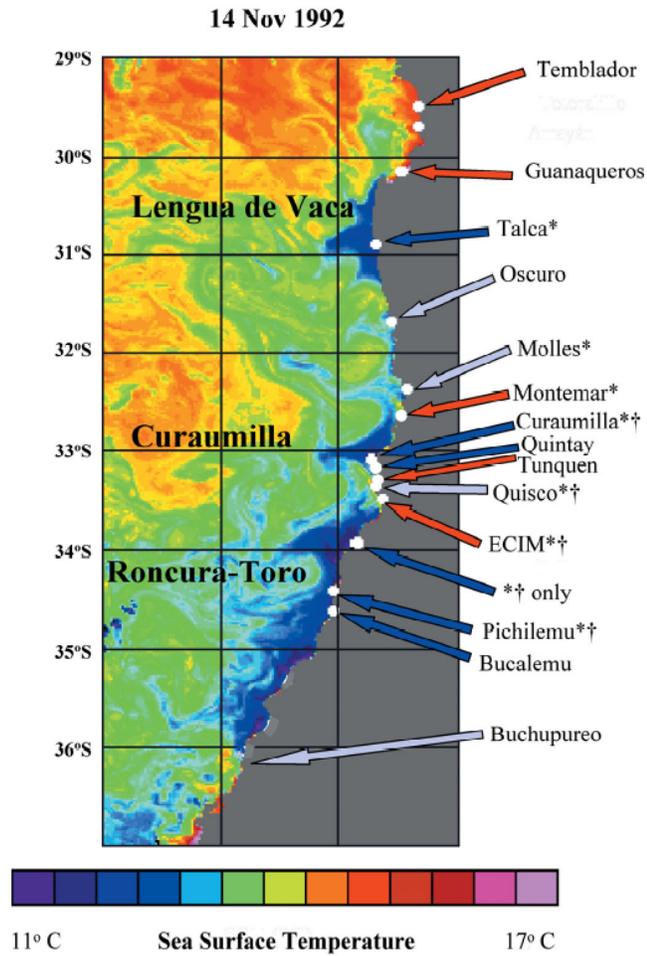


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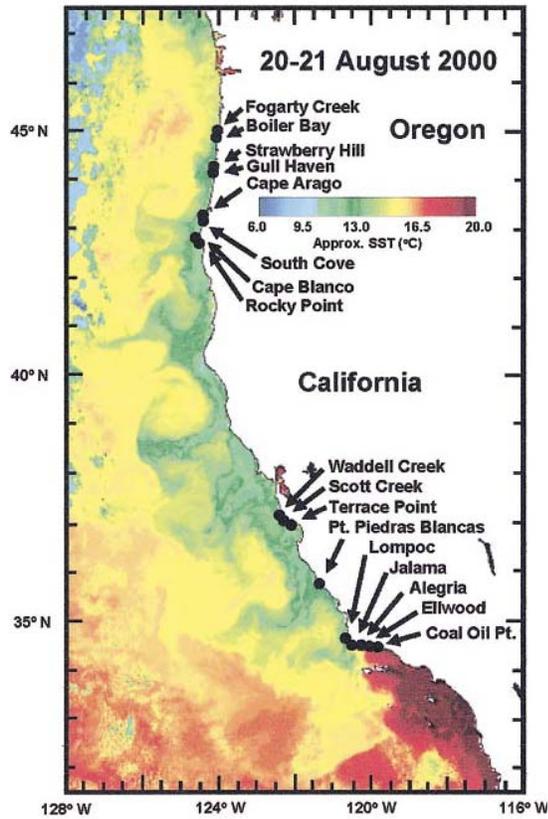
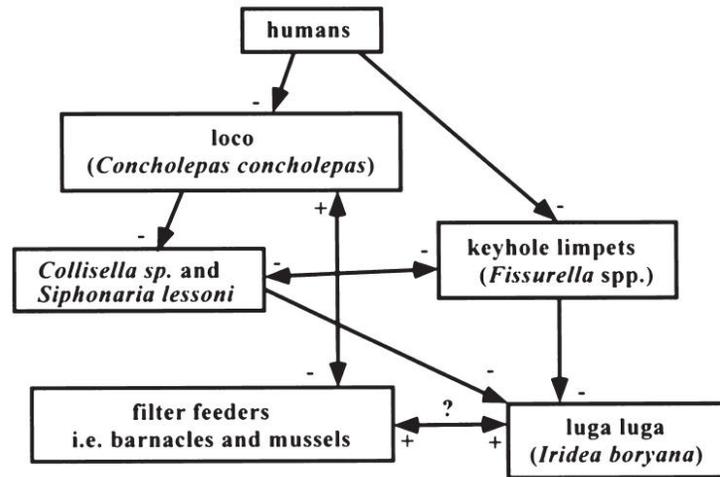


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Chile



Oregon

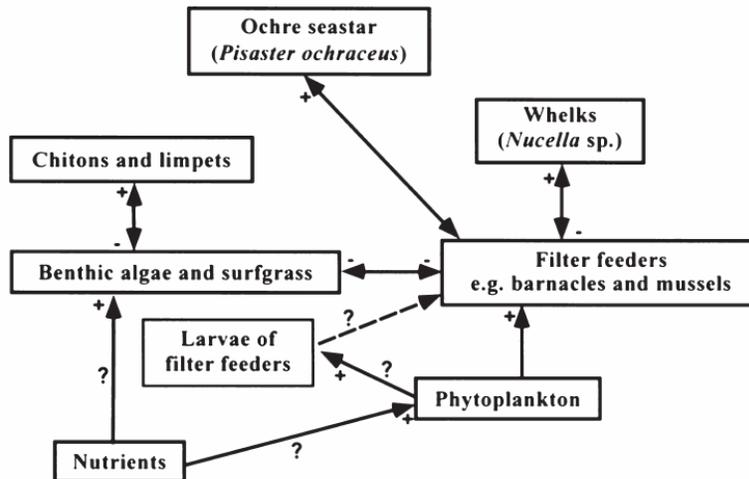


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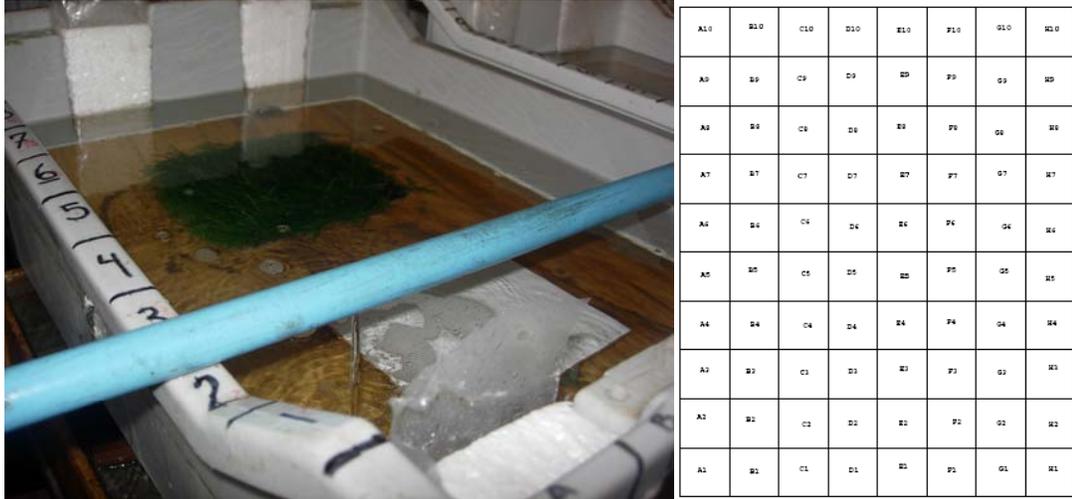


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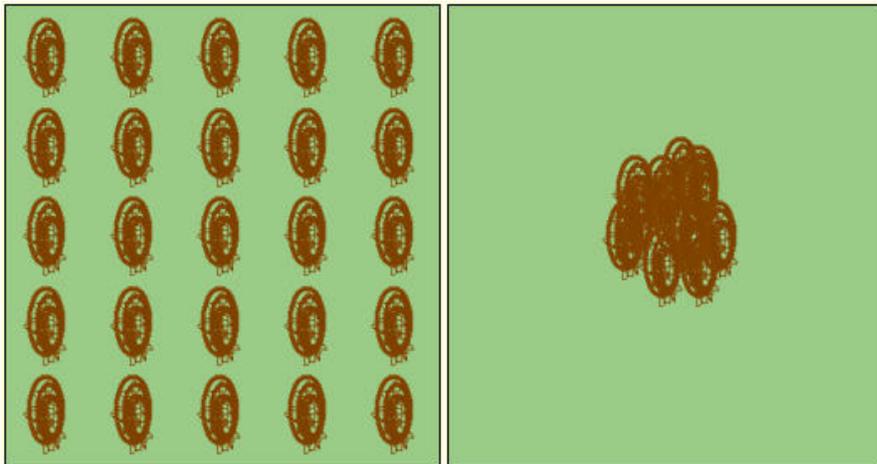


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Effect of turf height on crab feeding rate

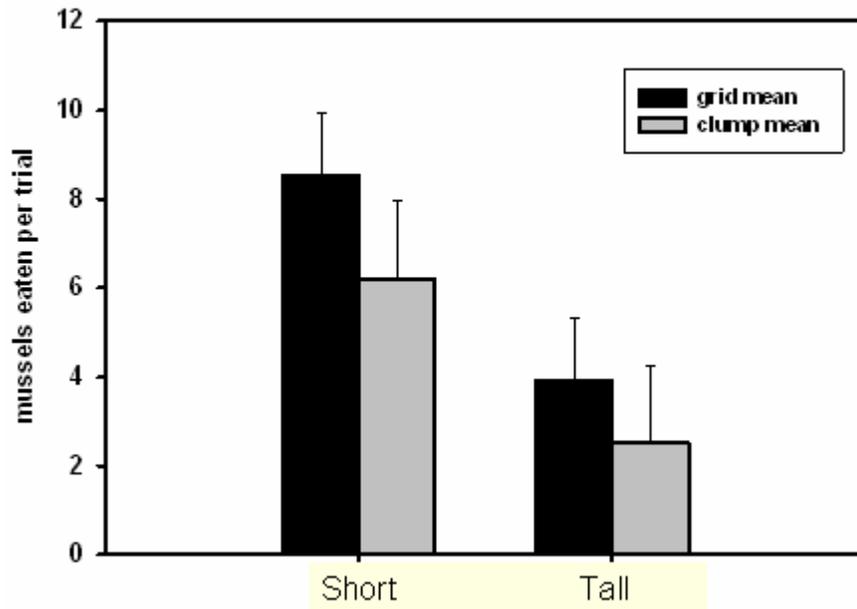


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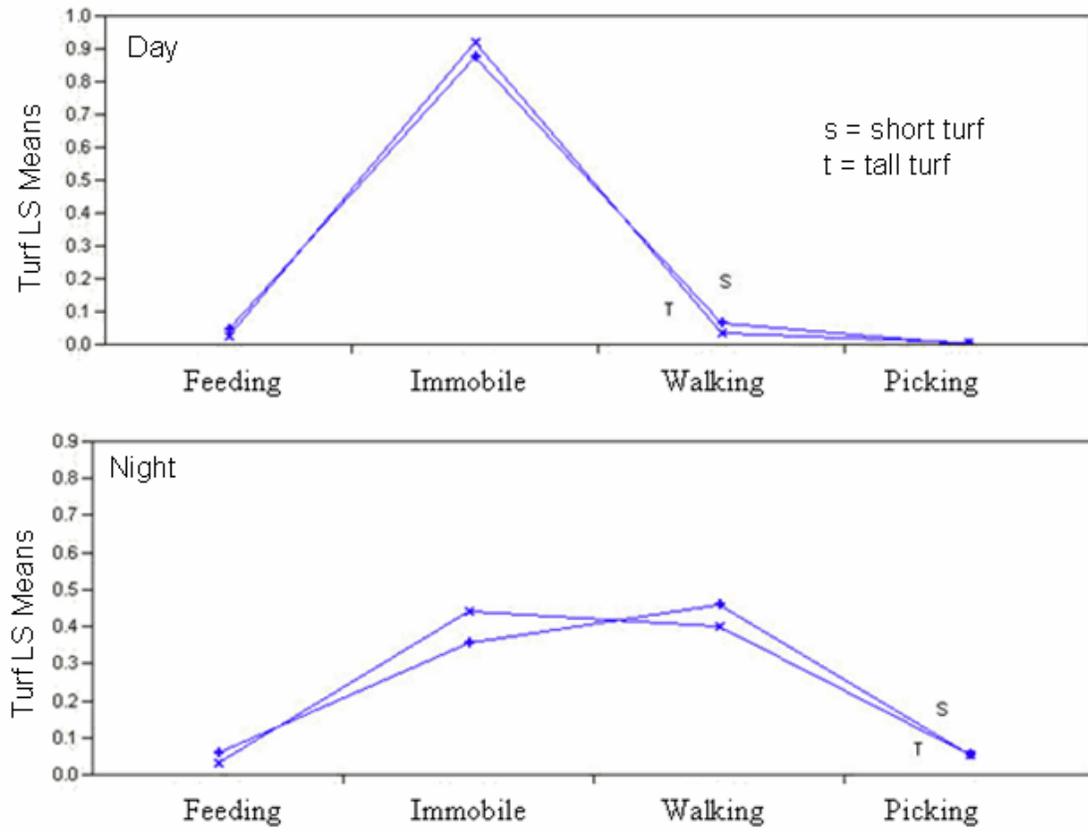


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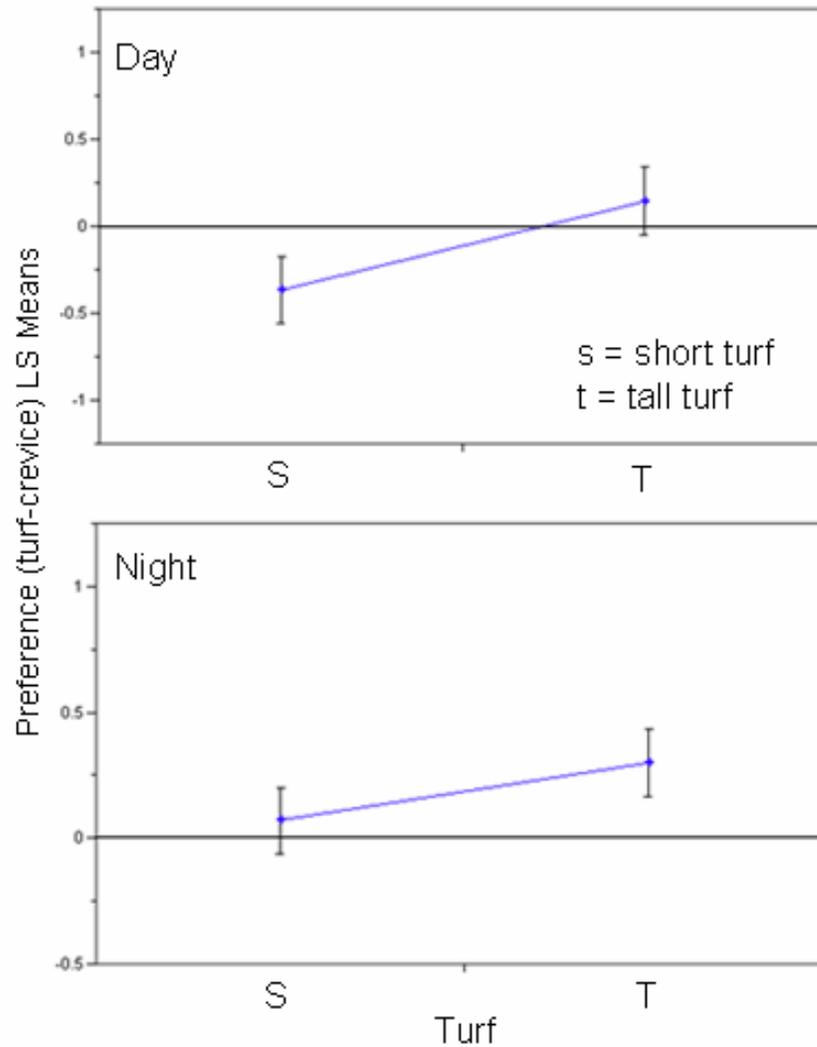


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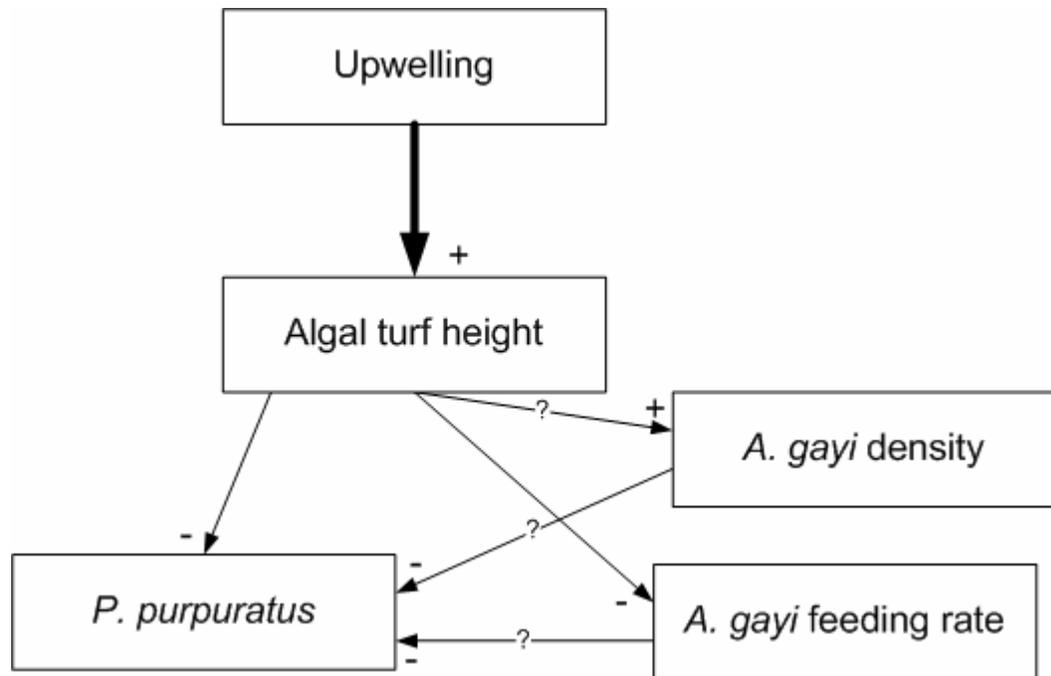


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