AN ABSTRACT OF THE DISSERTATION OF

Eric Sanford for the degree of Doctor of Philosophy in Zoology presented on September 3, 1999. Title: Oceanographic Influences on Rocky Intertidal Communities: Coastal Upwelling, Invertebrate Growth Rates, and Keystone Predation.

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The influence of large-scale processes on natural communities has become one of the central issues of modern ecology. I combined field and laboratory studies to investigate the effects of variation in coastal upwelling on rocky intertidal communities along the central Oregon coast.

I examined whether the growth of intertidal barnacles (*Balanus glandula* and *Chthamalus dalli*) at two sites was linked to nearshore phytoplankton abundance. Short-term growth rates were low during a persistent upwelling event and increased two to three-fold during the subsequent relaxation of upwelling. Although this increase coincided with a large phytoplankton bloom at one site, parallel increases in growth occurred at a second site where no bloom was recorded. Published analyses of barnacle stomach contents suggest that zooplankton may be an important component of barnacle

diets. Barnacle growth may thus be enhanced during upwelling relaxations through the combined benefits of more phytoplankton, more zooplankton, and warmer water temperatures.

In laboratory studies, I tested the hypothesis that upwelling-related variation in water temperature regulates the feeding, growth, and energetics of two intertidal predators, the sea star *Pisaster ochraceus* and whelk *Nucella canaliculata.* Sea stars and whelks maintained at 9°C generally consumed 30% fewer mussels than those at 12°C. Animals that were exposed to cyclic temperatures (alternating between 12°C and 9°C every two weeks) tended to grow faster than those held at constant temperatures. Consumers in upwelling systems may thus feed intensely during periods of warmer water while benefiting from reduced metabolic costs during cold-water intrusions.

I conducted field experiments to quantify the effect of small changes in water temperature on the interaction between a keystone predator, *Pisaster ochraceus*, and the intertidal mussel *Mytilus californianus.* Per capita and per population effects of sea stars on transplanted mussels were sharply reduced during a persistent cold-water upwelling event. Interannual variation in the frequency and intensity of upwelling may thus alter community dynamics through effects on this keystone interaction.

Taken together, these studies suggest that upwelling-related variation in nearshore conditions can profoundly influence intertidal systems at the organismal, population, and community level.

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Oceanographic Influences on Rocky Intertidal Communities: Coastal Upwelling, Invertebrate Growth Rates, and Keystone Predation.

by

Eric Sanford

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Doctor of Philosophy dissertation of Eric Sanford presented on September 3, 1999

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

Eric Sanford

Eric Sanford, Author

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CHAPTER 1

General Introduction

The influence of large-scale processes on natural communities has rapidly become one of the central issues of modern ecology. Historically, ecologists have investigated the role of local abiotic and biotic factors in small, well-defined systems (Menge & Olson 1990, Brown 1995). However, recent interest in topics such as dispersal, metapopulations, introduced species, climatic change, and the global nitrogen cycle has prompted ecologists to consider processes operating at larger spatial scales (Menge & Olson 1990, Lubchenco et al. 1991, Levin 1992, Vitousek 1994). The traditional distinction between basic and applied branches of ecology has also been blurred by the recognition that (1) large-scale processes contribute significantly to the structure of local communities, and (2) many of these processes are being altered by human activities (Vitousek et al. 1997). Addressing the role of large-scale processes is thus widely seen as the key to both predicting and managing the dynamics of biotic systems in an era of growing human impacts (Menge & Olson 1990, Lubchenco et al. 1991, Vitousek 1994).

Interest in large-scale processes is a relatively recent development in rocky intertidal ecology. As in most fields of ecology, marine researchers have traditionally worked at one or a few sites and have emphasized the importance of local physical and biotic factors (Menge & Olson 1990, Menge 1992). This tendency has been particularly strong in rocky intertidal communities where organisms generally exhibit conspicuous patterns of local distribution. Intertidal species are often confined within narrow vertical zones and large shifts in species composition and abundance are frequently observed across short horizontal distances (meters to 10's of meters).

In seeking to explain these dramatic patterns of local variation, ecologists working on rocky shores were naturally drawn to conspicuous local abiotic and biotic factors. For example, it has long been recognized that differing periods of aerial exposure produce a strong vertical gradient of heat and desiccation in the intertidal zone (Doty 1946). Horizontal positions on the shore also vary dramatically in degree of exposure to wave forces. In addition, species interactions may have strong local effects that are readily demonstrated by manipulating intertidal organisms with cages or other simple equipment. Therefore, it is not surprising that classic experimental studies in rocky intertidal systems focused on local processes including the effects of environmental stress, competition, predation, herbivory, and disturbance (Connell 1961, Paine 1966, Dayton 1971, Menge 1976, Lubchenco 1978, Sousa 1979).

Although these and similar studies were successful in explaining many patterns in rocky intertidal communities (see Paine 1994 for a review), local processes were often unable to fully explain variation among sites separated by 10's to 100's of km (Menge 1992). This observation prompted ecologists to seek explanations that included the influence of large-scale processes. In particular, a number of influential papers published in the 1980's sparked a renewed interest in larval transport and recruitment (Doherty 1981, Underwood & Denley 1984, Connell 1985, Gaines & Roughgarden 1985, Roughgarden et al. 1988; see reviews by Grosberg & Levitan 1992, Caley et al. 1996).

These papers suggested that (1) larval recruitment was an important factor structuring marine communities, and (2) recruitment often varied predictably in space and time as a result of persistent oceanographic features.

Strong interest in recruitment focused the attention of benthic marine ecologists on oceanographic transport processes, including coastal upwelling (Roughgarden et al. 1988, 1991, Farrell et al. 1991, Wing et al. 1995). Upwelling is driven by strong equatorward winds that occur during spring and summer along the Pacific coast of North America. Surface waters that are pushed offshore by the combined action of winds and the Coriolis effect are replaced by the upwelling of cold, nutrient-rich waters from deeper layers (Smith 1983). Along the Oregon coast, upwelling events last for several days to three or more weeks (Menge et al. 1997b; Chapter 3). Roughgarden et al. (1988, 1991) suggested that during upwelling, larvae in nearshore waters are advected offshore and accumulate in a frontal boundary. When alongshore winds relax, upwelling ceases, and the offshore front may return to shore producing a recruitment pulse (Roughgarden et al. 1988, 1991, Farrell et al. 1991, Wing et al. 1995). Spatial and temporal variation in recruitment may in turn influence the density of adults and the strength of competition for space (Gaines & Roughgarden 1985, Menge & Sutherland 1987, Roughgarden et al. 1988, Caley et al. 1996).

As links were investigated between upwelling and larval recruitment, it also became clear that, as a result of headlands and shelf bathymetry, upwelling plumes and offshore gyres generally recurred in the same locations (Ebert & Russell 1988, Roughgarden et al. 1988). These observations raised the possibility that, in addition to influencing recruitment, persistent oceanographic features might influence intertidal communities by generating predictable variation in nutrients and nearshore productivity

(Menge & Olson 1990, Menge 1992). This was an important development because ecologists had previously perceived nearshore waters as being relatively homogeneous at regional scales (i.e., 100's of kilometers)(Menge 1992).

Recent studies along the Oregon coast have identified persistent variation in productivity among sites separated by 10's to 100's of kilometers (Menge et al. 1997a, b, B. A. Menge, *unpublished data*). These and similar studies in South Africa (Bustamante et al. 1995) suggest that productivity differences may drive predictable "bottom-up" influences in intertidal communities. Consistently high levels of nearshore productivity may fuel high levels of prey and algal production that in turn support high consumer densities (Menge 1992, Bustamante et al. 1995, Menge et al. 1997b, 1999).

Despite these recent advances, research has only just begun to address the nature of oceanographic influences on rocky intertidal communities. The importance of understanding these links is enhanced by the fact that upwelling patterns within the California Current have changed substantially in recent decades (Bakun 1990, Roemmich & McGowan 1995, Schwing & Mendelssohn 1997, McGowan et al. 1998). Coastal upwelling and oceanographic processes are strongly affected by El Niño-Southern Oscillation events and longer-term geophysical changes including regime shifts (e.g., the Pacific Interdecadal Oscillation) and perhaps global warming (Bakun 1990, Roemmich & McGowan 1995, Peterson et al. 1990).

Predicting the impact of short and long-term changes in large-scale processes (such as upwelling) requires mechanistic studies that link these processes to effects at the organismal, population, and community level. In this dissertation, I present field and laboratory studies that examine the influence of coastal upwelling and related oceanographic factors on rocky intertidal communities along the central Oregon coast.

In Chapter 2, I examine a hypothesized link between nearshore phytoplankton abundance and the growth of two intertidal barnacle species, *Balanus glandula* and *Chthamalus dalli*. I tested the strength of this link by quantifying the short-term growth of barnacles at two sites that varied consistently in productivity. In Chapter 3, I examine the effect of variable water temperature on the feeding, growth, and energetics of two intertidal predators: the sea star *Pisaster ochraceus*, and whelk *Nucella canaliculata*. In the laboratory, I maintained sea stars and whelks under three temperature regimes: constant 9°C, constant 12°C, and an alternating treatment that simulated episodic upwelling. In Chapter 4, I report field experiments that investigated the effects of water temperature on a keystone predator, the sea star *P. ochraceus*. I quantified sea star predation on transplanted mussel clumps during 14-day intervals that encompassed periods with and without upwelling.

Taken together, the results of these studies provide strong evidence that upwelling-related variation in nearshore conditions may profoundly influence intertidal systems at the organismal, population, and community level. More broadly, these studies provide mechanistic understanding of how large-scale processes may interact with local processes to structure communities. In linking local and large-scale processes, this work explores pathways through which El Niños and longer-term climatic changes may alter natural communities.

CHAPTER 2

Spatial and Temporal Variation in Barnacle Growth In a Coastal Upwelling System

ABSTRACT

Recent studies suggest that large-scale variation in nutrients and phytoplankton may strongly influence the structure of rocky intertidal communities. Among the hypothesized effects is a presumed link between nearshore phytoplankton abundance and the growth of barnacles and other suspension feeders. I tested the strength of this association by quantifying water-column Chl-a concentrations and the growth of two intertidal barnacles (*Balanus glandula* and *Chthamalus dalli*) during consecutive 13-day intervals.

Individual barnacles were photographed through time on mid-intertidal growth plates attached in wave-exposed and wave-protected habitats at two sites known to differ strongly in nearshore productivity: Strawberry Hill (SH) and Boiler Bay (BB), Oregon. *B. glandula* grew more rapidly in wave-exposed areas than wave-protected habitats, presumably because higher flows delivered more food to passively feeding barnacles. Both species grew faster and attained a larger adult size at SH, the site with consistently higher phytoplankton abundance.

Surprisingly, short-term growth rates only partially matched spatial and temporal variation in phytoplankton. Growth rates were low during a persistent upwelling event, and increased two to three-fold during the subsequent upwelling relaxation. At SH, this

increase coincided with a major phytoplankton bloom, but growth rates remained high well after Chl-a concentrations returned to lower levels. Moreover, parallel increases in growth were recorded at BB, despite the fact that no bloom occurred at this site.

These results imply that factors other than phytoplankton contributed to variation in barnacle growth. Records of barnacle settlement suggest that water-column concentrations of larvae increased dramatically at both sites during the period of high barnacle growth. Published analyses of stomach contents suggest that zooplankton may be an important food source in other barnacle species. Increased barnacle growth during the upwelling relaxation may thus have arisen from the combined benefits of more phytoplankton, more zooplankton, and warmer water temperatures. Incorporating the influence of zooplankton and water temperature into studies of bottom-up influences may improve our ability to explain variation among intertidal communities.

INTRODUCTION

Biologists have long been intrigued by the life history and growth of barnacles. Some of the earliest observations of barnacle growth were made by Charles Darwin who measured the size of barnacles on the hull of the *H.M.S. Beagle*. Darwin estimated growth rates based upon the diameter of these individuals and the number of days that the ship was at sea (Darwin 1851). In the years since Darwin's voyage, the effects of water column conditions on barnacle growth have been well described. Although acorn barnacles are capable of generating feeding currents by actively sweeping their cirri through still water, feeding is generally passive at all but the lowest flow speeds (Trager et al. 1990, Sanford et al. 1994). In most habitats, barnacles simply orient their cirral net into the flow and passively collect suspended particles. Therefore, the flux of food to barnacles can be viewed as a function of both flow speed and particle concentration.

Not surprisingly, many early studies documented faster growth of acorn barnacles in areas that were exposed to either high flow (Hatton & Fischer-Piette 1932, Moore 1935, Crisp 1960) or a high concentration of suspended matter (Moore 1936). Crisp (1960) suggested that factors influencing barnacle growth rates could be divided into local factors (including water flow and barnacle density) and regional factors (including temperature and 'richness of suspended nutrients'). Several recent studies support the idea that regional factors may influence rates of barnacle growth. In the Aleutian Islands, Duggins et al. (1989) found that intertidal barnacles (*Balanus glandula*) grew up to five times faster in kelp-dominated environments. The results of $\delta^{13}C$ analysis confirmed that much of the input received by barnacles in these systems was derived from kelps, presumably in the form of suspended detritus. Bertness et al. (1991) found that growth of the barnacle *Semibalanus balanoides* was greater in Narragansett Bay, Rhode Island, than at outer coast sites where mean Chl-a concentrations were ~6x lower. Within a site, barnacles grew more rapidly in areas of higher flow than in more sheltered areas (Bertness et al. 1991, Sanford et al. 1994).

Connections among suspended food, barnacle growth, and population dynamics have thus been suggested by a number of studies. However, only recently have such connections been viewed within a broader community or ecosystem context (Duggins et al. 1989, Menge 1992, Menge et al. 1997a, b). Attempts to understand variation among rocky intertidal communities have traditionally focused on local processes such as predation, herbivory, competition, and disturbance (see Paine 1994 for a general review). Potential effects of variation in pelagic productivity were largely overlooked, presumably because nearshore waters were perceived as being relatively homogeneous at regional scales (i.e., 100's of kilometers)(Menge 1992).

However, recent studies along the Oregon coast have identified persistent variation in phytoplankton abundance among sites separated by 10's to 100's of kilometers (Menge et al. 1997a,b; B. A. Menge, *unpublished data*). Moreover, this variation appears to have a strong "bottom-up" influence on intertidal communities. Sites with consistently higher levels of productivity appear to have greater rates of recruitment and growth of sessile suspension feeders. Rates of grazing and predation also appear to be higher at these sites (Menge 1992, Menge et al. 1996, 1997a). These and similar studies in South Africa (Bustamante et al. 1995) suggest that high levels of nearshore productivity may increase prey and algal production and thus support greater consumer abundances. These consumers may in turn exert stronger "top-down" forces on lower trophic levels. If patterns of among-site variation in productivity are consistent through time (e.g., related to continental shelf bathymetry or other persistent oceanographic features), then pelagic-benthic links may play a critical role in explaining mesoscale variation among marine communities (Menge et al. 1997b, 1999).

As interest in large scale processes has grown, ecologists have been forced to grapple with many new challenges (Menge & Olson 1990, Lubchenco et al. 1991, Levin 1992). In particular, it is often impractical or impossible to manipulate factors and processes that vary at large scales. Several recent studies in marine systems have advocated the use of comparative approaches to examine the influence of large-scale oceanographic factors such as currents, nutrients, temperature, and phytoplankton abundance (Roughgarden et al. 1988, Menge 1992, Bustamante et al. 1995, Leonard et al. 1998, Menge et al. 1999).

Caution must be used in drawing inferences from comparative studies because they necessarily rely on correlation. One approach to strengthen confidence in such studies has been to combine spatial and temporal investigations of the factor of interest (Menge 1991). Previous studies have implicated the role of phytoplankton in barnacle growth by contrasting sites that vary in phytoplankton abundance (Moore 1936, Bertness et al. 1991, Menge 1992). In this study I attempt to strengthen these inferences by adding a short-term temporal component to the quantification of barnacle growth.

Phytoplankton blooms along the central Oregon coast are short-lived (days to weeks) and appear to be linked to episodic upwelling. Blooms typically occur in nearshore waters within a few days of the cessation of strong northerly winds and thus appear to coincide with periods of upwelling relaxation (Menge et al. 1997b). I hypothesized that if growth is directly linked to phytoplankton abundance, then blooms should be reflected as brief spikes of rapid barnacle growth. I tested this hypothesis by quantifying short-term variation in phytoplankton abundance and barnacle growth rates. I focused on two species of acorn barnacles (*Balanus glandula* and *Chthamalus dalli*) at two sites on the central Oregon coast known to have large, persistent differences in phytoplankton abundance. My results document strong spatial and temporal variation in barnacle growth but suggest that phytoplankton abundance alone is insufficient to explain these patterns.

METHODS

Study Sites

In 1994-95, barnacle growth was quantified in the mid-intertidal zone at Strawberry Hill (SH)(44°15' N, 124°07'W) and Boiler Bay (BB)(44°50' N, 124°03'W), two sites separated by 83 km on the central Oregon coast. These sites were selected because previous research indicated that the adjacent waters differed strongly in phytoplankton abundance during upwelling season (typically May through September). Whereas Chl-a was consistently low at BB (generally < 5 µg/l), SH was washed by episodic phytoplankton blooms during which Chl-a reached extremely high levels (> 30 µg/l) (Menge et al. 1997a,b).

The intertidal communities at these sites are similar to those found at outer coast locations throughout the Pacific Northwest (e.g., Dayton 1971, Paine 1980). The high intertidal zone is dominated by fucoid algae and the acorn barnacles *Balanus glandula* and *Chthamalus dalli*. The mid-intertidal zone is characterized by dense beds of the California mussel *Mytilus californianus*. Disturbance gaps within these beds contain a mixture of macroalgae and sessile suspension feeders including acorn barnacles (*B. glandula*, *C. dalli*, and *Semibalanus cariosus*), gooseneck barnacles (*Pollicipes polymerus*), and mussels (the bay mussel, *Mytilus trossulus*, and juvenile *M. californianus*). The low intertidal zone differs strongly between SH and BB. At BB, the low zone is dominated by macroalgae (*Hedophyllum sessile* and red algal turfs) and surfgrass (*Phyllospadix* spp.), whereas the low zone at SH has a much lower cover of macrophytes and a higher abundance of sessile suspension feeders, grazers (limpets and chitons), and predators (sea stars and whelks) (Menge et al. 1997b). Additional descriptions of these sites are published elsewhere (Menge 1992, Menge et al. 1994, 1997b).

In addition to examining the effects of variation in phytoplankton abundance, I quantified barnacle growth in wave-exposed and wave-protected habitats at each site. At SH, the wave-exposed area was a series of irregular outcrops and benches broken up by large pools and surge channels. This area was directly exposed to breaking waves. In contrast, the wave-protected area was sheltered by numerous outcrops. The BB site consisted of three benches (each ~75m long) that ran perpendicular from the shore out into the ocean. Barnacle growth was examined at the extremes of this wave-exposure gradient (i.e., on the most exposed outer bench and on the most protected land-ward bench). Previous work at BB and SH quantified variation in flow (using rates of erosion of cylinders made of dental chalk) and maximum wave forces (using dynamometers) at these same locations (Menge et al. 1996).

Growth Plate Design

I quantified the growth rates of barnacles on 10cm x 13cm clear plexiglass plates (thickness: 6mm). Small pits (1.5mm diameter, 0.5mm deep) were drilled into each plate in a 6 x 7 rectangular array with 14mm separating adjacent pits. Pitted plates are ideal for following the growth of solitary individuals through time (Crisp 1960). Previous work has indicated that barnacle growth and morphology are strongly influenced by crowding (Moore 1935, Barnes & Powell 1950, Crisp 1960, Bertness et al. 1998). Although barnacle cyprids are rarely able to persist on smooth plexiglass, they will readily settle into shallow pits. By controlling the distance between pits, barnacles can be maintained on plexiglass plates under uncrowded conditions (Crisp 1960).

Plates were attached to horizontal surfaces within pre-existing gaps in mid-intertidal beds of the California mussel, *Mytilus californianus*. Efforts were made to ensure that barnacles growing on plates experienced environmental conditions similar to individuals growing on adjacent rock surfaces. Because a hydrodynamic boundary layer may form at the rock surface, barnacles growing on plates raised above the surrounding rock may experience greater flows and wave forces than those on the rock (Denny 1988). To make the surface of plates flush with the rock, I used a rock hammer and chisel to create flat depressions, approximately 14cm wide x 17cm long x 0.6cm deep (Fig. 2.1). To ensure that plates fit snugly into these hollows, I placed a 2cm strip of marine epoxy putty (Z-spar™ Splash Zone Compound, Seattle Marine, Seattle, WA) around the irregular edges of each depression. While the putty was hardening, I positioned a sample plate in the depression, pressing the edges of the plate into the putty. The plate was removed leaving a depression with straight edges into which a plate fit exactly. In addition to minimizing flow artifacts, recessing plates into the rock probably kept them from overheating during periods of aerial exposure. Plates were held in place by a single stainless steel screw passing through a countersunk hole near the center of the plate and into a plastic wall anchor in the rock (Fig. 2.1). The underside of each plate was engraved with a unique number for identification.

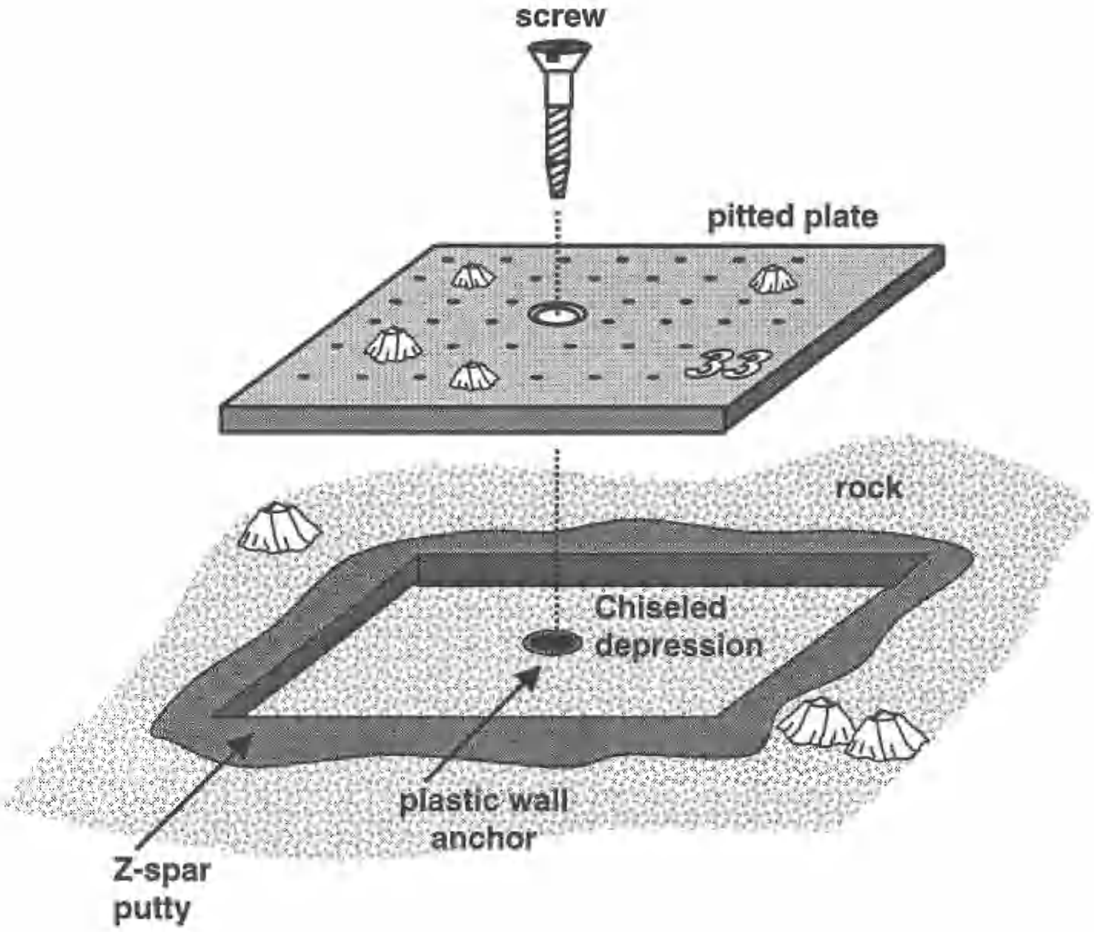


Figure 2.1 Design of barnacle growth plates. Plexiglass plates (10 x 13cm) were drilled with a regular array of pits and secured into shallow depressions chiseled into the rock. Plates were easily removed for censusing and photographic monitoring.

Growth and Mortality of Naturally Settling Barnacles

Fifteen plates were spaced along approximately 35-40m of shore within each of the four study areas (SH exposed, SH protected, BB exposed, BB protected). All plates were haphazardly placed in mussel bed gaps at approximately +1.5m above MLLW. Plate sites were chiseled and prepared in March-April 1994 and all plates were deployed on April 25 and 26.

In some geographic regions (e.g., New England and Scotland), barnacle settlement is limited to a discrete season lasting < 2 months (Connell 1961, Wethey 1984, Bertness et al. 1998). By contrast, along the Pacific coast of North America, although many *B. glandula* and *C. dalli* cyprids arrive onshore during episodes of heavy settlement, small numbers of barnacle larvae settle intermittently throughout the year (Gaines et al. 1985, Strathmann 1987, Pineda 1994; B. A. Menge, *unpublished data*). In addition, post-settlement mortality of barnacles is often high (Wethey 1984, Gosselin & Qian 1996; also see Results below). Therefore, it is difficult to know the age of barnacles on plates in Oregon without regular observations through time.

Plates were thus briefly removed from the rock and censused in the field every 12-14 days until early September. Each pit was assigned a letter and number to denote its position on the plate, and I recorded the presence or absence of cyprids and recent settlers in each pit. In this way, the settlement date and age of all barnacles growing on plates was known to within ± 6 days.

In addition to verifying the age of barnacles, the regular monitoring of plates allowed me to estimate variation in post-settlement mortality between sites, wave-exposures, and settlement dates. I selected two monitoring dates (21/22 June and 18/20 August) that had a large number of cyprids and newly metamorphosed settlers on all plates. The settlement date of these individuals was easily estimated (± 6 days) because their pits had been empty during the previous census. I examined post-settlement mortality of these cohorts by quantifying the percent of newly occupied pits on each plate that were empty after approximately 25 days. Cases where an individual died and was replaced before the next sampling date were easily detected because of the small size of the new settler. *B. glandula* and *C. dalli* were grouped together for this analysis because it was not always possible to distinguish cyprids of the two species in the field. Estimates of mortality were conservative because I did not record cases where pits contained more than one cyprid (i.e., an occupied pit that was empty after 25 days may have represented the mortality of two individuals, rather than one).

Growth of Transplanted Barnacles

During the first month of this study, settlement of *Chthamalus dalli* was very low on wave-exposed plates. I therefore decided to transplant *Chthamalus* recruits to the study areas from an area of higher settlement. To do so, I constructed a separate set of 10cm x 13cm plexiglass plates. Pits were the same size and depth as above, but since *Chthamalus* grows to a smaller adult size, the pits were more closely spaced (8mm apart in an 11 x 13 grid). On 28 May, 14 plates were attached to the low intertidal zone on the wave-protected bench at Boiler Bay (a location known to receive heavy settlement of *Chthamalus*). By late June, recent *Chthamalus* settlers and smaller numbers of *B. glandula* were present on most plates.

On 9 July, I randomly divided the plates into two groups and transplanted them to pre-chiseled locations within the exposed areas at Strawberry Hill and Boiler Bay (n = 7 plates per site). All plates were removed and transplanted during a single low tide period of aerial exposure. Prior to being transplanted, plates were photographed and censused to record the presence or absence of barnacles in each pit. It was thus possible to quantify the growth of barnacles that settled at the source site, rather than individuals that may have subsequently filled empty pits at the site of transplant. Transplanted barnacles were all of a similar size and represented a cohort of individuals that settled at the same location during the same time period. This design minimized potential differences that could arise from settlers arriving naturally at SH and BB on different days after experiencing different planktonic conditions.

Photographic Monitoring

Plates were generally photographed every 13 days between 28 June and 8 September 1994. In total, short-term barnacle growth was assessed during 5 consecutive periods for the natural settlement plates, and 4 consecutive periods for transplanted plates. On consecutive days, all plates at a site were briefly removed from the rock, placed on a blue background, and photographed with a 35mm camera equipped with a macro-lens and mounted on a frame stand. A ruler was included in each photograph for scale. Although limpets on the plates generally kept barnacles free of algal growth, it was occasionally necessary to remove diatoms using a soft toothbrush.

Following the intensive monitoring of short-term growth rates, long-term growth rates were monitored by photographing plates on a less frequent schedule. Plates were photographed on 17/19 October 1994, 1/3 December 1994, 14/16 April 1995, 12/13 June 1995, and 25/26 August 1995.

Image Analysis: Short-Term Barnacle Growth

Slides of barnacle plates were digitized and stored on a computer as JPEG images. I used image analysis software (SigmaScan Pro v.4.0, Jandel Scientific Software, San Rafael, CA) to measure the maximum basal diameter (mm) and the basal area (mm^2) of individual barnacles on plates. Measurements were calibrated using the ruler present in each photograph. Each barnacle was assigned a unique number based on its plate and location within the array of pits.

For the natural settlement plates, individual *Balanus glandula* were measured through time if they were present in the first photographs (28/29 June 1994) and persisted through all five growth periods (until 7/8 Sept 1994). For these individuals, I measured both maximum basal diameter (the longest linear dimension) and basal area from images taken on each of the 6 sampling dates. For the transplant plates, I quantified the growth of all individuals (both *B. glandula* and *C. dalli*) that were present during all four periods. For barnacles on transplant plates, only basal area was measured. Data confirmed that maximum basal diameter and basal area were tightly correlated (see Results, below) and thus either measure was a sufficient indicator of size. In some photographs, small barnacles were obscured by diatoms. Because the size of these individuals could not be accurately measured, they were removed from the analysis.

Image Analysis: Long-Term Growth and Growth Curves

To assess variation in long-term *B. glandula* growth, I examined a separate group of barnacles that recruited to the natural settlement plates at SH exposed and BB exposed during August 1994. Since these individuals were known to have settled within the same three week period, I simply measured their final basal area in mid-April 1995, after approximately 8 months of growth. Photographs from September, October, and December 1994 were inspected to ensure that the same individuals were present throughout the entire growth period. For *C. dalli*, I assessed long-term growth on transplant plates by measuring the basal area of all individuals that persisted from June 1994 until mid-June 1995.

Whereas the above measures of long-term growth focused on the final size attained, I also characterized the growth curve of wave-exposed *B. glandula* and *C. dalli* by examining changes in basal diameter across all sampling dates. For *B. glandula*, I identified all individuals that settled in May and June 1994 and persisted until late August 1995. For these individuals (n = 17 at SH; n = 66 at BB), I measured maximum basal diameter from the 11 images taken of each plate between June 1994 and August 1995.

For *C. dalli* I characterized the growth curve of individuals transplanted to the exposed area at Strawberry Hill. From the large number of *C. dalli* that survived from June 1994 to June 1995, I randomly selected 10 individuals per plate. I followed these barnacles through time by measuring their basal diameter from the images taken on all 9 sampling dates.

Water Temperature and Chlorophyll Concentrations

Water temperatures were recorded every hour by data-loggers (Model 9102, Alpha Omega, Corvallis, OR) attached in the low intertidal zone in the wave-exposed areas at SH and BB. From these data I calculated High Tide Water Temperatures, defined as the mean of all readings during the period from two hours before to two hours after each high tide (as estimated from NOAA tide charts). For graphical presentation, these data were smoothed using a running means function that averaged each High Tide Water Temperature with those of the two preceding and two following high tides.

To assess variation in phytoplankton abundance, Chl-a concentrations were quantified from water samples collected at SH and BB on 3-14 days during each of the five barnacle growth periods (n = 33 dates between 29 June and 8 September 1994). On sampling dates, five water samples were taken at low tide from the wave-exposed areas at each site. Samples were collected from a depth of 15cm in acid-washed 250ml HDPE Nalgene dark bottles (5 bottles per site). Bottles were stored in a cooler with ice, returned to Hatfield Marine Science Center in Newport, and processed according to established methods (Parsons et al. 1984, Menge et al. 1997a).

I filtered a 50ml subsample from each collection bottle. Subsamples were first poured through a 100μm Nytex prefilter (to remove any large matter), and then filtered on a 25mm glass fiber filter that had previously been baked in a combustion oven at 450°C for 4-24 hours (to remove any contaminants). After filtering, the paper was removed with forceps and placed in a 15ml centrifuge tube. To extract Chl-a, 10ml of 90% HPLC acetone was added to each tube, and tubes were stored in a dark freezer for 24 hours.

Prior to analysis, samples were removed from the freezer and warmed to room temperature in the dark. I centrifuged the samples for 5 minutes, transferred the supernatant to a glass cuvette, and read its flourescence in a Turner AU10 Fluorometer. A second flourescence reading was taken after adding 2 drops of 10% HCl to each cuvette. The concentration of Chl-a was calculated based on these two readings and an equation generated from calibration standards. For samples with high concentrations of Chl-a, it was sometimes necessary to dilute samples with 90% HPLC acetone to remain within the scale of the fluorometer.

Statistical Analysis

Although growth rates generally decline with age, previous authors have noted that the basal diameter of several barnacle species increased at a linear rate over much of its early life history (Crisp 1960, Crisp & Bourget 1985). Inspection of growth curves for *B. glandula* and *C. dalli* (see Results, below) suggested that basal diameter increased as a roughly linear function of time for at least the first 3-4 months following settlement. I therefore assessed variation in short-term barnacle growth by comparing growth rates [i.e., slope of increase in basal diameter (mm/day)] among the 4-5 time intervals from late June to early September 1994.

In all analyses, growth plates were treated as the experimental units and barnacles on plates were regarded as sub-samples. Thus, I averaged the growth rate (mm/day) from all individuals on a plate to get a mean for each plate within each site x time period combination. Plates were only included in the analysis if they had a complete set of measurements for 2 or more individuals. Sample sizes thus varied among sites and analyses.

Since the growth of individual barnacles on plates was followed through time, data were analyzed in a repeated measures analysis of variance (RM-ANOVA). Three separate RM-ANOVAs were conducted on the short-term growth rates of (1) *Balanus glandula* on natural settlement plates, (2) *B. glandula* on transplanted plates, and (3) *Chthamalus dalli* on transplanted plates. Site (SH vs. BB) was regarded as a fixed effect in all models. The first analysis incorporated the additional factor of wave-exposure (exposed vs. protected), which was also treated as a fixed effect.

There are both univariate and multivariate approaches to repeated measures designs (von Ende 1993). Although the univariate approach is more powerful, it requires that data exhibit homogeneity in the variance of the difference between all possible pairs of repeated measures (a condition known as sphericity). When sphericity is not met, F statistics for the within-subject factor are inflated, and it is necessary to use either the multivariate approach, or decrease the degrees of freedom in the univariate analysis using the Huynh-Feldt adjustment (von Ende 1993).

I tested whether sphericity was met using Mauchly's sphericity test applied to the orthonormalized form of the variance-covariance matrix. The assumption was satisfied for the transplant study (growth of transplanted *B. glandula* and *C. dalli*), but not for the growth of *B. glandula* on natural settlement plates. In this case, I present the univariate results with more conservative Huynh-Feldt (H-F) adjusted p-values. In all cases, multivariate repeated measures analyses are presented for comparison. As in all ANOVA designs, normality and homogeneity of variance are also required, and I tested these assumptions by visual inspection of normal probability plots and residual plots. In all cases the untransformed data satisfied these assumptions reasonably well.

If the RM-ANOVA indicated significant variation in growth between sites and/or among time periods, I conducted separate tests to determine which specific contrasts were significant. Within each time period I tested whether barnacle growth varied between sites by conducting a two sample t-test with a Bonferroni adjusted critical p-value to control for multiple comparisons across the 4-5 time periods. Within each site, I used ANOVA and the Tukey-Kramer procedure for multiple comparisons to identify significant differences in growth among time periods.

For the analysis of post-settlement mortality, the percents of settlers surviving on each plate after ~25 days were arcsine-square root transformed and examined in a three-way ANOVA with site, wave-exposure, and settlement date as fixed effects. Replicate plates were removed from the analysis if they had fewer than 4 new settlers present at the beginning of the mortality period.

RESULTS

Post-Settlement Mortality

Mortality of barnacles during their first 25 days on pitted plates was relatively high (50.3% overall), but variable (Fig. 2.2). Survivorship of new settlers was dependent on site, wave-exposure, and settlement date (Table 2.1; site x exposure x date, $p = 0.008$). Barnacles usually survived better on wave-exposed plates than wave-protected ones (exposure, $p = 0.0019$), presumably because wave splash reduced thermal stress. For the cohort that experienced greater overall mortality (i.e., barnacles that settled on ~17 June), mortality was greater at SH than BB. The high degree of post-settlement mortality contributed to variation in barnacle size on the plates. Because individuals frequently died and were replaced by new settlers, plates quickly developed a mixture of barnacles of different ages and sizes.

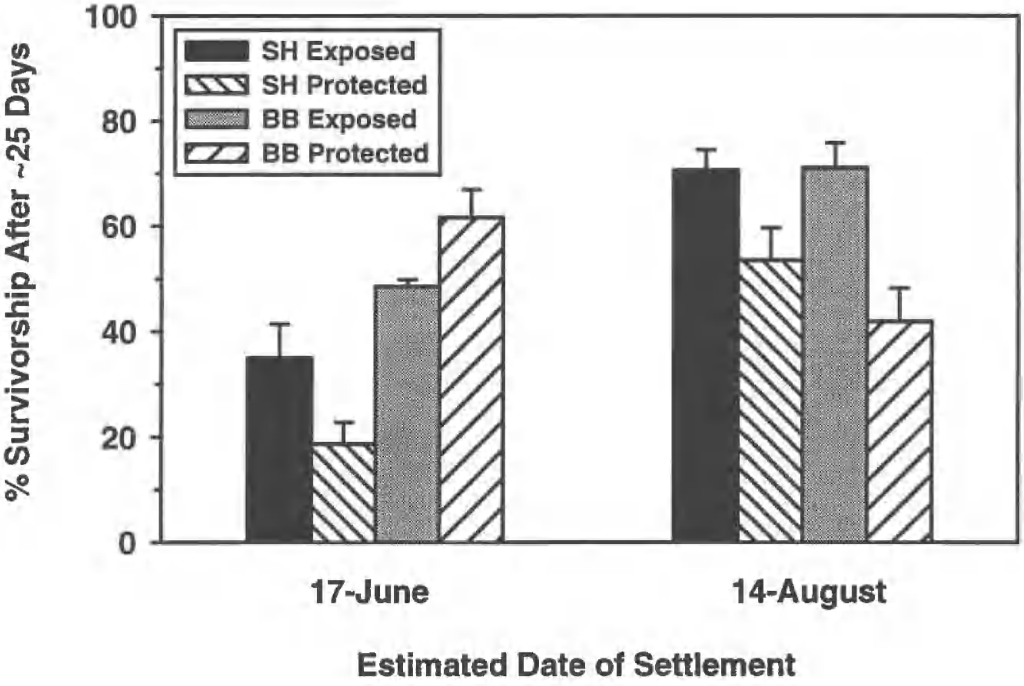


Figure 2.2 Post-settlement mortality of barnacles on growth plates. Bars are the mean % survivorship (+SEM) of newly-settled barnacles (*B. glandula* and *C. dalli* combined) after ~25 days on the shore (n = 13-15 plates per site x exposure combination, each with 4-42 new settlers; mean = 18.0 per plate). Mortality of cohorts settling on 17 June 1994 and 14 August 1994 (± 6 days) was evaluated in four areas: SH exposed, SH protected, BB exposed, and BB protected.

Table 2.1 Analysis of variance of the effects of site, wave-exposure, and settlement date on the survivorship of newly-settled acorn barnacles (*Balanus glandula* and *Chthamalus dalli*, combined). The dependent variable was arcsine-square root transformed percents of settlers surviving on each plate after ~25 days. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

SOURCE	df	MS	F	P
Site	1	0.564	10.41	**0.0017**
Exposure	1	0.552	10.19	**0.0019**
Settlement Date	1	1.307	24.12	**< 0.0001**
Site x Exposure	1	0.079	1.47	0.2288
Site x Date	1	1.106	20.41	**< 0.0001**
Exposure x Date	1	0.323	5.97	**0.0163**
Site x Exposure x Date	1	0.397	7.33	**0.0080**
Error	103	0.054		

Allometric Relationships and Growth Curves

As expected, basal diameter and basal area were tightly correlated for both *Balanus glandula* and *Chthamalus dalli* (Fig. 2.3). Thus, for barnacles growing on transplanted plates, only basal areas were measured from digitized slides. Basal diameters used in the analysis of short-term growth were estimated using measured basal areas and the regression equations (Fig. 2.3).

Growth curves for both *B. glandula* and *C. dalli* indicated that the increase in basal diameter was roughly linear for at least the first 3-4 months following settlement (Figs. 2.4, 2.5). Basal diameter increased rapidly during the summer before reaching a site-specific plateau by fall. Despite this general trend of rapid summer growth, there appeared to be short-term variation in growth within this season. In particular, growth

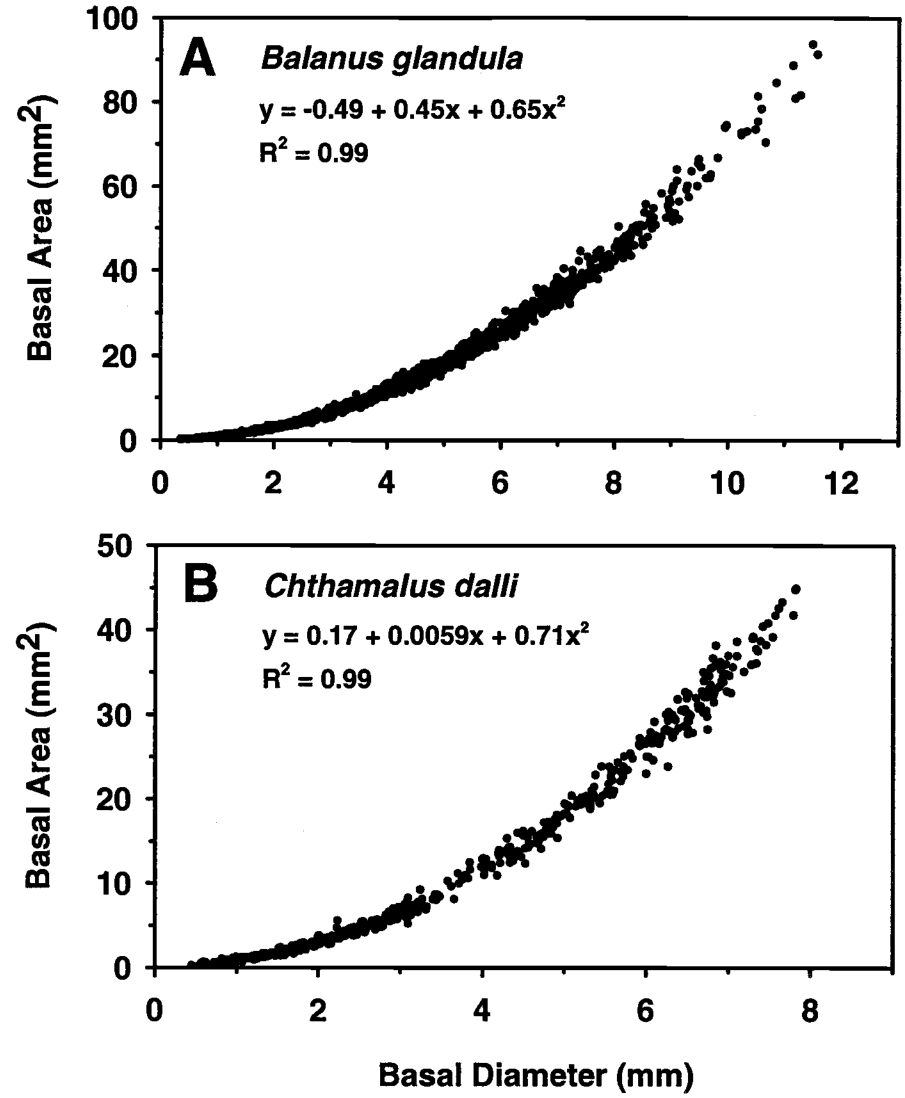


Figure 2.3 Maximum basal diameter vs. basal area relationships for *Balanus glandula* and *Chthamalus dalli* growing in wave-exposed areas. (A) The *B. glandula* curve was generated from successive measurements through time of 181 individuals on 21 plates at SH exposed and BB exposed (n = 1145 measurements total). (B) The *C. dalli* curve was generated from successive measurements through time of 59 individuals on 6 plates transplanted to SH exposed (n = 531 measurements total). R-square values and equations for the polynomial fits are reported in each panel.

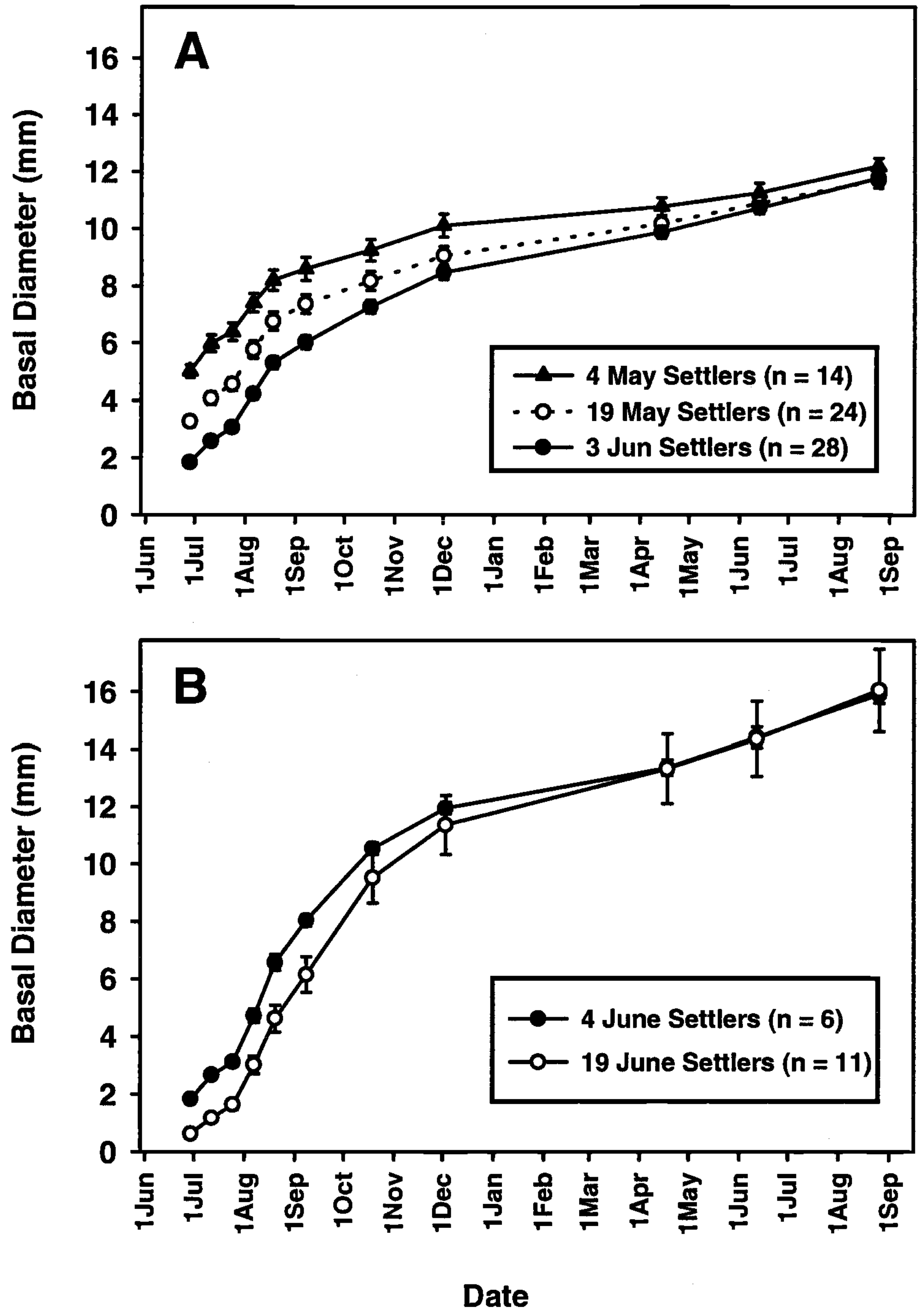


Figure 2.4 Growth curves for *Balanus glandula*. Data are mean basal diameter (± SEM) on successive sampling dates for all individuals that persisted from May/June 1994 through late August 1995 at (**A**) Boiler Bay exposed, and (**B**) Strawberry Hill exposed. Growth trajectories are separated by date of settlement (estimated ± 6 days).

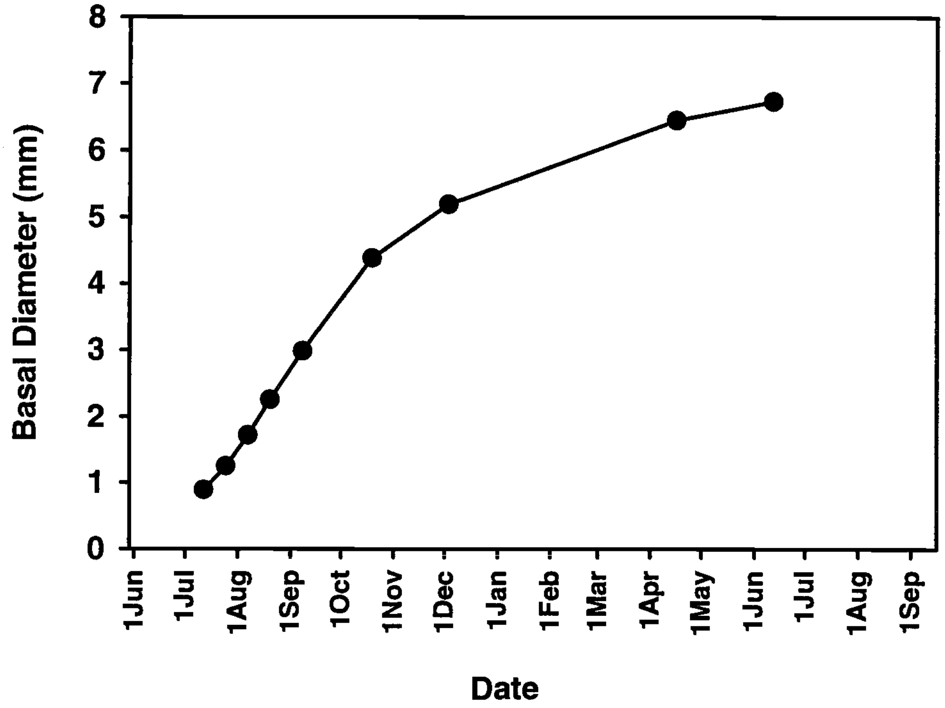


Figure 2.5 Growth curve for *Chthamalus dalli.* Data are mean basal diameter on successive sampling dates for 59 individuals on 6 transplanted plates at Strawberry Hill exposed. All individuals settled in June 1994. Error bars (SEM) are smaller than data points.

rates of *B. glandula* appeared to slow at both sites in late July, before accelerating in August (Fig. 2.4).

A non-linear growth curve could be generated if barnacle growth rate was size-dependent. Growth could accelerate after individuals reached some threshold size, perhaps due to unknown interactions among body size, hydrodynamic boundary layers, and feeding efficiency (Crisp 1960). To test this hypothesis, I separated individual *B. glandula* into cohorts based on when they first appeared on the settlement plates. This analysis revealed that all cohorts exhibited a phase of reduced growth in late July regardless of age and size (Fig. 2.4). For example, BB barnacles that settled a month apart (4 May and 3 June), and differed in size by ~3mm, showed parallel fluctuations in short-term growth (Fig. 2.4A). These results suggest that variation in growth rate was the result of external factors and not a size-dependent growth trajectory.

Oceanographic Variation and Predicted Patterns of Growth

Based on these data I assumed that, under constant environmental conditions, the basal diameter of *B. glandula* and *C. dalli* should increase at a roughly constant rate for at least the first few months after settlement. The results of other studies suggest that this may be a general pattern among barnacles (Crisp 1960, Crisp & Bourget 1985). I thus examined variation in short-term growth by testing whether the rate of increase in basal diameter (mm/day) varied among different time intervals. The influence of environmental factors was evaluated by comparing variation in barnacle growth rate with variation in Chl-a concentration, water temperature, and wave-exposure.

During this study, there was a persistent upwelling event lasting most of the month of July. This upwelling event was marked by strong northerly winds and water temperatures which remained well below 10°C for several weeks (Fig. 2.6A, see also Menge et al. 1997b). Upwelling-favorable winds ceased in late July, and soon thereafter a large phytoplankton bloom was observed at SH. Very high levels of Chl-a were recorded at SH on the six dates sampled during this "bloom period" (Fig. 2.6B, 25 July to 7August). In contrast, Chl-a remained low and fairly consistent at BB throughout the summer. If barnacle growth was strongly linked to phytoplankton abundance, I predicted that growth rates would be greatest during the bloom period at SH, and consistently lower at BB.

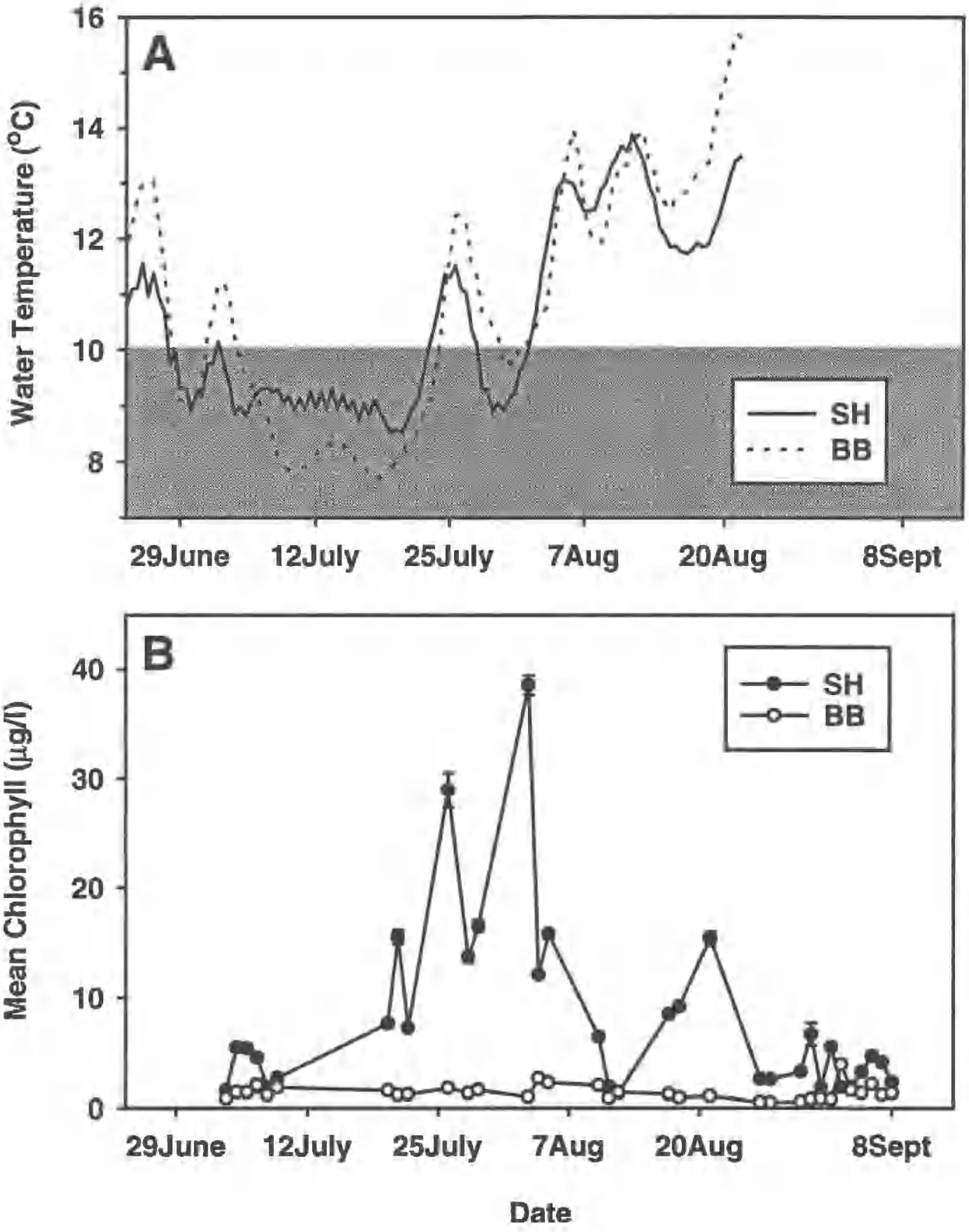


Figure 2.6 Oceanographic conditions at Strawberry Hill and Boiler Bay, Summer 1994. **(A)** High Tide Water Temperatures (mean data-logger reading during the period from 2 hours before to two hours after each high tide) at SH (solid line) and BB (dashed line). Data were smoothed using a running means function (see text for details). Temperature records are unavailable for the period after 21 August. **(B)** Mean Chlorophyll-a concentration (±SEM) in water samples collected from the exposed areas at SH (closed circles) and BB (open circles) (n = 5 samples/ site/ date).

Short-Term Growth on Natural Settlement Plates: Balanus glandula

The analysis of *B. glandula* growth on natural settlement plates indicated that wave-exposure had a significant effect on growth rate, regardless of site (Table 2.2; exposure, $p < 0.001$, site x exposure, $p = 0.32$). As expected, barnacles grew more quickly in areas that experienced greater flows. By early September, wave-exposed barnacles at Strawberry Hill had mean basal diameters 1.6x greater than wave-protected barnacles (Fig. 2.7). Similarly, wave-exposed barnacles at Boiler Bay had diameters 2.5x greater than those in the protected area. Previous work at these same locations quantified relative differences in flow by measuring the rates of dissolution of blocks of dental chalk attached in the mid-intertidal zone (Menge et al. 1996). These data confirmed that flow rates were significantly greater in the areas directly exposed to wave action.

There was significant variation in *B. glandula* growth among time periods (Fig. 2.7, Table 2.2; time, $p < 0.001$), but changes with time were dependent on both site and wave exposure (Table 2.2; time x site x exposure, $p < 0.001$). In both the exposed and protected areas at SH, growth rate was significantly greater during the bloom period (25July – 7Aug) than during the first two periods (29June -12July, and 12July – 25July), but did not differ from the final two periods (7Aug - 20Aug, and 20Aug - 8Sept)(Tukey-Kramer, $p > 0.05$).

Surprisingly, *B. glandula* growth showed similar variation through time at BB exposed where little variation in Chl-a was recorded (Figs. 2.7, 2.6B). Growth was significantly greater during the "bloom period" (25July – 7Aug) than during either the

Table 2.2 Repeated measures analysis of variance of the effects of site and wave exposure on *Balanus glandula* growth during five consecutive time periods. Barnacles were allowed to settle naturally on replicate plates in wave-exposed and wave-protected areas at Strawberry Hill and Boiler Bay. The dependent variable was the mean rate of increase in basal diameter (mm/day) for all individuals on a replicate plate. Data did not exhibit homogeneity of treatment differences variance (test for sphericity, $p = 0.006$). Univariate results are therefore presented with Huynh-Feldt adjusted probabilities, and multivariate results are provided for comparison. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Site	1	0.01478	22.41	**< 0.0001**
Exposure	1	0.05854	88.75	**< 0.0001**
Site x Exposure	1	0.00066	1.01	0.3228
Error	35	0.00066		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	H-F p-value	num df	den df	Wilks' λ	p-value
Time	4	0.01020	69.83	**<0.0001**	4	32	0.1304	**<0.0001**
Time x Site	4	0.00351	24.01	**<0.0001**	4	32	0.1872	**<0.0001**
Time x Expos	4	0.00344	23.54	**<0.0001**	4	32	0.2948	**<0.0001**
Time x Site x Exposure	4	0.00096	6.58	**0.0001**	4	32	0.6049	**0.0024**
Error	140	0.00015						

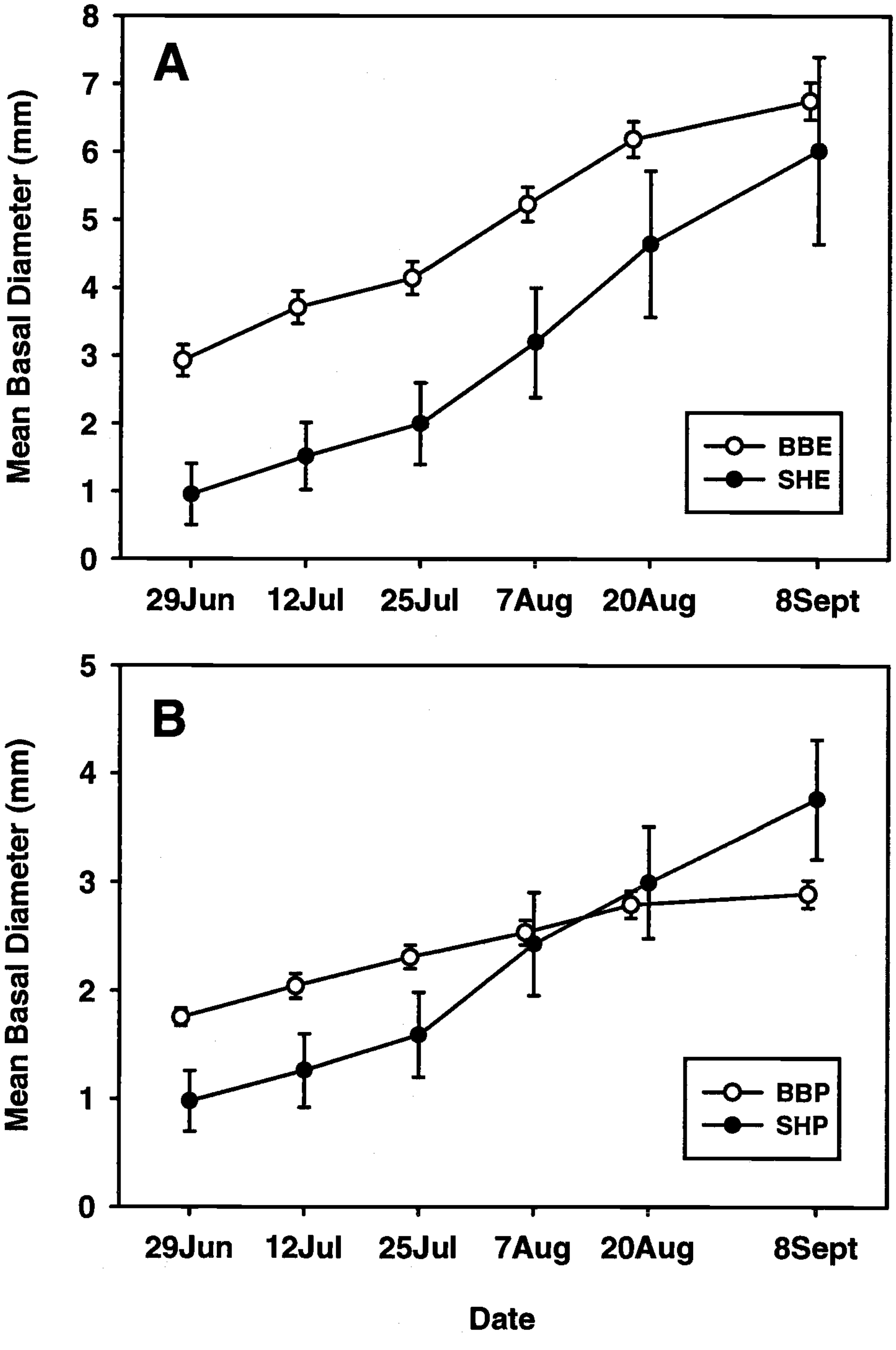


Figure 2.7 Growth of naturally settling *Balanus glandula* on mid-intertidal plates at Boiler Bay and Strawberry Hill. Data are means (± SEM) of the mean basal diameter on 7-14 plates in (**A**) wave-exposed and (**B**) wave-protected areas. Sample sizes varied with the number of plates that had 2 or more individuals persisting in all five periods. BBE = Boiler Bay exposed (n =14), SHE = Strawberry Hill exposed (n = 7), BBP = Boiler Bay protected (n = 10), SHP = Strawberry Hill protected (n = 8).

first two periods or the final period (20Aug-8Sept)(Tukey-Kramer, $p< 0.05$). At BB protected, there was little variation in growth through time (Fig. 2.7B).

Also surprising was the observation that growth rate did not vary significantly between SH exposed and BB exposed during the bloom period (25July-7Aug; t-test, $t_{19} = -0.799$, $p = 0.43$) despite the fact that a dramatic increase in Chl-a was recorded at SH, but not at BB (Figs. 2.7; 2.6B). Interestingly, during the two periods *after* the bloom (7Aug-8Sept), the mean growth rate at SH was 0.4x and 1.6x greater (respectively) than at BB (t-tests, $p < 0.01$).

Short-term Growth on Transplanted Plates: __Balanus glandula__

B. glandula transplanted to SH exposed and BB exposed showed very similar growth patterns to barnacles settling naturally at those sites (Fig. 2.8). Since plates were transplanted on 9 July, growth was quantified in four periods rather than five. Growth varied significantly between sites (Table 2.3; site, $p = 0.004$) and among time periods (Table 2.3; time, $p < 0.001$). At SH exposed, growth rate during the bloom period (25 July-7Aug) was significantly greater than during the preceding upwelling period (12 July-25 July), but did not differ from the final two periods (7Aug - 8Sept)(Tukey-Kramer, $p < 0.05$). At BB exposed, growth during the bloom period was significantly greater than during the upwelling period (25July-7Aug) and the final period (20Aug-8Sept)(Tukey-Kramer, $p < 0.05$).

As on natural settlement plates, *B. glandula* growth did not vary significantly between sites during the bloom period (Fig. 2.8; t-test, $t_{12} = -2.26$, $p = 0.043 >$ than a

Bonferroni adjusted critical p-value = 0.0125), but was significantly greater at SH than BB during the following two periods (t-tests, $p < 0.01$).

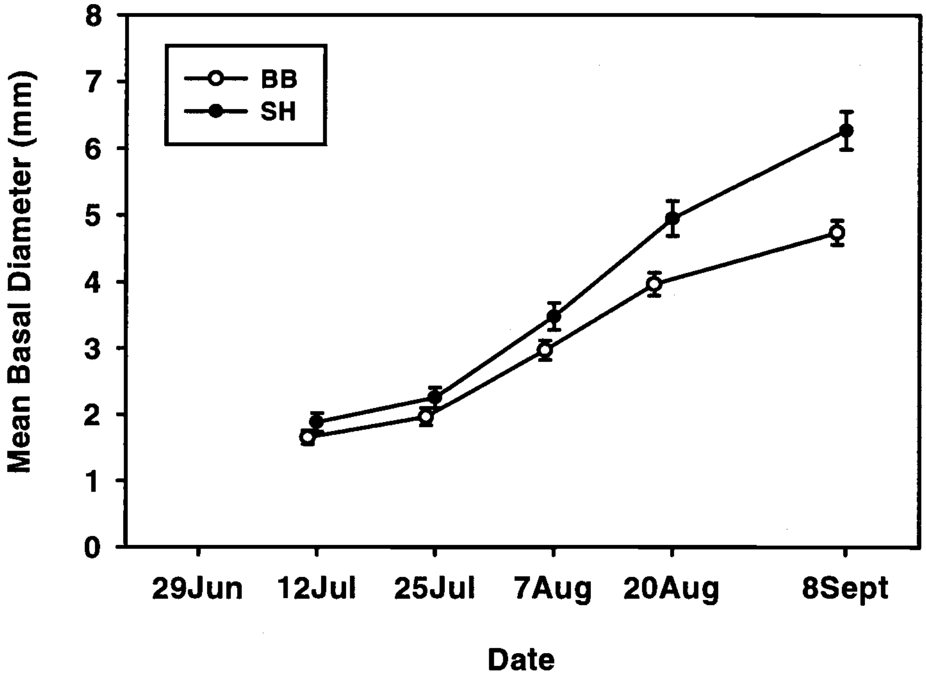


Figure 2.8 Growth of *Balanus glandula* on mid-intertidal plates transplanted from a common source to the exposed areas at Boiler Bay and Strawberry Hill. Data are means (± SEM) of the mean basal diameter on 7 plates per site, each with ~ 13 individuals / plate.

In summary, growth rate of *B. glandula* on both natural settlement plates and transplanted plates was low in all areas during the upwelling event and more than doubled when upwelling ceased (Figs. 2.9, 2.6). This increase in growth coincided with a large phytoplankton bloom that occurred at SH (25 July through 7August). Contrary to my prediction, barnacles at BB grew at the same rate as those at SH during this period, despite the fact that no bloom was recorded at BB. Barnacles did, however, grow significantly faster at SH than BB during the two periods following the peak bloom period (Fig. 2.9).

Table 2.3 Repeated measures analysis of variance of the effects of site on the growth of transplanted *Balanus glandula* during four consecutive time periods. Replicate plates were transplanted to wave-exposed areas at Strawberry Hill and Boiler Bay. The dependent variable was the mean rate of increase in basal diameter (mm/day) for all individuals on a replicate plate. Data exhibited homogeneity of treatment differences variance (test for sphericity, $p = 0.88$). Univariate results are therefore presented with unadjusted probabilities, and multivariate results are provided for comparison. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Site	1	0.005945	12.45	**0.0041**
Error	12	0.000478		

C. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	p-value	num df	den df	Wilks' λ	p-value
Time	3	0.01460	130.0	**<0.0001**	3	10	0.0277	**<0.0001**
Time x Site	3	0.00054	4.77	**0.0067**	3	10	0.4444	**0.0372**
Error	36	0.00011						

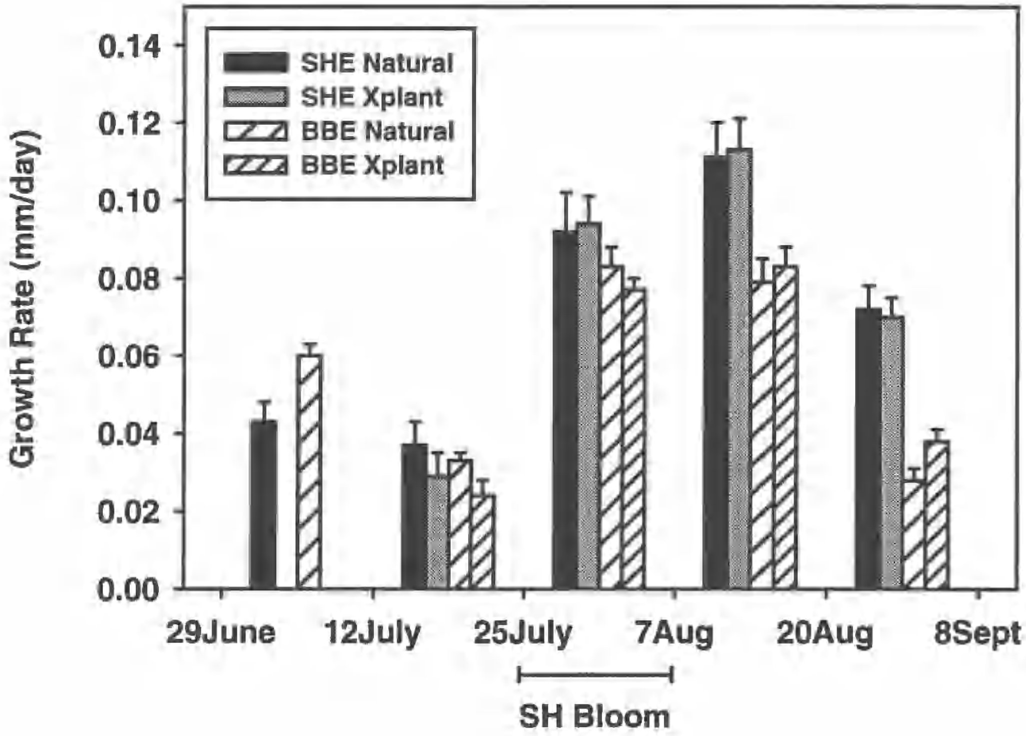


Figure 2.9 Summary of *B. glandula* growth rates during five consecutive periods. Bars are mean growth rate (+SEM) in mm/day; SHE = Strawberry Hill exposed, BBE = Boiler Bay exposed, Natural = natural settlement plates, Xplant = transplanted plates. A major phytoplankton bloom was recorded at SH during the period 25July - 7August (see Fig. 2.6B).

Short-Term Growth on Transplanted Plates: *Chthamalus dalli*

Temporal variation in *C. dalli* growth was less dramatic than that observed in *B. glandula* (Fig. 2.10). Nevertheless, there were significant differences in growth rates among the four time periods, and this variation was dependent upon site (Table 2.4; time x site, $p = 0.0097$). At SH exposed, growth during the bloom period was significantly greater than during the preceding upwelling period (Tukey-Kramer, $p < 0.05$), but did not differ from the final two periods. At BB exposed, growth during the bloom period was greater than during any of the other periods (Tukey-Kramer, $p < 0.05$).

Comparing growth between sites, *C. dalli* grew faster at SH than BB during the period from 7Aug to 20Aug (t-test, $t_{11} = -3.850$, $p = 0.0027$), but growth rates did not differ between sites during the other three periods (Fig. 2.10, t-tests, $p > 0.10$). Thus, as with *B. glandula*, *Chthamalus* growth was low during the upwelling event and subsequently increased. However, there was little variation between sites, despite the strong differences in Chl-a concentrations.

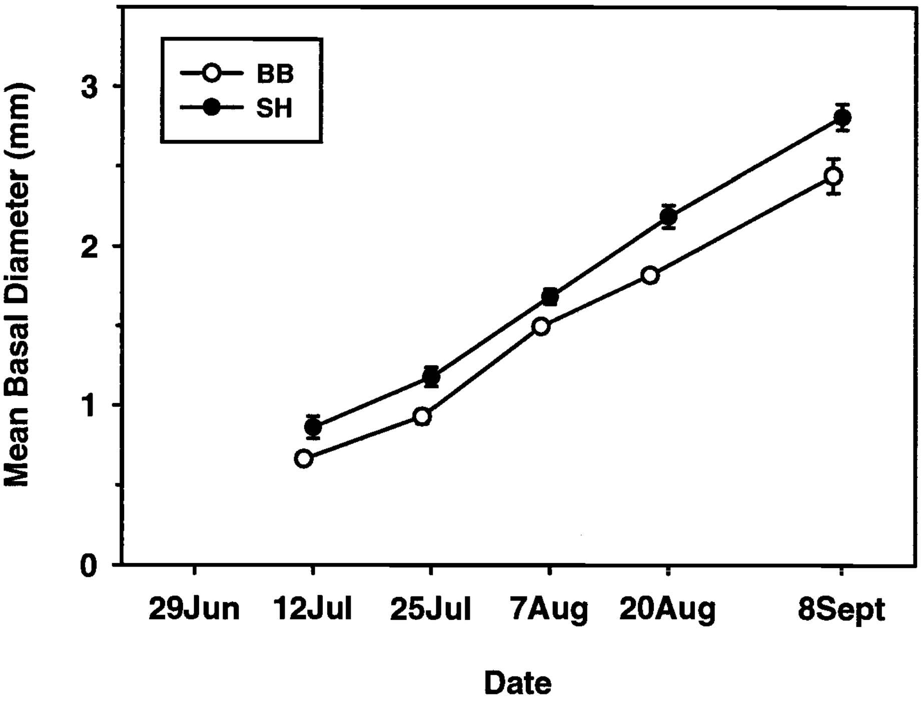


Figure 2.10 Growth of *Chthamalus dalli* on mid-intertidal plates transplanted from a common source to the exposed areas at Boiler Bay and Strawberry Hill. Data are means (± SEM) of the mean basal diameter on 7 plates per site, each with ~ 34 individuals / plate.

Table 2.4 Repeated measures analysis of variance of the effects of site on *Chthamalus dalli* growth during four consecutive time periods. Replicate plates were transplanted to wave-exposed areas at Strawberry Hill and Boiler Bay. The dependent variable was the mean rate of increase in basal diameter (mm/day) for all individuals on a replicate plate. Data exhibited homogeneity of treatment differences variance (test for sphericity, p = 0.76). Univariate results are therefore presented with unadjusted probabilities, and multivariate results are provided for comparison. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Site	1	0.000127	2.10	0.175
Error	11	0.000060		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	p-value	num df	den df	Wilks' λ	p-value
Time	3	0.00073	21.69	**<0.0001**	3	9	0.2014	**0.0018**
Time x Site	3	0.00015	4.47	**0.0097**	3	9	0.3602	**0.0219**
Error	33	0.00003						

Long-Term Growth Rates

The growth curves of *Balanus glandula* at wave-exposed locations indicate that barnacles at SH attained a much larger adult size than those at BB (Fig. 2.4). Barnacles that settled in May and June 1994 were 2.0mm larger at SH by late October, and 4.1mm larger at SH by the following August (mean basal diameter).

I followed a separate set of *B. glandula* that settled on exposed plates at SH and BB during August 1994 (Fig. 2.11A). By mid-April 1995 (after ~8 months of growth) these individuals were significantly larger at SH than BB (t-test, $t_{22} = -13.92$, $p < 0.001$; per plate mean basal area ± SEM = 91.0 ± 3.1 mm^2 vs. 35.5 ± 2.3 mm^2).

For *Chthamalus dalli* I measured the basal area of all individuals that persisted on transplanted plates from June 1994 to June 1995 (Fig. 2.11B). After approximately one year of growth, *C. dalli* at SH were significantly larger than those at BB (t-test, $t_8 = -4.65$, $p = 0.002$; per plate mean basal area ± SEM = 31.3 ± 1.6 mm^2 vs. 17.9 ± 2.4 mm^2).

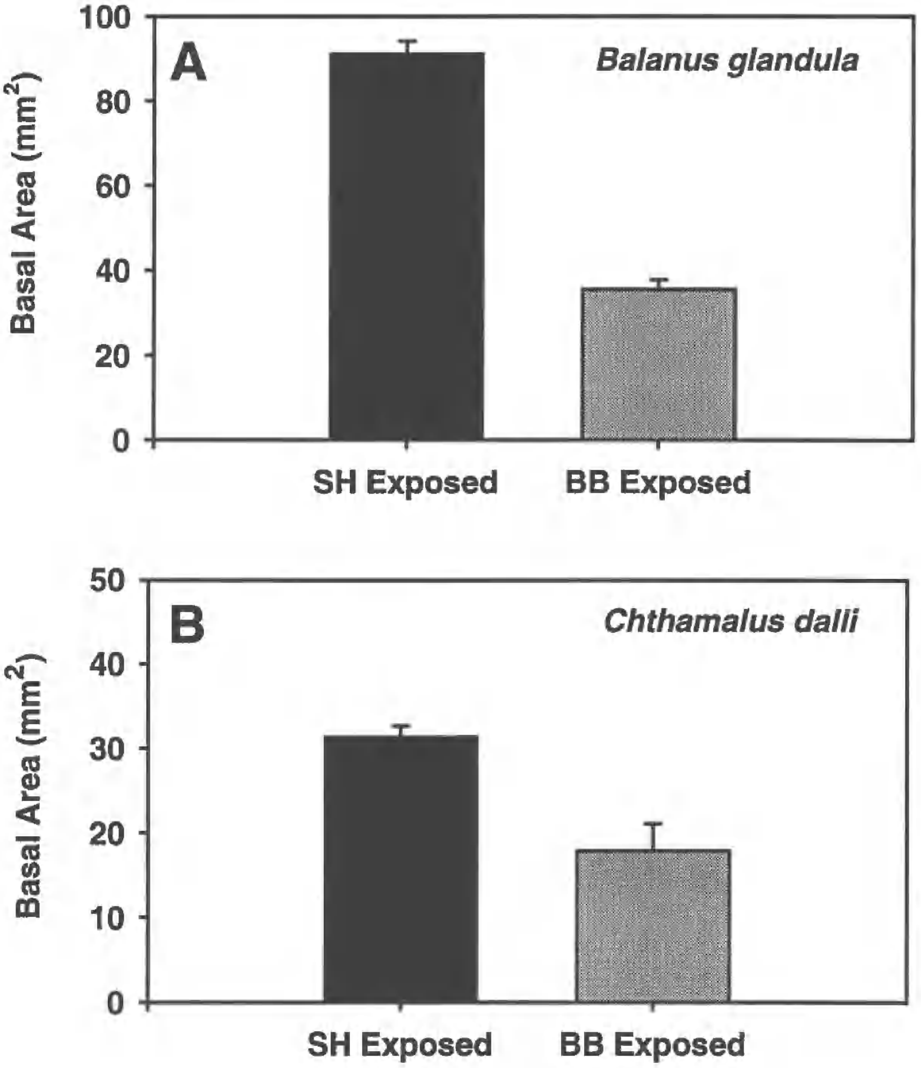


Figure 2.11 Long-term growth of *B. glandula* and *C. dalli* in exposed areas at Strawberry Hill and Boiler Bay. Bars are mean basal area (+SEM). **(A)** For *B. glandula*, individuals settling in August 1994 were measured in April 1995 following ~ 8 months of growth (SH, n = 13 plates; BB, n = 11). **(B)** For *C. dalli*, individuals on transplanted plates were measured in June 1995 after ~ 1 year of growth (SH, n = 7 plates; BB, n = 3 due to plate loss).

DISCUSSION

The Effects of Wave-Exposure on Growth

My results suggest that barnacle growth rates varied dramatically at a variety of spatial and temporal scales, and that this variation was tightly linked to oceanographic conditions. Within a site, barnacles grew more rapidly in wave-exposed habitats than wave-protected ones. Quantification of relative flow rates within these areas confirmed that the exposed areas generally experienced greater flows (Menge et al. 1996). Many studies have found that barnacles grow faster in areas of higher flow, presumably because of the increased delivery of suspended particles to passively feeding barnacles (Hatton & Fischer-Piette 1932, Moore 1935, Crisp 1960, Bertness et al. 1991, Sanford et al. 1994, Bustamante et al. 1995, Leonard et al. 1998). Barnacles on wave-exposed plates may also have experienced longer submergence times and hence greater opportunities for feeding. Although plates were positioned at the same tidal height, wave swell in exposed areas shortened periods of aerial exposure on some days (E. Sanford, *personal observation*). Growth rates in exposed areas may also have been enhanced if these barnacles experienced reduced thermal stress, a possibility suggested by the lower rates of post-settlement mortality in these habitats (Fig. 2.2).

The Effects of Phytoplankton Abundance

Determining whether barnacle growth rates were directly correlated with phytoplankton abundance was the central goal of this study. My results documented extreme short-term variation in barnacle growth rates; in the two weeks immediately following an extended upwelling period, growth rates in wave-exposed areas increased by 2.5-3.3x for *Balanus glandula* and 1.6-2.1x for *Chthamalus dalli* (Figs. 2.8, 2.9). At SH, this increase in growth was associated with a dramatic three to five-fold increase in Chl-a concentrations (Fig. 2.6B).

However, two lines of evidence suggest that phytoplankton abundance does not fully explain variation in barnacle growth. First, a well-defined spike in barnacle growth was not apparent at SH. Although *B. glandula* growth increased at SH during the peak bloom period (25July-7Aug), it remained high during the following two periods (7Aug-20Aug, 20Aug-8Sept), despite the fact that Chl-a levels dropped sharply and returned to lower levels (Fig. 2.9, 2.6B). Secondly, growth rates at BB also increased dramatically following the upwelling event, despite the fact that no increase in Chl-a concentration was recorded at this site (Figs. 2.9, 2.6B).

Although water samples were not collected on a daily basis, it seems unlikely that a phytoplankton bloom occurred and went unnoticed at BB. The bloom at SH lasted at least 10 days during which the nearshore waters were strikingly brown in color. On six days dispersed throughout this period (July 26, 28, 29, Aug 3, 4, 5), Chl-a concentrations were very high at SH and consistently low at BB.

Potential Influence of Zooplankton and Water Temperature

These patterns suggest that factors in addition to phytoplankton may have influenced barnacle growth rates. One possibility is that barnacle growth responded to changes in zooplankton concentration. Although I am aware of no data regarding the diet of *Balanus glandula* or *Chthamalus dalli*, stomach content analyses and laboratory feeding observations suggest that zooplankton is consumed by many barnacle species. *Semibalanus balanoides*, an Atlantic barnacle similar in size and habitat to *B. glandula*, readily consumed 300µm barnacle nauplii in the laboratory (Crisp & Southward 1961). The stomachs of field-collected individuals also contained a variety of invertebrate larvae and small crustaceans (Barnes 1959). Stomach contents of *Semibalanus cariosus* and *Balanus nubilis*, two larger intertidal barnacles common in Oregon, revealed barnacle nauplii and cyprids, small copepods, detritus, detached algal filaments, and diatoms (Barnes 1959, Zardus et al. 1991, Navarrete & Wieters, unpub. manuscript).

Barnacles are thus capable of consuming a variety of suspended food representing a large range of particle sizes (Anderson 1994). A comparison of five barnacle species in Chinese waters suggested that phytoplankton was dominant in the stomachs of smaller species, whereas zooplankton was the primary food of larger species (Jianping et al. 1996). Although this pattern suggests that the size of particles captured may be a function of body size, I am aware of only one study that has examined whether the composition of a barnacle's diet changes with growth and development. In the gooseneck barnacle *Pollicipes polymerus*, gut content analysis suggested that recently settled individuals (1-6mm across) were more dependent on detritus and diatoms than larger individuals whose diet included copepods and other crustaceans (Lewis 1981). Even so, more than half of the small individuals sampled had recently consumed crustaceans.

It is thus possible that the newly-settled barnacles on my plates were large enough to consume zooplankton. In a laboratory flowtank, small *Semibalanus balanoides* (mean basal diameter = 3.7mm) readily captured relatively large pieces of macroalgae (1000-2000μm in length)(Trager et al. 1990). Thus even small *B. glandula* and *C. dalli* may have been capable of capturing early-stage barnacle nauplii (200-300μm in length; Strathmann 1987), and perhaps larger zooplankton as well. If this was this case, then variation in zooplankton concentration may have contributed to patterns of barnacle growth.

As an indicator of spatial and temporal variation in zooplankton abundance, I examined data collected from barnacle settlement plates attached within the mid-intertidal zone at the same four study areas (SH exposed, SH protected, BB exposed, BB protected; n = 5 plates per area). These 10 x 10cm plates were covered with a textured surface (Safety-Walk™, 3M, St. Paul, MN) and deployed for 30 day periods as part of a long-term monitoring program (B. A. Menge, *unpublished data*). Data from the periods of my study suggest that settlement of both *B. glandula* and *C. dalli* was very low during upwelling (22June-22July) and dramatically higher during the upwelling relaxation (22July-20Aug) (Figs. 2.12, 2.6). These results are consistent with the offshore advection of larvae during upwelling and onshore transport during periods of upwelling relaxation (Roughgarden et al. 1988, 1991, Farrell et al. 1991).

Whereas Chl-a differed strongly between sites during the upwelling relaxation, patterns of settlement varied little between sites, implying similar water-column concentrations of barnacle larvae. In addition, although phytoplankton abundance peaked and returned to lower levels within 2-3 weeks, concentrations of barnacle larvae may have remained high throughout August at both sites. Plates collected on August 20th had high densities of both recently settled juveniles and cyprids (Fig. 2.12). Because cyprids metamorphose shortly after settlement, their presence on the plates indicates that barnacle larvae were abundant in the water column on or just before August 20th. To the

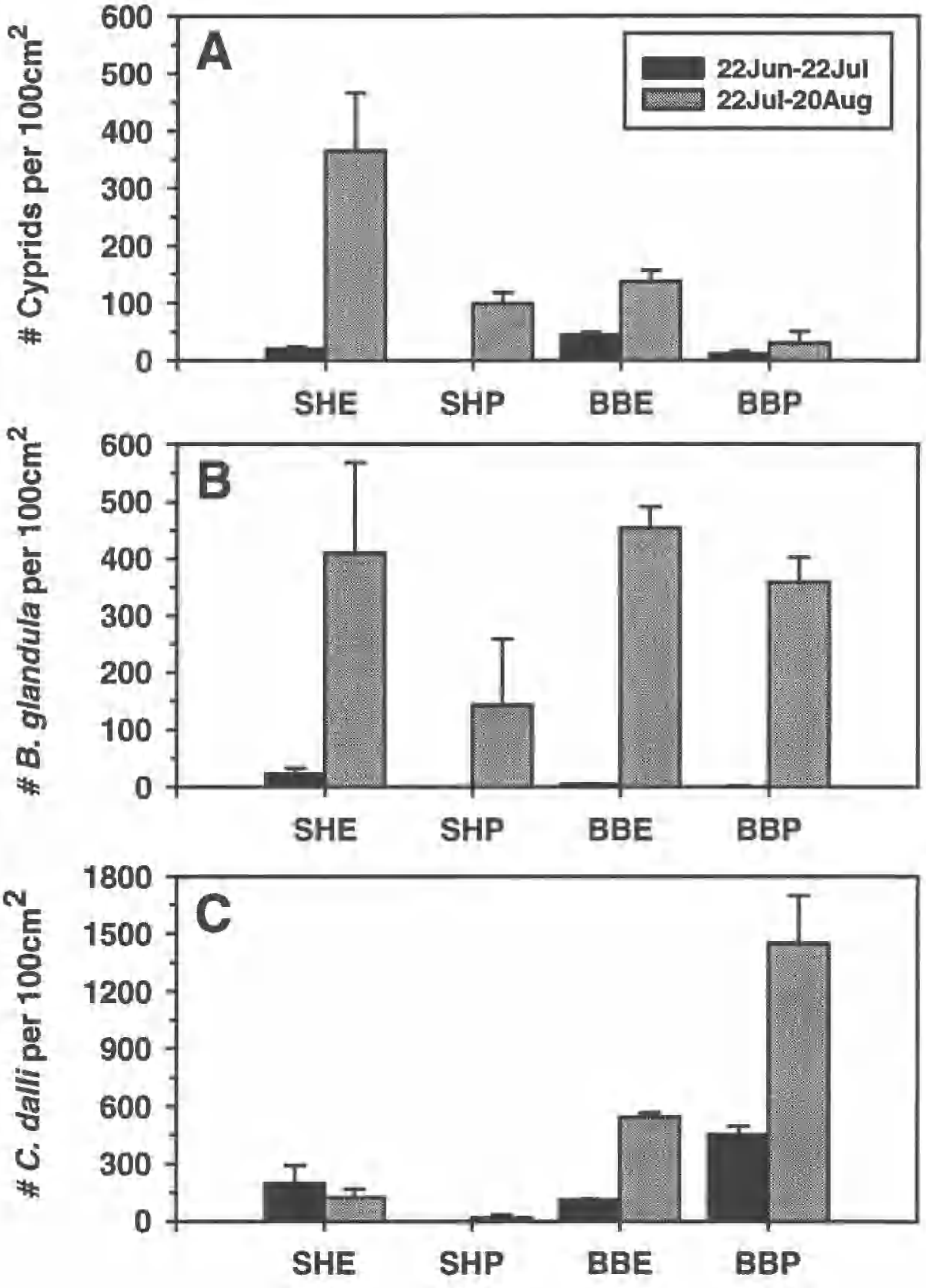


Figure 2.12 Mid-intertidal barnacle settlement, Summer 1994 (B. A. Menge, unpublished data). Mean density (+SEM) of **(A)** cyprids, **(B)** newly-settled *B. glandula*, and **(C)** newly-settled *C. dalli* on 10 x 10cm textured plates deployed for ~30 days during a persistent upwelling event (22June-22July, black bars) and an upwelling relaxation (22July-20August, gray bars). Plates were deployed in all four study areas (n = 5 plates per area); SHE = Strawberry Hill exposed, SHP = Strawberry Hill protected, BBE = Boiler Bay exposed, BBP = Boiler Bay protected.

extent that high concentrations of cyprids are indicative of onshore transport of a variety of zooplankton, these results imply that the period of enhanced barnacle growth at both sites was strongly associated with an increase in zooplankton concentrations. Therefore, the increase in barnacle growth during the relaxation of upwelling may have resulted from an increase in the concentration of both phytoplankton and zooplankton.

Increased water temperature may be an additional factor that contributed to enhanced barnacle growth rates. Water temperatures were consistently at or below 9°C during the July upwelling event and climbed to >13°C during the upwelling relaxation (Fig. 2.6A). Upwelling temperatures were thus lower than winter water temperatures which rarely dip below 10°C (see Chapter 3, Fig. 3.12). Barnacle growth rate is assumed to increase at higher temperatures because of enhanced cirral activity, food intake, and assimilation (Crisp & Bourget 1985, Anderson 1981, Sanford et al. 1994). Therefore, faster growth rates during the upwelling relaxation may have arisen from the combined benefits of more food and warmer water temperatures.

Long-Term Variation in Growth Between Sites

The short-term measures of barnacle growth indicated that *B. glandula* grew significantly faster at SH exposed than BB exposed during two of five time intervals, and that *C. dalli* grew faster at SH during one of four periods. The cumulative effect of these short-term differences in growth rate was apparent in the growth curves of *B. glandula.* By the time growth rates began to plateau in the late fall, *B. glandula* had attained a significantly larger body size at SH than at BB (Fig. 2.4). Measurements of long-term growth indicated a similar pattern; after eight months of growth at SH, *B. glandula* were

2.6x larger than at BB (Fig. 2.11A). For *C. dalli*, individuals were 1.7x larger at SH than at BB after a year of growth (Fig. 2.11B).

These results thus support the hypothesis that consistently higher levels of productivity at SH translate into stronger "bottom-up" forces (Menge 1992, Menge et al. 1997b); both *B. glandula* and *C. dalli* grew more rapidly and attained a larger adult size at SH. Previous studies indicate that the recruitment and growth of mussels (*Mytilus californianus* and *M. trossulus*) are also higher at SH than BB (Menge 1992, Menge et al. 1997b). The consistently higher prey production at SH, in turn, appears to support higher densities of sea stars that exert more intense predation pressure (Menge et al. 1994, 1996, 1997b, Navarrete & Menge 1996). Efforts are underway to expand the scale of these studies to test whether variation in productivity generates similar differences among multiple sites along the coasts of Oregon and California (Menge et al. 1997b; B. A. Menge et al., *unpublished data*).

Conclusions

Interest has grown rapidly in the effects that oceanographic factors such as currents, temperature, nutrients, and phytoplankton abundance may have in generating large-scale variation among rocky intertidal communities (Roughgarden et al. 1988, Menge 1992, Bustamante et al. 1995, Menge et al. 1997b, 1999, Sanford 1999). In this study, long-term growth rates of *Balanus glandula* and *Chthamalus dalli* were higher at the site with consistently higher Chl-a abundance. However, detailed analysis of growth during short time intervals suggests that changes in phytoplankton abundance are unable to fully explain variation in barnacle growth rates. During upwelling relaxations, phytoplankton blooms may be accompanied by onshore transport of zooplankton and significant increases in water temperatures. It seems likely that the combination of all three factors enhances barnacle growth rates. Incorporating the influence of zooplankton and water temperature into large-scale studies of bottom-up influences may thus improve our ability to explain variation among intertidal communities.

CHAPTER 3

The Influence of Variable Water Temperature on the Feeding, Growth, and Reproduction of Two Rocky Intertidal Predators

ABSTRACT

It is widely assumed that small changes in temperature may alter population abundance through effects on the growth and fitness of individuals. Although a number of recent studies have correlated population and climatic changes, the mechanisms underlying such associations are seldom identified. Population changes may often be driven by short-term impacts on critical phases of an organism's life history. Patterns of seasonal upwelling along the Pacific coast of North America are highly variable among years and extremely sensitive to atmospheric and oceanographic conditions. I tested the hypothesis that upwelling-related variation in water temperature regulates the feeding, growth, and energetics of two rocky intertidal predators, the sea star *Pisaster ochraceus* and the whelk *Nucella canaliculata*.

Sea stars and whelks were maintained in laboratory tanks at a constant 9°C, a constant 12°C, or a treatment that simulated the influence of episodic upwelling by cycling between 14-day periods of 12°C and 9°C. Early in the experiments, sea stars and whelks held at 9°C consumed about 30% fewer mussels than those in warmer tanks. Individuals of both species grew at similar rates in 9°C and 12°C tanks, suggesting that reduced consumption under cold conditions was balanced by reduced metabolic costs.

In contrast, there appeared to be an energetic advantage to living in the temperature regime characteristic of episodic upwelling. Sea stars alternately exposed to 12°C and 9°C had a significantly higher growth rate, conversion efficiency, and storage of reserves in the pyloric ceca than individuals in the constant 12°C tanks. Similarly, whelks maintained under fluctuating temperatures tended to have a greater growth rate than those held at constant 12°C or 9°C. Consumers experiencing cyclic temperatures may feed intensely during periods of warmer water while benefiting from reduced metabolic costs during cold-water intrusions.

From 1995 to 1999, I monitored the condition of *Pisaster ochraceus* at two sites on the central Oregon coast: Strawberry Hill and the Newport South Jetty. Changes in energy storage (pyloric ceca) and gonad production were cyclical and inversely related. The frequency and intensity of upwelling varied among years and was sharply reduced during the 1997-98 El Niño. The laboratory results suggested that reduced upwelling and persistent warm water conditions would reduce energy storage in the pyloric ceca. Results were consistent with this expectation at the South Jetty, but not at Strawberry Hill. Gonad production varied among years and between sites, but was not clearly related to variation in water temperature or prey availability. Differences among years and sites in the allocation of energy to growth, storage, and reproduction may obscure the effects of temperature variation.

This study suggests that simple models relating temperature to individual growth and fitness are unlikely to predict the effects of climatic changes on natural populations. There is a strong need for models that incorporate greater mechanistic understanding, including the influence of variable temperature and episodic events on critical phases of an organism's life history.

INTRODUCTION

Climatic Effects on Population Abundance

Surprisingly little is known about how small changes in climate may impact natural populations despite a long history of interest in this area (Gleason 1926, Andrewartha & Birch 1954, Hutchinson 1957). This lack of understanding attests to the challenges of (1) untangling the relative contributions of multiple demographic parameters to population size, and (2) causally linking these parameters to complex environmental variation. The importance of exploring such links has grown in recent decades with the accumulation of evidence that global temperatures are increasing at an unprecedented rate (IPCC Report 1996, Mann et al. 1998, Pollack et al. 1998).

It is widely predicted that increasing temperatures will shift species' geographic ranges to higher latitudes or altitudes (Davis & Zabinski 1992, Lubchenco et al. 1993, Brown & Lomolino 1998). On a local scale, communities are expected to gradually shift in composition, as species with affinities for warmer temperatures become more abundant. In some cases, this response may arise from mobile species migrating to new locations. More commonly it is assumed that subtle temperature change will impact local populations by altering birth or death rates (Parmesan et al. 1999).

Although drawn from classic principles of biogeography, this assumption has seldom been tested. An organism's "performance" (defined as growth or efficiency of operation) has long been thought to vary as a roughly bell-shaped function of temperature or other climatic variables (Fig. 3.1A) (Shelford 1913, Whittaker 1956, Hutchinson 1957, Huey & Stevenson 1979, Huey & Kingsolver 1993, Gates 1993).

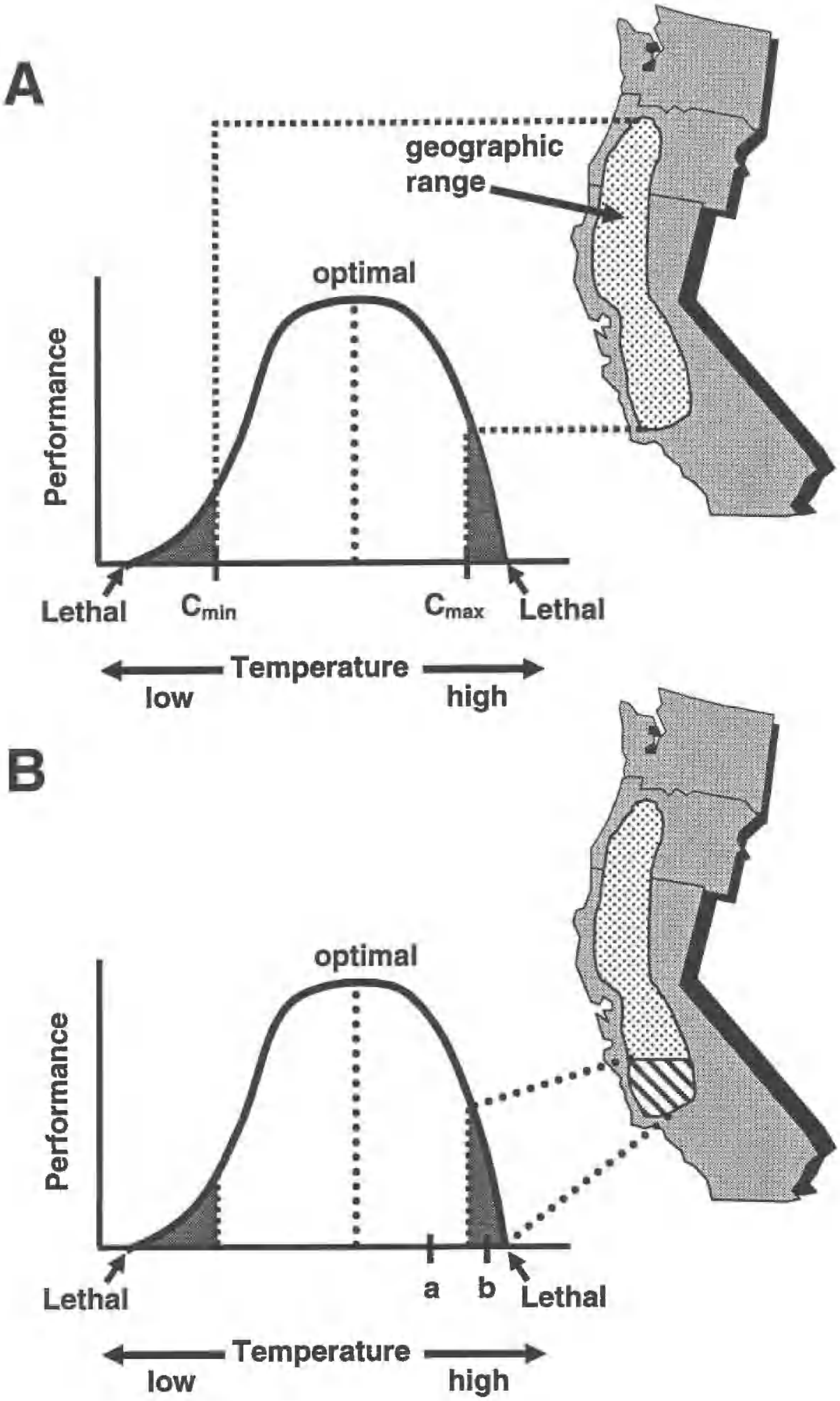
These species-specific relationships are determined by the effect of temperature on the efficiency of underlying physiological processes. Optimal performance should occur in the middle of this temperature range. At high and low temperatures there are critical limits, beyond which an organism is no longer able to reproduce successfully. These upper and lower critical limits are thought to set the geographic boundaries of a species range (Fig. 3.1A).

This model provides the basis for the predicted response of species to climatic warming. Given this model, a population living near its southern boundary may disappear when a small temperature increase pushes individuals beyond their upper critical limit (Fig. 3.1B). As populations are eliminated from this southern margin, the geographic range would contract. At the same time, climatic warming may allow populations to shift northward into regions that previously had conditions below a species' lower critical limit.

Importantly, changes in temperature closer to the middle of a species range may still lead to measurable impacts on population size by altering the fitness or survival of individuals. Thus, as local temperatures change, the composition of communities may also change as species with affinities for warmer temperatures gradually increase in abundance relative to more cold-adapted species. Such changes have been documented in the fossil record in response to historical climate change (e.g., Addicott 1962, Graham 1992, Webb 1992).

More recently, compositional shifts have been observed in both marine and terrestrial communities in association with increased regional temperatures. For example, at a site in Monterey Bay, Barry et al. (1995) examined shifts in the abundance

Figure 3.1 A simple model relating temperature and the geographic range of a hypothetical sedentary species in California and Oregon. **(A)** Individual performance varies as a species-specific function of temperature. Geographic range limits are set by a critical minimum (C_{min}) and critical maximum (C_{max}) temperature, beyond which the organism is unable to successfully reproduce (shaded regions under curve). **(B)** Dynamics of a hypothetical range contraction. A small temperature increase occurs throughout the geographic range. Individuals near their southern range limit formerly experienced temperature "a", but now experience a higher temperature "b" within the species' upper critical range. Individuals are unable to successfully reproduce and southern populations ultimately disappear (cross-hatched region of geographic range). Analogous processes may expand the northern range limit, leading to a northward shift of the entire range.


A
geographic range
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b
Lethal
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Figure 3.1

of intertidal invertebrates by re-sampling permanently marked quadrats established in 1931-33. Invertebrates were classified as southern, northern, or cosmopolitan species based on their geographic ranges. Although many cosmopolitan species showed significant changes in abundance, there was a roughly equal mix of increases and decreases. In contrast, 8 of 9 southern species increased in abundance, while 5 of 8 northern species decreased in abundance. These changes were consistent with predictions, since annual mean water temperature increased by approximately 0.75°C over this sixty year period.

It is significant that the changes observed in the Barry et al. study were mostly shifts in the relative abundance of species, rather than local extinctions or introductions of new species. Most of the southern and northern species that changed in abundance at this site were several 100 km away from their published northern and southern range limits (respectively). This suggests that shifts in population abundance may have been driven by sub-lethal temperature changes within these species' hypothetical critical limits.

Similar changes appear to be occurring in terrestrial systems. At a short-grass steppe site in Colorado, the abundance of the dominant C_4 grass decreased over the last 15 years while the abundance of exotic and native C_3 forbs increased (Alward et al. 1999). This shift was strongly associated with a gradual increase in average minimum temperatures. In the highland forests of Costa Rica, the relative abundance of bird, amphibian, and reptile species appears to have shifted along an altitudinal gradient in recent decades (Pounds et al. 1999). Birds that formerly bred only at lower altitudes have extended their distribution upslope in association with a decline in mist frequency (i.e., low-intensity windblown precipitation). In contrast, those species of highland frogs, toads, and lizards that are dependent on moisture have declined in abundance.

What are the causes of such changes in population abundance? In all of these studies, the relative abundance of different species generally shifted in the direction predicted based upon knowledge of these species' geographic ranges or climatic tolerances. In the studies where abundance was monitored over time, the changes typically occurred gradually over many years, and local extinctions were rare. Although population changes were associated with climatic changes, none of these studies identified the mechanism through which these changes occurred. Without such mechanistic understanding it is difficult to predict future impacts or identify management efforts that might help declining populations.

Changes in individual fitness (and ultimately population abundance) may be driven predominantly by short-term impacts on critical phases of the life cycle (Gates 1993, Bhaud et al. 1995). Therefore, annual mean temperatures may be relatively unimportant relative to seasonal means, variation in thermal maxima, minima, and range, or changes in the frequency and intensity of episodic events (Gates 1993, Harrington et al. 1993, Root & Schneider 1993, Bhaud et al. 1995). Thus, it is necessary to identify both the relative importance of different phases of the life cycle to overall fitness, and the sensitivity of these phases to various forms of climatic variation.

Such links have been established in some studies of plant populations. For example, several studies of alpine plants have identified growing season length as a primary determinant of variation in reproductive success (e.g., Billings & Bliss 1959). In many high alpine environments, growth and reproduction occur during a brief window of one or two months. Galen and Stanton (1993) manipulated snowmelt schedule and observed the effects on a population of an alpine buttercup. Experimentally advancing snowmelt by two weeks increased the time available for growth and seed maturation, and resulted in larger seeds. Seedlings that germinated from larger seeds in turn had a six-fold higher rate of survival (Galen & Stanton 1991). This study thus suggested a plausible mechanism through which the abundance of alpine buttercups may be modified by the effects of global warming on the timing of snowmelt.

Such mechanistic understanding has seldom been achieved in studies of animal populations (Kingsolver 1989). In part this may be due to the difficulty of observing mobile animals and experimentally manipulating their local climate. Another complication is that many mobile poikilotherms such as fishes, lizards, and insects may be able to mediate the effects of minor temperature change by selecting preferred microhabitats or limiting activity to certain times (Caulton 1982, Christian et al. 1983, Whicker & Tracy 1987, Gates 1993, Lin & Regier 1995). In many freshwater and terrestrial systems the thermal environment may be heterogeneous over small spatial scales (e.g., stratified lakes, shaded microhabitats, above vs. below-ground habitats, etc.), providing mobile animals with considerable opportunity for behavioral thermoregulation.

In contrast, investigation of thermal effects is simplified in benthic marine systems since such opportunities are reduced or absent. Most benthic invertebrates and fishes are largely sedentary, with a range of daily movement (cm to m's) that is far less than the spatial scale at which ocean temperature varies (km's). Thus, changes in water temperature are generally experienced directly as changes in the body temperature of these consumers.

Temporal variation in water temperature could impact benthic marine populations at multiple points during an organism's life cycle. It is generally believed that the environmental conditions required for successful reproduction are more restrictive than those required for adult survival (Orton 1920, Hutchins 1947), and there is some evidence for this from both invertebrates (Lewis 1986, Bhaud et al. 1995) and fishes (Gates 1993). Thus, climatic impacts on population abundance may be driven primarily by effects on reproduction or repopulation (Lewis 1986).

Certainly, there is strong evidence that recruitment to marine populations varies among years as a result of many factors (Loosanoff 1964, Gaines & Roughgarden 1985, Pearse & Hines 1987, Rumrill 1989, Menge 1991, Sewell & Watson 1993, Doherty & Fowler 1994, Connell et al. 1997). While in the water column larvae may be influenced by currents (Roughgarden et al. 1988), food supply (Birkeland 1982, Menge 1992), and pelagic predators (Thorson 1950, Gaines & Roughgarden 1987). Once larvae settle in benthic habitats, densities may be altered by physical stress and biotic interactions (e.g., Robles et al. 1995, Hixon & Carr 1997).

However, another possible source of variation in recruitment is the influence of water temperature at various stages in the recruitment process. Temperature could potentially alter (1) the growth and fecundity of adults, (2) the physiological condition and survival of eggs and larvae, or (3) the survivorship of larvae after settling on the shore (Bailey & Incze 1985). In this study I focus on the first of these three possibilities, and examine the effects of small temperature changes on rates of feeding, resource accrual, growth, and reproduction of two rocky intertidal predators, the sea star *Pisaster ochraceus* and the whelk *Nucella canaliculata.* In particular, I explore potential links between variation in coastal upwelling patterns, and the energetics, growth and reproductive output of these consumers.

Study System

Pisaster ochraceus and *Nucella canaliculata* are abundant and important predators in wave-exposed rocky intertidal communities in the Pacific Northwest (Paine 1966, 1969, 1974, Dayton 1971, Menge et al. 1994, Navarrete & Menge 1996). Despite considerable overlap in habitat and diet, these species differ strongly in life history and taxonomy; *Pisaster* is a broadcast spawning asteroid (Phylum: Echinodermata), whereas *Nucella* is a muricid gastropod (Phylum: Mollusca) with direct development (Morris et al. 1986).

Both species show highly seasonal patterns of feeding in the Pacific Northwest (Mauzey 1966, Dayton 1971, Paine 1974, Robles et al. 1995). Along the central Oregon coast, intertidal densities of *Pisaster* and *Nucella canaliculata* are highest from May through September, and low during the remainder of the year (Navarrete 1994; see also Chapter 4). At many sites these predators feed voraciously during the spring and summer on ephemeral low zone patches of the mussel *Mytilus trossulus* (Menge et al. 1994, Navarrete & Menge 1996). These mussels recruit to the low zone during the fall, grow over winter when predator densities are low, and are eliminated by sea stars and whelks by late summer. Thus, feeding by these two consumers appears to be concentrated primarily in the late spring and summer.

Sea stars possess pyloric ceca, extensions of the stomach which serve as storage organs for food reserves (Lawrence & Lane 1982). The ceca grow rapidly in size during the summer (when feeding activity is high) and then shrink over winter as stores are converted to gonads prior to spawning in the spring (Mauzey 1966, Lawrence & Lane 1982). Laboratory studies of *Pisaster* suggest that when food intake is low, resources are channeled to routine body maintenance and growth before reproduction (Mauzey 1967, Harrold & Pearse 1980). This is clearly the strategy that would be expected for a long-lived iteroparous organism. Several studies of *Pisaster* (Mauzey 1967, Feder 1970) and other sea star species (Pearse 1965, Crump 1971, Barker & Xu 1991) have identified differences in growth or gonad production between field populations living in areas of differing food availability; where food is plentiful, sea stars appear to have greater energy available for reproduction. Taken together, these studies suggest that gonad production of individual *Pisaster* may be dependent upon accruing surplus resources during a relatively short window of intensive feeding (May-September).

In Oregon, *Nucella canaliculata* lay egg capsules on the shore during the summer (B.A. Menge, *personal communication*; E. Sanford, *personal observation*). Reproductive output of *Nucella* spp. is directly proportional to body size, and whelks grow to larger sizes in areas where prey are abundant (Spight & Emlen 1976, Spight 1982, Navarrete & Menge 1996). Consequently, growth and reproductive success of both *Pisaster* and *Nucella* should be extremely sensitive to variation in (1) resource quantity and quality, and (2) factors which alter feeding rates during the limited feeding season.

Preliminary observations and subsequent field experiments suggested that water temperature may be one factor that influences the feeding rate of *Pisaster* (Sanford 1999; Chapter 4). Along the Oregon coast, water temperature varies within a relatively narrow range of 8-15°C. Between October and May, water temperatures are consistently within the range 10-12 °C, and changes within this range occur gradually over several weeks. In contrast, both annual maxima and minima typically occur during the summer as a consequence of warmer summer waters punctuated by episodic upwelling of cold water. During upwelling events, strong northerly winds and the Coriolis effect push surface waters offshore (Smith 1983, Bakun 1990). These waters are replaced by cold, nutrient-rich waters which rise from depth. Along the Oregon coast, water temperatures typically drop 3-5°C during these upwelling events that last from several days to three or more weeks (Menge et al. 1997b). Upwelling-favorable winds generally occur from May through September along the Oregon coast (Smith 1983) coinciding with the seasonal peak in sea star and whelk feeding.

Patterns of upwelling are highly variable among years. In particular, the frequency and intensity of upwelling are generally reduced during El Niño-Southern Oscillation events (Barber 1988, Lange et al. 1990). On longer-time scales, upwelling in the California Current may be altered by interdecadal regime shifts in the North Pacific (Lange et al. 1990, Roemmich & McGowan 1995, McGowan et al. 1998). Finally, since the strength of upwelling favorable winds is largely determined by atmospheric conditions, there is great potential for climatic change to modify upwelling patterns (Bakun 1990, Peterson et al. 1993). Evidence suggests that upwelling patterns in the California Current have in fact changed substantially in recent decades, perhaps due in part to global warming (Bakun 1990, Roemmich & McGowan 1995, Schwing & Mendelssohn 1997, McGowan et al. 1998).

Despite considerable spatial and temporal variation in upwelling patterns, I am aware of no previous studies that have considered how this upwelling-associated variability in water temperature might impact benthic marine populations. Field measures of *Pisaster* predation on transplanted mussels demonstrated that the intensity of sea star predation was sharply reduced during periods of cold water upwelling (Sanford 1999; Chapter 4). These results suggested that variation in upwelling patterns can regulate the strength of sea star predation and thus may have important effects on community dynamics. The strong influence of water temperature on sea star feeding also suggested that changes in upwelling patterns might influence the physiological condition and ultimately the population abundance of sea stars and other consumers.

In this study, I tested the effects of small differences in water temperatures on the feeding and growth of sea stars and whelks maintained under controlled conditions in the laboratory. In addition, I compared these laboratory results to observations of field populations of *Pisaster* and examined whether interannual variation in water temperature generated predictable variation in sea star energy reserves and reproductive output.

METHODS

Laboratory Experiments

Experimental design

I examined the effects of water temperature on feeding and growth rates of *Pisaster ochraceus* and *Nucella canaliculata* under controlled conditions at Hatfield Marine Science Center in Newport, Oregon. In separate experiments, sea stars (in 1996) and whelks (in 1997) were maintained under three temperature treatments: (1) constant 9°C ("cold"), (2) constant 12°C ("warmer"), and (3) a treatment that alternated between two weeks at 12°C, and two weeks at 9°C. This final "upwelling" treatment was designed to simulate the fluctuating water temperatures typically generated by episodic upwelling along the Oregon coast. Transitions between the 12°C and 9 °C states were made gradually at a rate of 1°C per 12 hours which is comparable to temperature changes observed in the field during transitions between upwelling and relaxation periods. The constant "cold" and "warmer" treatments simulate water temperatures that organisms would experience during summers with either very intense upwelling or no upwelling, respectively.

Animals were kept in 12, closed Nalgene™ tanks (110-liter capacity, dimensions: 60cm L, 45cm W, 45cm H) filled with filtered seawater. All tanks were held in a cold room (5.6m x 2.7m) with ambient temperature that cycled between ~6 and 8°C. Two tanks were placed in each of 6 rectangular plastic bins (725-liter capacity, dimensions: 120 cm L, 79 cm W, 79 cm H; Chem-Tainer Industries, Los Angeles, CA) that were filled with freshwater and functioned as water baths (Fig. 3.2). By controlling the temperatures of these large bins, I maintained water temperatures within the closed tanks. Water temperatures in the bins were elevated to set levels and self-regulated to ± 0.1°C using heaters and controllers. A 240-volt immersion heater (Model PTH-102, Omega Engineering, Inc., Stamford, CT) and temperature sensor (Model CPSS-18G-18-PFA, Omega Engineering, Inc.) were positioned between the two closed tanks in each bin. A submersible pump (Penguin Powerhead™ Model 1140, 1000-liters per hour, Marineland Aquarium Products, Moorpark, CA) kept the water bath mixed, circulating water past the heater and around the outside of the two tanks. The heater and sensor were connected to a controller (Controller Model CN76120, Omega Engineering Inc). This unit continuously monitored how far the water temperature of the bin was from the set-point, and turned the heater on for an appropriate proportion of every 10 second interval. Thus, this system (termed Proportional Integral Derivative control, Omega Temperature Handbook 1995) continuously supplied small pulses of heat, and provided very accurate temperature control without cycling.

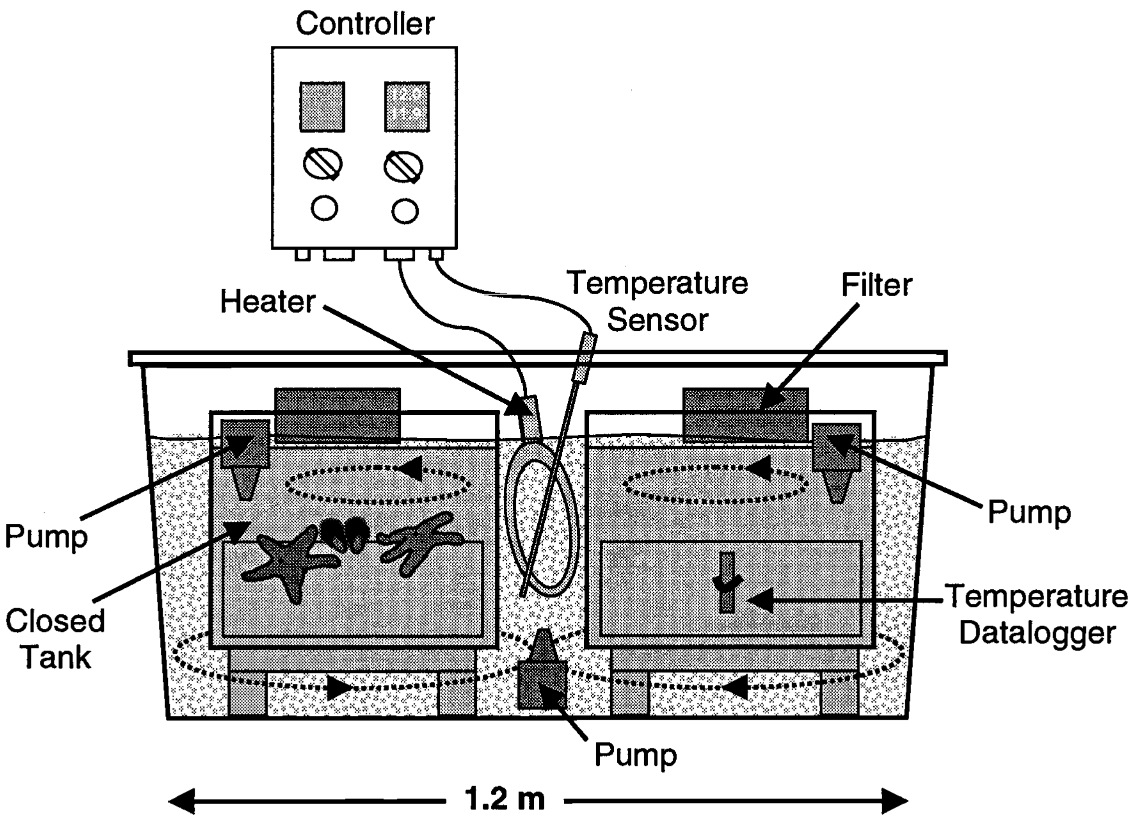


Figure 3.2 Design of controlled temperature tanks. Two closed tanks were submerged in each large bin. A heater and controller self-regulated the temperature of these water baths. Dotted arrows indicate the circulation of water. Each closed tank (n = 4 per temperature treatment) contained 4 sea stars (during 1996) or 8 whelks (during 1997) fed mussels *ad libitum.*

Temperatures in treatments were verified independently throughout the experiments by spot checks with a mercury thermometer and data-loggers (Optic StowAway™, Onset Computer Corp., Pocasset, MA) that were submerged in the 110-liter closed tanks and recorded temperatures hourly. Water within each tank was vigorously circulated and oxygenated by two pumps (Penguin Powerhead 1140). Water quality was maintained by an *in situ* wet/dry filter (Bio-Wheel™, Marineland Aquarium Products) and foam fractionater (Protein Skimmer, Lee's Aquarium Products) in each tank. Routine water changes were also conducted weekly during the sea star experiment, and every two weeks during the whelk experiment. I siphoned any accumulated waste from the bottom of each tank, and replaced 25% of the total volume with filtered seawater (cooled or warmed to the temperature of that treatment). Salinity was monitored regularly and maintained at 36 ± 1‰ by the addition of small volumes of distilled water. Light in the cold room was provided by two 100-watt ceiling light bulbs positioned to provide equal lighting to all tanks. Lights were operated by a timer, and the experiments were conducted under a 12 hour light:12 hour dark schedule.

Pisaster feeding experiment

The sea star experiment began in early June 1996, soon after *Pisaster* had spawned in the field, and ran for 4.5 months. This is the time of the year when *Pisaster* are feeding most actively in the field and are storing energy in the pyloric ceca (Mauzey 1966, Paine 1974; see also this chapter, Fig. 3.15). This period also corresponds to the upwelling season on the Oregon coast, when sea stars typically experience fluctuating water temperatures.

On 7 June 1996, I collected 48 sea stars (wet weight: range = 118-138 g) from a single location on the central Oregon coast (Strawberry Hill: 44°15'N, 124°07'W, see site description below). Sea stars were immediately brought to the laboratory where they were assigned a number and weighed. I photographed the aboral disk of each sea star so that I could later re-identify individuals by unique characteristics (i.e., color and patterns of tubercles around the madreporite). Four individuals were randomly assigned to each of the 12 tanks. After exploring their tanks on the first day, sea stars did not attempt to crawl out, and remained submerged throughout the experiment.

All sea stars were initially acclimated for 10 days at 11°C without food. The three treatments were then randomly assigned among the tanks (n = 4 tanks/treatment) and sea stars were provided with mussels *ad libitum*. *Mytilus trossulus* (shell length: range = 32-42 cm) were collected from a common source (Bob Creek Wayside, 1 km south of Strawberry Hill). In the lab, mussels were cleaned of any epibionts and were arranged in groups of 25 in numbered plastic petri dishes (10 cm diameter). Prepared dishes were stored in seawater tables supplied with running, unfiltered seawater. Mussels reattached byssal threads to the petri dish and each other and formed clusters very similar to those found in the field.

At the start of each period, each tank was supplied with 3-4 petri dishes. A plexiglass box was placed in each tank that added surface area to the tank and functioned as a horizontal shelf (28 x 43 cm) about 20 cm below the surface of the water. All petri dishes added to the tank were placed on this shelf. As mussels were consumed, fresh petri dishes were added so as to keep the level of food at about 75-100 mussels/tank. The number of mussels consumed per tank was recorded every 14 days. It was impossible to determine individual feeding rates within tanks, so I estimated per capita feeding rates based on the assumption that the four sea stars within each tank contributed equally to predation totals. At the conclusion of the experiment, I quantified mussel survivorship in the absence of sea stars, by holding mussels in 9°C and 12°C tanks (n = 4 per temperature) for 14 days.

Data were also collected to estimate the amount of mussel tissue consumed per tank and time period. Prior to being added to tanks, mussel clusters in pre-weighed petri dishes were dried upside down on paper towels for 1 hour and then weighed. At the end of each 14-day period, uneaten mussels and empty shells were removed from each tank, dried on paper towels for 1 hour, and re-weighed. I also randomly selected 144 eaten mussels per period (12 per tank, where possible) and measured the lengths of these shells to the nearest 0.1 mm using calipers.

In addition to living tissue, mussels that were consumed also contained some water in the mantle cavity when initially weighed. I therefore estimated the average weight of water in a mussel by weighing individual mussels, cutting the abductor muscle, and drying the open mussels on paper towels for 30 minutes (n = 51, shell length: range = 32 - 41 mm). I re-weighed the mussels and assumed the weight difference represented water content. Thus, mussel tissue consumed in each tank was estimated as:

tissue consumed = (mussel weight added) – (uneaten mussel weight + empty shells) – (# mussels consumed x estimated water weight/mussel)

Mussels were inadvertently not weighed during the first period, but shell lengths were measured from a random sample of eaten mussels (n = 144). I therefore estimated tissue consumed for this period from a shell length vs. tissue weight regression based on a separate sample of *M. trossulus* [tissue weight (g) = 0.0825 * shell length (mm) – 1.495, $R^2 = 0.66$, n = 58].

To monitor sea star growth, I recorded the wet weight of individuals at the beginning, middle, and end of the experiment. Since *Pisaster* may cease feeding after repeated handling (Landenberger 1968, Menge & Menge 1974, Sloan 1980), sea stars were only weighed once after the first day and otherwise were not handled. At the conclusion of the experiment, all sea stars were dissected and I calculated pyloric ceca indices (see methods below). In addition, pyloric ceca of each individual were dried to a constant weight at ~60°C and then weighed to the nearest 0.002 g.

Nucella canaliculata feeding experiment

Whelks were maintained for three months under the same three temperature treatments and conditions used in the sea star experiment. On 11 June 1997 I collected *Nucella canaliculata* from low and mid-intertidal wave-exposed areas at Bob Creek Wayside. Whelks were returned to the laboratory and shell lengths were measured to the nearest 0.1mm using calipers. All whelks selected for the experiment (n = 96) had a shell length of 15.0 ± 0.2mm, obviating the need for marking individuals; individual growth was simply estimated by subtracting 15mm from measured lengths. I divided snails into twelve groups so that each group contained eight whelks representing all sizes within this narrow range (i.e., 14.8-15.2mm). Each group was placed in one of twelve identical plastic containers (Tupperware™, dimensions: 25cm L, 25cm W, 10cm deep) that had the top and sides removed and replaced with mesh screen. Each container was then randomly assigned to one of the twelve 110-l tanks. The container was placed on a plexiglass shelf so that snails were constantly submerged in vigorously circulated water, approximately 20cm below the surface of the water.

Whelks were initially acclimated for 8 days at 10.5°C without food. The three treatments were then randomly assigned among the tanks (n = 4 tanks / treatment) and whelks were provided with mussels *ad libitum*. *Mytilus trossulus* (shell length: range = 25-31mm) were collected from a common source (Bob Creek Wayside) and arranged in groups of 20 in plastic petri dishes stored in seawater tables. At the start of each period, each plastic container was supplied with two petri dishes. Every 14 days, all mussels were removed and mussels that had been drilled by whelks were counted and measured. In many cases whelk feeding was interrupted at the end of a period, so some mussels were not completely consumed. Mussels were defined as "drilled" if the drill hole went completely through the mussel shell. As with the sea star experiments, it was impossible to know how many mussels were drilled by individual snails within a container. Rather, I calculated per capita feeding rates based on the assumption that the number of mussels drilled was divided equally among the eight whelks in a container.

Mean whelk growth per container was quantified after 4, 8, 10, and 12 weeks by recording the shell length of the eight snails in each container. In addition, at the start of the experiment, I used a file to create two small notches at the margin of the outer body whorl on each individual. At the conclusion of the experiment, I measured the addition of shell to the body whorl (indicated by new growth beyond the repaired notches).

Coastal Water Temperature, Prey Abundance, and Pisaster Condition

I tested whether results from the *Pisaster* laboratory experiment were consistent with natural patterns by monitoring the condition of field populations in relation to variation in water temperature and prey abundance. From 1995-1999, I examined variation in *Pisaster* pyloric ceca and gonad indices at two wave-exposed sites separated by 34 km on the central Oregon coast: Strawberry Hill (44°15'N, 124°07'W) and the South Jetty in Newport (44° 36'N, 124° 04'W). Strawberry Hill (hereafter SH) is composed of extensive rocky benches, pools, and surge channels, and is described in detail elsewhere (D'Antonio 1985, Menge 1992). The South Jetty is a human-made breakwater of large boulders that extends out approximately 1 km WSW from the shore and protects the south side of the entrance to Yaquina Bay.

These sites were selected because preliminary observations suggested that available prey items differed markedly between the sites. At SH, mussels (*Mytilus trossulus*) and goose-neck barnacles (*Pollicipes polymerus*) were abundant in the low intertidal zone. In contrast, mussels and gooseneck barnacles were uncommon at the South Jetty. At this site, low intertidal surfaces were dominated by algal turf, coralline algae, and clonal anemones (*Anthopleura elegantissima*), and the most abundant prey were acorn barnacles (*Balanus glandula* and *Chthamalus dalli*) on mid and high intertidal boulder faces.

Sea stars were routinely sampled from the same locations within these sites. At SH, I selected a rocky outcropping that was isolated by deep surge channels, and surrounded by sand. The South Jetty is isolated from other rocky habitats by sandy beach to the south and the mouth of the Yaquina Bay to the north. It seemed likely that the sand surrounding these locations minimized large-scale movements of sea stars; most individuals sampled probably fed and remained within these same areas throughout the year.

To characterize the shape and magnitude of seasonal cycles in the pyloric ceca and gonads, I collected sea stars (n = 12 per site) during the first spring tide series of every other month between August 1995 and August 1997. Less frequent collections were made between August 1997 and May 1999 to record the seasonal peaks in the pyloric ceca and gonads. I haphazardly collected individuals and weighed them in the field using a battery-powered digital balance (Portable Plus™, Ohaus Corporation, Florham Park, NJ). Individuals were retained if their wet weight fell within the range of

170-260 g. *Pisaster ochraceus* reaches sexual maturity at 70-90 g wet weight (Menge 1974). Sea stars were brought to Hatfield Marine Science Center in Newport, held in seawater tables for 24 hours, and then dissected following the methods of Farmanfarmaian et al. (1958) and Mauzey (1966).

Prior to dissection sea stars were anesthetized for 15-20 minutes in a solution of $MgCl_2$ and seawater. I used sewing scissors (Soft Touch Micro-Tip Scissors™, Fiskars Inc., Madison, WI) to make radial and interradial cuts along the aboral surface of each individual. Gonads and pyloric ceca were removed from each arm and separated into dishes. The eviscerated sea star was weighed and the removed organs were blotted on paper towels for 15 minutes to remove excess water. The volume of the pyloric ceca and gonads were then determined by their displacement of known volumes of water in a graduated cylinder (Mauzey 1966). By convention, the gonad index was defined as the ratio of the gonad volume to eviscerated body weight x 100 (Lawrence & Lane 1982). Similarly, the pyloric ceca index was defined as the ratio of the pyloric ceca volume to eviscerated body weight x 100. Some studies of asteroid condition have quantified organ wet weight rather than volume (Lawrence & Lane 1982). The specific gravity of the pyloric ceca, gonads, and sea water are essentially equivalent (Mauzey 1966), so that indices determined with either organ wet weight or volume are comparable.

I quantified sea star diet within the collection areas at SH and the South Jetty in July 1995, May 1996, and August 1996. At each site, two 30m transect lines were laid parallel to the water in the low intertidal zone. I examined the first 100 sea stars within 1m of each transect line and noted prey items that were being consumed. If an individual was preying on one or more mussels, I recorded the shell length of the largest mussel being consumed.

At SH, I also quantified interannual variation in prey availability. Recruitment of most barnacle and mussel species is highest along the Oregon coast during the fall (B. A. Menge, *unpublished data*). Intertidal densities of *Pisaster* and *Nucella* are low from late fall to early spring. I therefore censused invertebrate abundance just prior to the onset of intense sea star and whelk predation, during the first week of May 1996, 1997, and 1998. I placed two 30m transects parallel to the water in the low intertidal zone within the area from which sea stars were regularly collected. I photographed the biota within 30 x 40 cm quadrats randomly located within each meter (n = 60-62 total). I later quantified percent cover by placing transparent plastic sheets with 100 random dots over these photographs, and recording the identity of sessile invertebrate and macroalgal species beneath each dot.

I examined seasonal and interannual variation in water temperature using data-loggers (Optic StowAway) attached under stainless steel mesh in the low intertidal zone at Strawberry Hill. In most cases, temperatures were recorded by two data-loggers separated by several hundred meters. At this scale, water temperature readings generally varied $< 0.2^{\circ}C$ between pairs of data-loggers. Data-loggers were set to record temperatures every 30 minutes during upwelling season (May through September), and every hour during the remainder of the year. From these data I calculated High Tide Water Temperatures, defined as the mean of all readings during the period from two hours before to two hours after each high tide (as estimated from NOAA tide charts). For graphical presentation, these data were smoothed using a running means function that averaged each High Tide Water Temperature with those of the two preceding and two following high tides. Although water temperatures were recorded at SH, there is relatively minor spatial variation in water temperature among sites extending 80 km to the north (Menge et al. 1997b, B. A. Menge, *unpublished data*). Thus, the South Jetty probably experienced similar temperature patterns as those recorded at SH.

Statistical Analysis

For analysis of the laboratory experiments, closed tanks were treated as the experimental units. To avoid pseudoreplication (Hurlbert 1984), analyses were conducted on mean feeding and growth per tank (i.e., calculated from all individuals within a tank). Although two tanks shared the same large water bath, I considered these tanks to be independent because the tanks were closed units with separate animals and environments. Data-loggers within the tanks verified that all four tanks within a treatment experienced the same water temperatures. Moreover, there was no evidence of non-independence in the data; variation among the two tanks within the same water bath was generally ≥ variation between tanks in different baths belonging to the same treatment.

Sea star and whelk feeding rates, and the size of mussels drilled by whelks were recorded through time in replicate tanks. I therefore used a one-way repeated measures analysis of variance (RM-ANOVA) to account for temporal correlation in replicate tanks (JPM Version 3.2.2, SAS Institute, 1997). As in all ANOVA designs, normality and homogeneity of variance are required and these assumptions were checked by visual inspection of residual plots and normal probability plots, and by using the Brown-Forsythe (1974) and O'Brien's (O'Brien 1979) tests for unequal variances. For both the sea star and whelk feeding data, assumptions of homoscedasticity were met reasonably well. Although there were minor departures from normality, these were not improved by data transformation, so analyses were conducted on untransformed data. The assumption of normality is not critical for ANOVA tests (Ramsey & Schafer 1997).

Repeated measures designs can be analyzed using either univariate or multivariate approaches (von Ende 1993). Although more powerful, the univariate approach requires the condition of sphericity (i.e., homogeneity in the variance of the difference between all possible pairs of repeated measures). When this condition is not met, F statistics for the within-subject factor are inflated, and it is necessary to either use the multivariate approach, or decrease the degrees of freedom in the univariate analysis using the Huynh-Feldt adjustment (von Ende 1993).

I tested whether sphericity was met by using Mauchly's sphericity test applied to the orthonormalized form of the variance-covariance matrix. The assumption was satisfied for all data sets except rates of sea star feeding estimated by tissue weight. In this case, I present results of the univariate approach with more conservative Huynh-Feldt (H-F) adjusted p-values, as well as the results from the multivariate repeated measures analyses. Multivariate analyses on sea star feeding data were conducted on the first seven periods of the experiment because insufficient degrees of freedom precluded analysis of all nine periods. Within each time period, separate one-way ANOVAs were used to test for differences in feeding rates among treatments, and significant differences between all treatment pairs were identified using the Tukey-Kramer procedure for multiple comparisons.

For the sea star experiment, effects of temperature treatment on total consumption (number of mussels and tissue weight), sea star growth, conversion efficiency, the pyloric ceca index, and dry weight pyloric ceca were examined using one-way analyses of variance (ANOVA). Similarly, for the whelk experiment I used separate one-way ANOVAs to examine the effect of temperature regime on total number of mussels drilled, whelk growth, and final shell length attained. In all cases, significant differences among treatment pairs were identified using the Tukey-Kramer procedure.

For data collected on sea star condition in the field, peak pyloric ceca and gonad indices were analyzed using a two-way ANOVA design with site and year as fixed factors. Since different sea stars were sampled during each collection, a repeated measures analysis was not necessary. For both indices, significant differences among years and sites were determined using the Tukey-Kramer procedure.

For the ANOVA tests described above, assumptions of normality and homogeneity of variance were checked by visual inspection of residual plots and by using the Brown-Forsythe and O'Brien's tests for unequal variances. Assumptions of normality and homoscedasticity were met reasonably well. In the few cases where variances were unequal it was because variance in one treatment was smaller than the other two, which is not a problem for ANOVA tests (Underwood 1997). Thus, it was not necessary to transform the data.

Finally, to test for variation among years in prey availability at SH, I conducted a multivariate analysis of variation (MANOVA) on the percent cover of sessile invertebrates and bare space with year as the main effect. Although the same reef was sampled each year, a repeated measures analysis was not necessary because quadrats were randomly placed in different positions each year. MANOVA was used to account for correlation among the following dependent variables: mussels (*Mytilus trossulus* and *M. californianus*), gooseneck barnacles (*Pollicipes polymerus*), small acorn barnacles (*Balanus glandula* and *Chthamalus dalli*), large barnacles (*Semibalanus cariosus* and *Balanus nubilis*), other sessile invertebrates (colonial hydriods and tubeworms), and bare space. Assumptions of normality and homogeneity of variance were checked by visual inspection of residual plots. Arcsin-square root transformed cover data exhibited more normal distributions and homogeneity of variances than the raw data. To test whether the cover of each prey type varied among years, separate ANOVAs were conducted for each, using a Bonferroni adjusted critical p-value (0.05/6) to control for multiple comparisons across the six categories (e.g., five prey types plus bare space).

RESULTS

Pisaster ***Laboratory Experiment***

Water temperatures were generally maintained within ± 0.1°C of the desired treatment levels throughout the 18 week long experiment (Fig. 3.3). All empty mussels were attributed to sea star predation since mussel mortality was negligible in tanks without sea stars (mean mortality ± SEM = 0.37 ± 0.25% per 14 days, n = 8 tanks). Most experimental sea stars appeared very healthy and fed readily throughout the experiment. However, late in the experiment (week 12), two sea stars (one in a 12°C tank and one in a 9°C tank) appeared infected by an unidentified disease. These individuals had lesions and contorted arms, remained inactive, and were not observed feeding. To prevent possible infection of other sea stars, I removed these individuals from their tanks. Surprisingly, once these individuals were removed, the other sea stars in these tanks fed at a greatly accelerated rate and several attained final weights greater than those of all other experimental sea stars. Since these sea stars apparently altered their feeding in response to the decrease in sea star density, I removed these replicates from analysis. Therefore, the sample sizes for most analyses were: cold (n = 3 tanks), warmer (n = 3), and upwelling (n = 4).

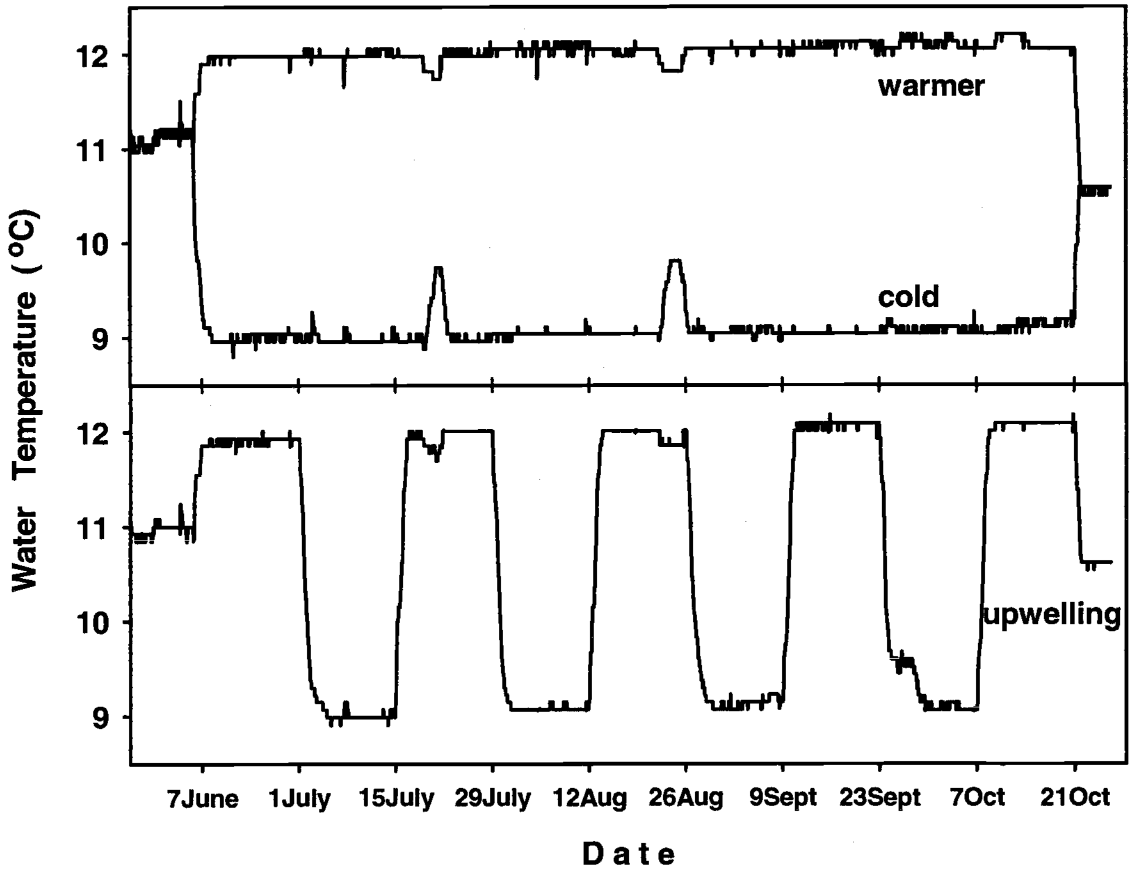


Figure 3.3 Water temperatures during the sea star feeding experiment. Sea stars were held in three treatments: constant 12°C ("warmer"), constant 9°C ("cold"), and alternating 12°C/9°C ("upwelling"). Temperatures were recorded hourly by data-loggers submerged in the closed tanks. Dates on the abscissa indicate starting dates for the nine consecutive 14-day periods. The small anomalies in the cold treatment during late July and late August were caused by technical problems with the refrigeration unit that cooled the cold room.

Although these treatments only differed by a few degrees, they produced surprisingly large differences in *Pisaster* feeding rates (Fig. 3.4). Feeding rates differed significantly among treatments and time periods, and the effect of treatment varied with time (Table 3.1, RM-ANOVA: Treatment, Time, and Time * Treatment are all significant, $p < 0.001$). During the first three periods of the experiment, sea stars in the 9°C tanks consumed 23-34% fewer mussels than sea stars kept at 12 °C. In the upwelling treatment, sea stars fed intensely at 12 °C, more slowly at 9 °C, then faster again at 12 °C (Fig. 3.4).

Later in the experiment, satiation appeared to modify consumption rates. After the first three periods, feeding rates declined sharply in the 12 °C tanks (Fig. 3.4). Sea stars in these tanks had consumed 40% more mussels than 9 °C sea stars, and presumably were satiated on the *ad libitum* diet. Feeding rates in the 12 °C tanks remained low during the fourth and fifth periods, and then these sea stars appeared to start a second feeding cycle. Similar cycles occurred in the 9°C and alternating 12 °C/9°C treatments, although the temporary reduction in feeding rates occurred later in these treatments. As a result of these offset cycles, cold sea stars actually consumed significantly more than warmer sea stars during some periods (e.g., four and five, Fig. 3.4, Tukey-Kramer, $p < 0.05$).

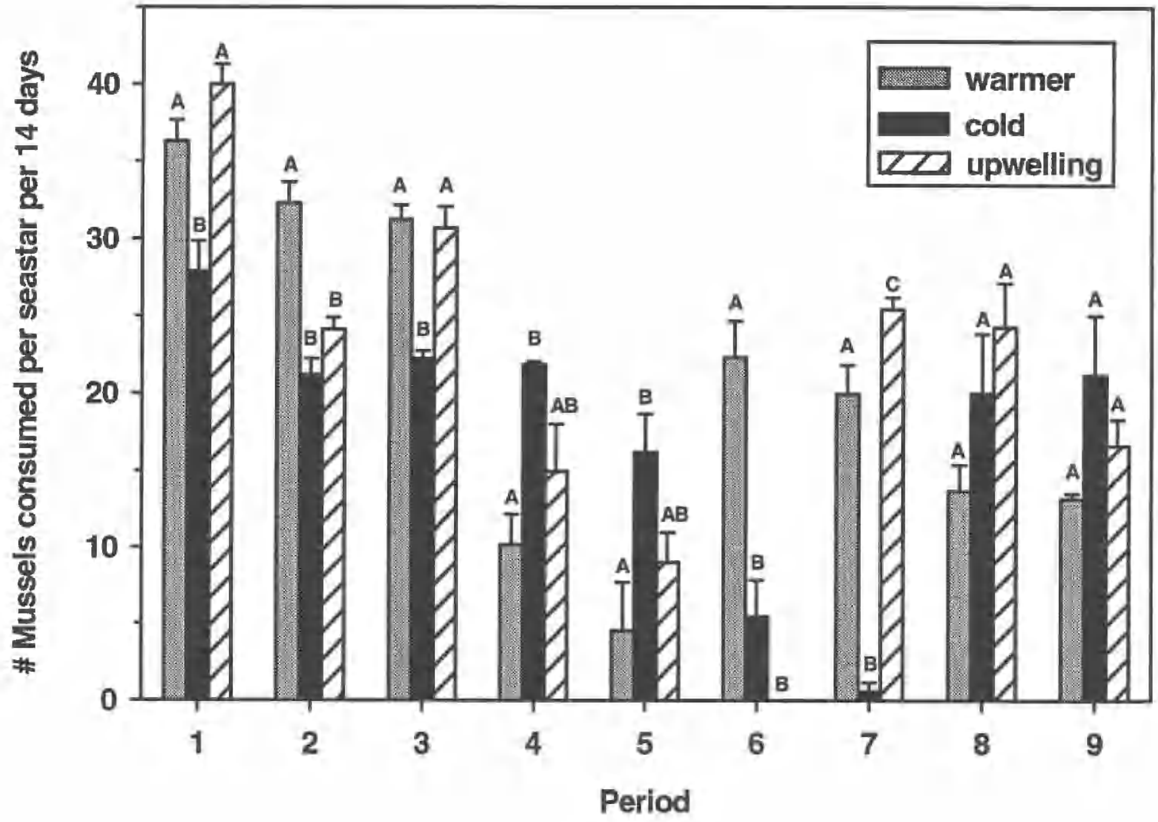


Figure 3.4 Rates of mussel consumption by *Pisaster ochraceus* in the three laboratory treatments. Bars are mean number of mussels consumed (+ SEM) per sea star per 14-day period (n = 3-4 tanks / treatment). Within each time period, shared letters above bars indicate groups whose means do not differ (Tukey-Kramer, $p > 0.05$). The "upwelling" treatment was held at 12°C during odd-numbered periods, and 9°C during even-numbered periods.

Table 3.1 Repeated measures analysis of variance of the effects of temperature treatment on the number of mussels consumed per *Pisaster* per 14 days. Data were analyzed for the first seven periods of the experiment. Data exhibited homogeneity of treatment differences variance (test for sphericity, p = 0.152). Univariate results are therefore presented with unadjusted probabilities, and multivariate results are provided for comparison. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	187.24	44.06	**0.0001**
Error	7	4.25		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	p-value	num df	den df	Wilks' λ	p-value
Time	6	907.47	69.20	**<0.0001**	6	2	0.0060	**0.0178**
Time x Treatment	12	236.94	18.07	**<0.0001**	12	4	0.0001	**0.0021**

Mussels used early in the experiment were slightly smaller than those collected later. As a result, the length of mussels consumed varied among time periods (ANOVA, $F_{8,1257} = 118.34$, $p < 0.001$); it was somewhat smaller during periods 1 and 2 than during periods 3-9 (mean length ± SEM = 31.4 ± 0.24 mm vs. 36.5 ± 0.09 mm, respectively). Since variation in mussel size could influence the number consumed, I also calculated feeding rates based on tissue weight consumed.

The pattern of consumption by tissue weight was similar and even more strongly cyclical (Fig. 3.5, Table 3.2, RM-ANOVA: Treatment, Time, and Time * Treatment are all significant, p< 0.001). In all treatments, feeding rates increased early in the experiment, then declined for about one month, and then increased sharply again. The timing of the temporary depression in feeding rates varied among treatments occurring first in the warmer tanks (periods 4 and 5), then in the upwelling tanks (periods 5 and 6), and finally in the cold tanks (periods 6 and 7).

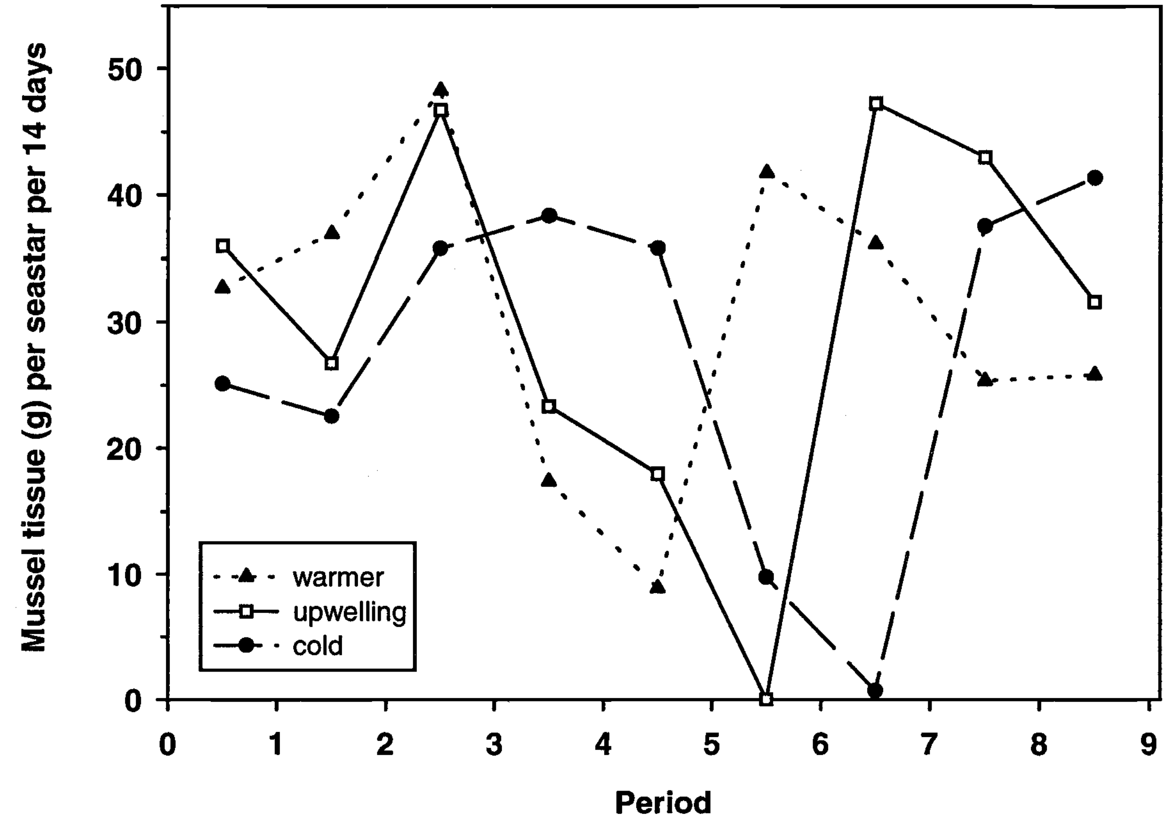


Figure 3.5 Rates of mussel tissue consumption by *Pisaster ochraceus* in the three laboratory treatments. Data points are mean estimated consumption of mussel tissue per sea star per 14-day period (n = 3-4 tanks / treatment). Error bars are similar in size to those in Fig. 3.4 and are omitted for clarity.

Table 3.2 Repeated measures analysis of variance of the effects of temperature treatment on the estimated amount of mussel tissue consumed per *Pisaster* per 14 days. Data were analyzed for the first seven periods of the experiment. Data did not exhibit homogeneity of treatment differences variance (test for sphericity, p = 0.012). Univariate results are therefore presented with Huynh-Feldt corrected probabilities (H-F p-value), and multivariate results are provided for comparison. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	331.98	14.34	**0.0034**
Error	7	23.15		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	H-F p-value	num df	den df	Wilks' λ	p-value
Time	6	669.69	15.72	**<0.0001**	6	2	0.0057	**0.0171**
Time x Treatment	12	815.13	19.13	**<0.0001**	12	4	0.0001	**0.0012**

At the conclusion of the experiment, there was significant variation among treatments in the total number of mussels consumed per individual (ANOVA, $F_{2,7}$ = 23.03, p < 0.001). Consumption did not differ significantly between the warmer and upwelling tanks (mean number consumed ± SEM = 181.4 ± 4.69 vs. 185.1 ± 1.15) but was about 15% lower in the cold tanks (mean number consumed ± SEM = 155.8 ± 4.12). There was suggestive but inconclusive evidence that 9°C sea stars consumed less mussel tissue than those in the other two treatments (Fig. 3.6A)(ANOVA, $F_{2,7}$=3.49, p = 0.089).

Although warmer and upwelling sea stars did not differ in the number of mussels or amount of tissue consumed, individuals in upwelling tanks grew significantly more than warmer sea stars over the course of the experiment (Fig. 3.6B)(ANOVA, $F_{2,7} = 6.71$, $p = 0.024$). Both upwelling and cold sea stars had a significantly greater "conversion efficiency" (i.e, the ratio of weight added to tissue consumed) than warmer sea stars (Fig. 3.6C)(ANOVA, $F_{2,7} = 10.33$, $p = 0.0082$). In addition, both upwelling and cold sea stars stored significantly more energy than warmer sea stars as indicated by the greater pyloric ceca index (Fig. 3.6D)(ANOVA, $F_{2,7} = 8.98$, $p = 0.012$). The index tends to obscure an even larger absolute difference between the pyloric ceca of upwelling vs. warmer sea stars. This occurs because the denominator of the index is eviscerated body weight, which was significantly larger for upwelling sea stars than warmer sea stars (ANOVA, $F_{2,7} = 5.13$, $p = 0.043$). Comparing the dry weight of the pyloric ceca (independent of sea star weight) indicates that the ceca of upwelling and cold sea stars were 25% larger than that of warmer sea stars (Fig. 3.6E)(ANOVA, $F_{2,7} = 11.84$, $p = 0.0057$). Thus, despite eating equivalent or greater amounts of food than upwelling and cold sea stars, individuals in constant 12°C tanks generally had lower growth rates, conversion efficiencies, and energy storage.

Figure 3.6 Summary of treatment effects at the conclusion of the 18 week *Pisaster* feeding experiment. All bars are mean (+SEM) values for 3-4 tank means / treatment. Each tank mean was based on measurements of the four sea stars. **(A)** Estimated total mussel tissue consumed per sea star, **(B)** Change in wet weight, **(C)** Ratio of change in wet weight to tissue consumed, **(D)** Ratio of pyloric ceca volume to eviscerated sea star wet weight, **(E)** Pyloric ceca dry weight. Horizontal lines above bars indicate groups whose means do not differ (Tukey-Kramer, $p > 0.05$).

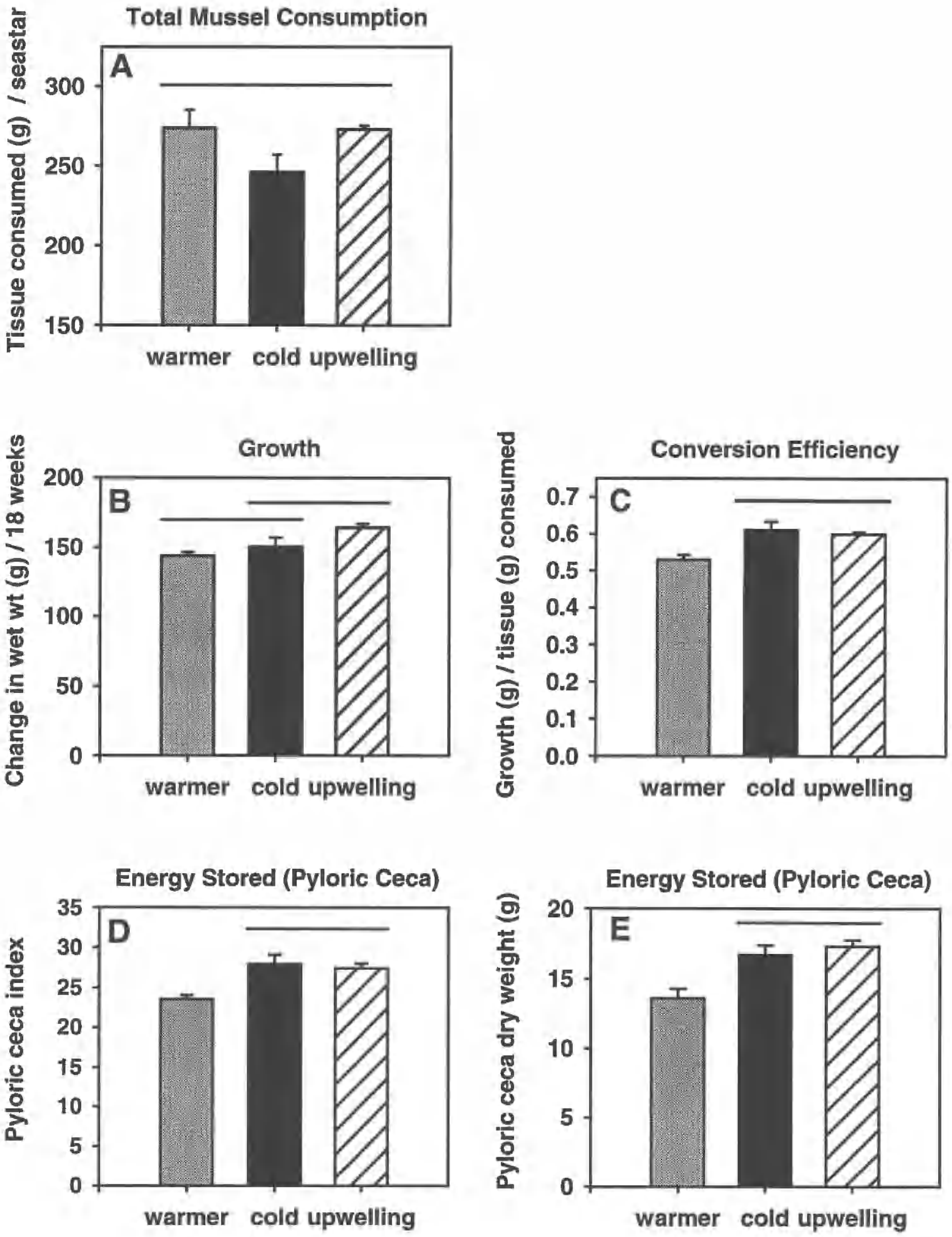

Total Mussel Consumption
A
Tissue consumed (g) / seastar
300
250
200
150
warmer
cold
upwelling
Growth
B
Change in wet wt (g) / 18 weeks
200
150
100
50
0
warmer
cold
upwelling
Conversion Efficiency
C
Growth (g) / tissue (g) consumed
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
warmer
cold
upwelling
Energy Stored (Pyloric Ceca)
D
Pyloric ceca index
35
30
25
20
15
10
5
0
warmer
cold
upwelling
Energy Stored (Pyloric Ceca)
E
Pyloric ceca dry weight (g)
20
15
10
5
0
warmer
cold
upwelling

Figure 3.6

Nucella Laboratory Experiment

Water temperatures during the *Nucella canaliculata* experiment were usually maintained within ± 0.1 °C of set treatment levels (Fig. 3.7). As in the *Pisaster* experiment, whelk feeding rates were extremely sensitive to small differences in water temperature (Fig. 3.8). Feeding rates varied significantly among treatments and time periods, and the effect of temperature on feeding rate changed with time (Table 3.3, RM-ANOVA: Treatment, Time, and Time * Treatment are all significant, $p< 0.005$). During the first four periods, whelks in 9 °C tanks consumed 27-43 % fewer mussels than those in 12 °C tanks. In both warmer and cold tanks, feeding rates increased steadily over the first four periods as whelks grew rapidly in size (Fig. 3.9). In the upwelling treatment, feeding rates increased in a step-like manner; they generally increased following the transition from 9 °C to 12°C phases, but remained consistent between consecutive 12°C and 9°C phases (Fig. 3.8). Later in the experiment, feeding rates in all three treatments leveled off or declined slightly. The mean length of mussels drilled varied among treatments during some periods, but these differences were small (< 2mm shell length) and were not consistent through time (Table 3.4, RM-ANOVA: Treatment and Time are non-significant, $p > 0.10$; Time * Treatment is significant, $p< 0.001$). The mean shell length (± SEM) of all drilled mussels was 28.36 ± 0.06mm ($n = 1190$).

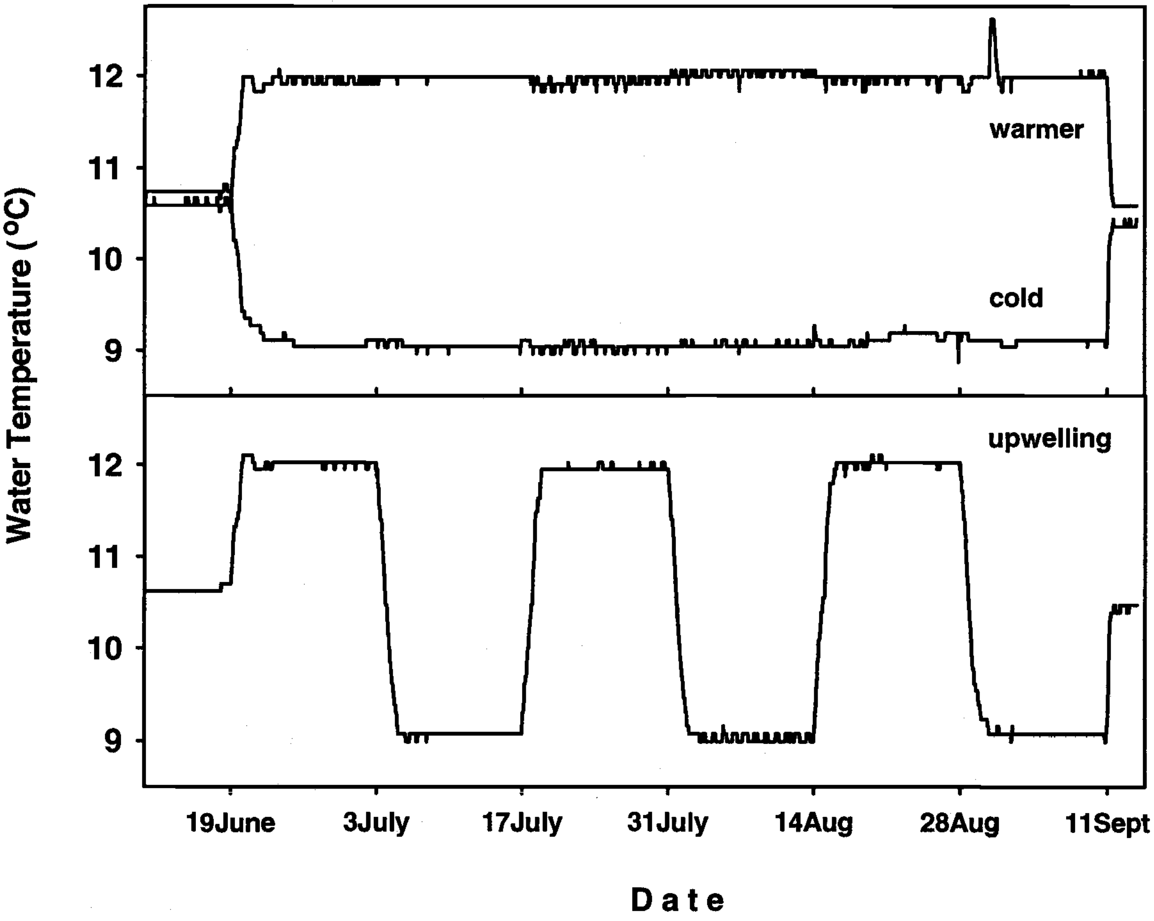


Figure 3.7 Water temperatures during the whelk feeding experiment. Whelks were held in three treatments: constant 12°C ("warmer"), constant 9°C ("cold"), and alternating 12°C/9°C ("upwelling"). Temperatures were recorded hourly by data-loggers submerged in the closed tanks. Dates on the abscissa indicate starting dates for the six consecutive 14-day periods.

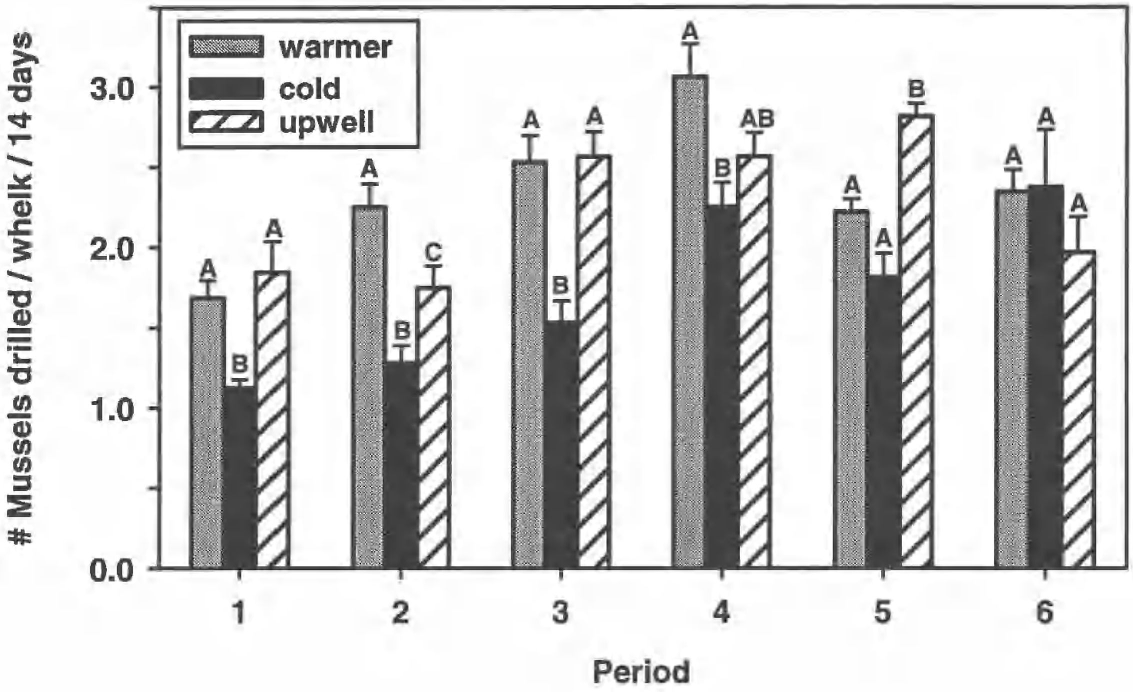


Figure 3.8 *Nucella canaliculata* feeding rates in the three laboratory treatments. Bars are mean number of mussels consumed (+ SEM) per whelk per 14-day period (n = 4 tanks / treatment). Within each time period, shared letters above bars indicate groups whose means do not differ (Tukey-Kramer, $p > 0.05$). The "upwelling" treatment was held at 12°C during odd-numbered periods, and 9°C during even-numbered periods.

Table 3.3 Repeated measures analysis of variance of the effects of temperature treatment on the number of mussels drilled per *Nucella* per 14 days. Data were analyzed for the six periods of the experiment. Data exhibited homogeneity of treatment differences variance (test for sphericity, $p = 0.221$). Univariate results are therefore presented with unadjusted probabilities, and multivariate results are provided for comparison. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	170.29	13.13	**0.0022**
Error	9	12.98		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	p-value	num df	den df	Wilks' λ	p-value
Time	5	115.49	19.95	**<0.0001**	5	5	0.0225	**0.0004**
Time x Treatment	10	27.06	4.67	**0.0001**	10	10	0.0637	**0.0508**

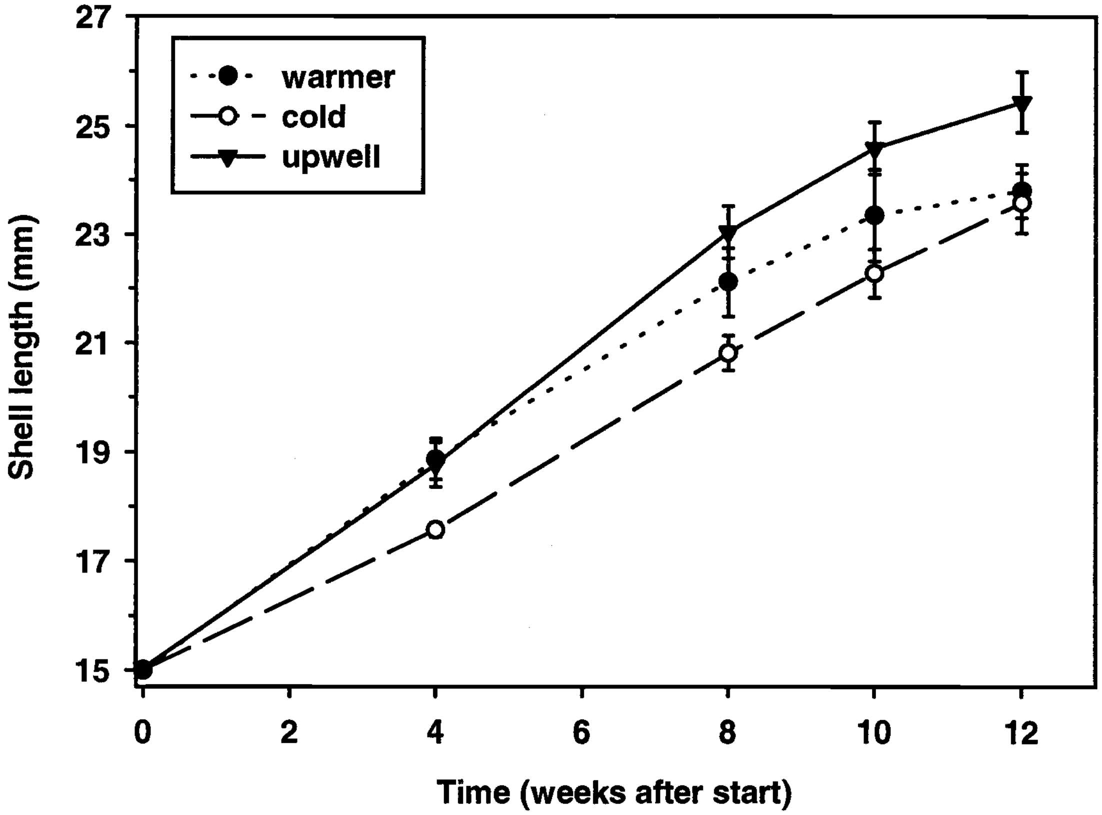


Figure 3.9 *Nucella canaliculata* growth rates in the three treatments. Data points are mean shell length (± SEM) per treatment (n = 4 tank means / treatment). Each tank mean was based on measurements of the 8 whelks in that tank. All whelks began at 15.0 ± 0.2mm.

Table 3.4 Repeated measures analysis of variance of the effects of temperature treatment on the mean size (shell length) of mussels drilled by *Nucella* during the six periods of the experiment. Data exhibited homogeneity of treatment differences variance (test for sphericity, $p = 0.376$). Univariate results are therefore presented with unadjusted probabilities, and multivariate results are provided for comparison. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

A. BETWEEN SUBJECTS

SOURCE	df	MS	F	P
Treatment	2	0.269	0.581	0.5792
Error	9	0.464		

B. WITHIN SUBJECTS

	Univariate Analysis				Multivariate Analysis			
SOURCE	df	MS	F	p-value	num df	den df	Wilks' λ	p-value
Time	5	0.343	1.71	0.1518	5	5	0.3450	0.2494
Time x Treatment	10	0.826	4.12	**0.0005**	10	10	0.0696	0.0605

At the conclusion of the experiment, whelks in 9 °C tanks had consumed significantly fewer mussels than whelks in warmer or upwelling tanks (Fig. 3.10A) (ANOVA, $F_{2,9} = 13.12$, $p = 0.002$). Trends in growth rates generally paralleled the results from the sea star experiment. There was suggestive evidence that whelks in the upwelling treatment added more new shell to the body whorl than did whelks in the warmer or cold treatments (Fig. 3.10B)(ANOVA, $F_{2,9} = 3.01$, $p = 0.099$). Of the ten whelks that added $\geq$ 40mm of new shell, eight were in upwelling tanks. There was also suggestive evidence that upwelling snails attained a larger final shell length than those in the other two treatments (Fig. 3.10C)(ANOVA, $F_{2,9} = 3.64$, $p = 0.069$).

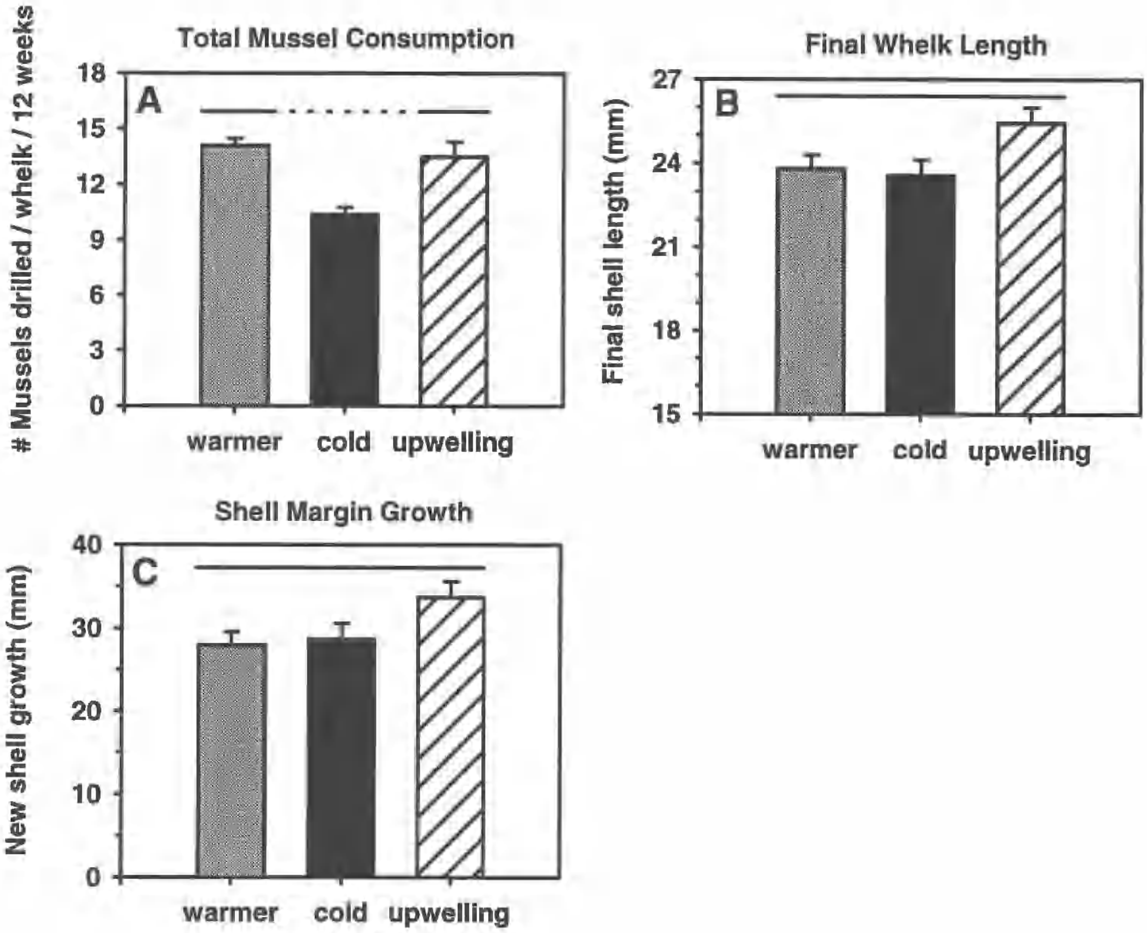


Figure 3.10 Summary of treatment effects at the conclusion of the 12 week *Nucella* experiment. All bars are mean (+SEM) values for 4 tank means / treatment. Each tank mean was based on measurements of the 8 whelks. **(A)** Total number of mussels drilled per whelk, **(B)** Final shell length, **(C)** New shell added to body whorl. Horizontal lines above bars indicate groups whose means do not differ significantly (Tukey-Kramer, $p > 0.05$).

Coastal Water Temperature, Prey Abundance, and Pisaster Condition

Variation in Water Temperature

There was strong seasonal variation in water temperature at Strawberry Hill. During the upwelling season (predominantly May through August on the central Oregon coast), water temperatures often fluctuated several degrees over short time scales (days to weeks)(Fig. 3.11). Water temperatures typically dropped to 9-10°C during periods of upwelling, and quickly rose to 12-13°C when winds relaxed. In contrast, during the remainder of the year (October through April) water temperatures seldom dropped below 10°C (except in 1998-99) and were remarkably stable over time, often fluctuating less than 1°C for several months (Fig. 3.12).

The years of my study encompassed considerable interannual variation in water temperature, largely because of the major El Niño-Southern Oscillation event of 1997-98. In particular, the frequency and intensity of upwelling was very low during the El Niño summer of 1997 (Fig. 3.11). In contrast, the summer of 1996 was characterized by frequent, very cold upwelling events. Water temperatures during the non-upwelling season (October through April) also varied strongly among years (Fig. 3.12). During the 1997-98 El Niño water temperatures remained around 12°C throughout the winter, whereas during winter 1998-99 water temperatures were consistently below 10°C, perhaps as a result of La Niña conditions in the North Pacific.

Figure 3.11 Spring-Summer water temperature at Strawberry Hill, OR, during 1995-1998. Data are High Tide Water Temperatures (the mean from two hours before to two hours after each high tide) recorded by intertidal data-loggers. Shaded region indicates temperatures ≤ 10°C. Data were smoothed using a running means function (see text for details).

Figure 3.12 October-April water temperature at Strawberry Hill, OR, during 1995-1999. Data are High Tide Water Temperatures (the mean from two hours before to two hours after each high tide) recorded by intertidal data-loggers. Shaded region indicates temperatures ≤ 10°C. Data were smoothed using a running means function (see text for details).

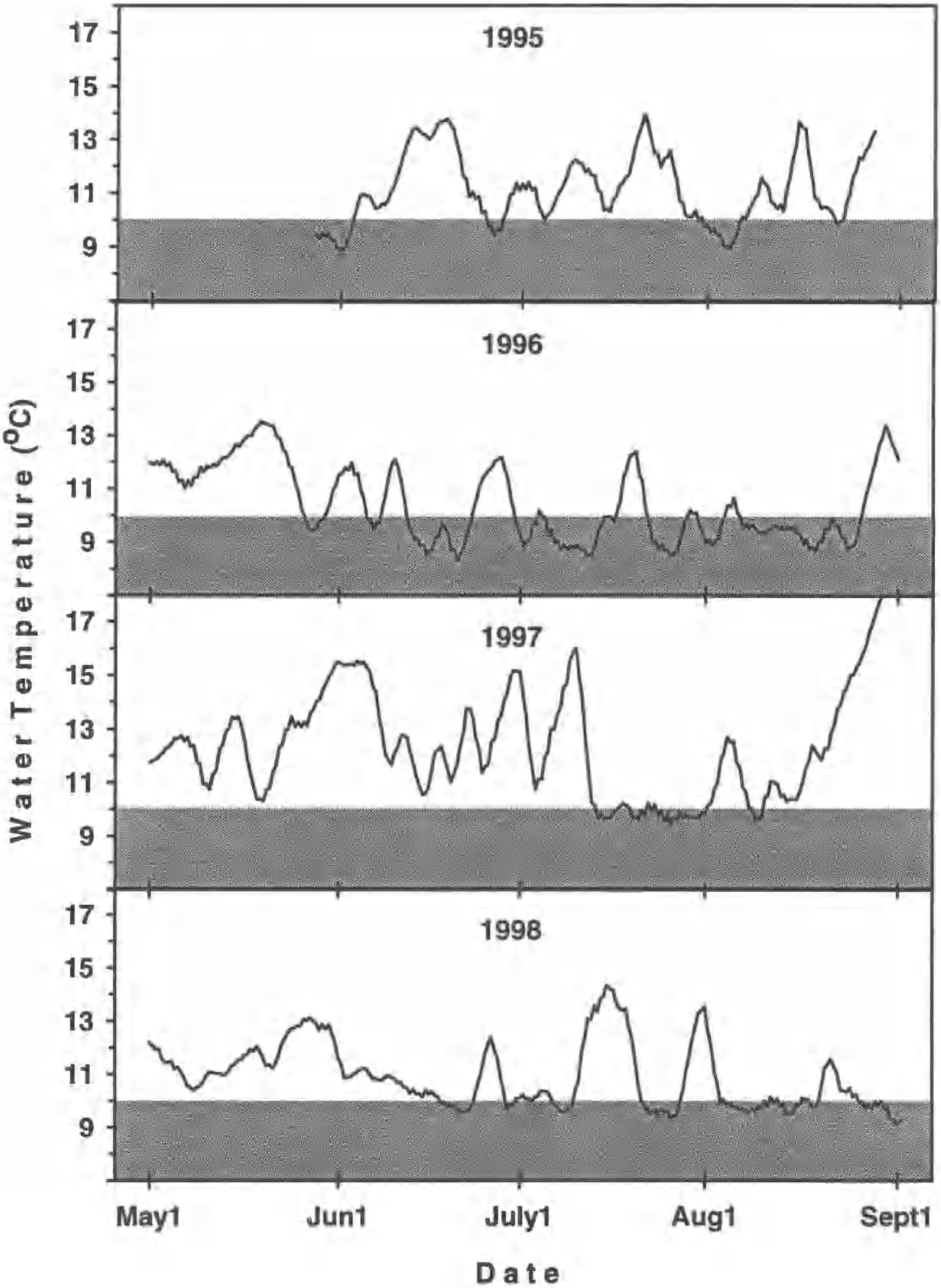

1995
1996
1997
1998
17
15
13
11
9
Water Temperature (°C)
May1
Jun1
July1
Aug1
Sept1
Date

Figure 3.11

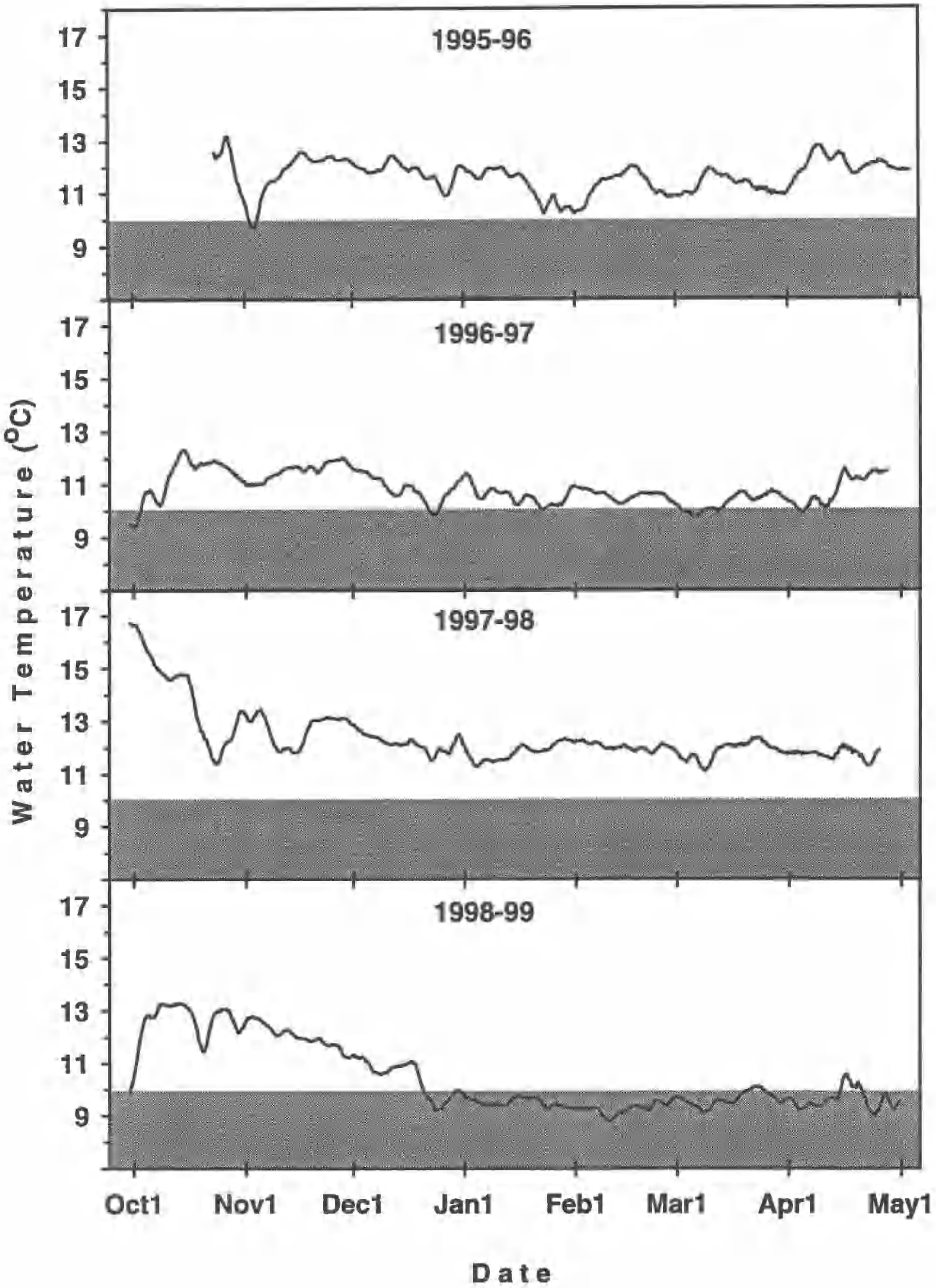

1995-96
1996-97
1997-98
1998-99
17
15
13
11
9
Water Temperature (°C)
Oct1
Nov1
Dec1
Jan1
Feb1
Mar1
Apr1
May1
Date

Figure 3.12

Variation in prey abundance and *Pisaster* diet

Sampling of feeding sea stars at Strawberry Hill and the Newport South Jetty confirmed the initial observations that *Pisaster* diet differed dramatically between these two sites (Fig. 3.13). At SH, prey were predominantly *Mytilus trossulus* and gooseneck barnacles (*Pollicipes polymerus*). At the South Jetty, most sea stars were eating sheets of densely packed acorn barnacles (*Balanus glandula* and *Chthamalus dalli*). Although 33% of sea stars feeding at the South Jetty were also feeding on *M. trossulus*, these mussels were generally recent recruits that had settled among acorn barnacles, and were significantly smaller than those consumed at SH (mean shell length ± SEM = 9.22 ± 0.4 vs. 22.40 ± 0.44 mm; t-test, $t_{333} = -20.27$, one-sided $p < 0.001$). Thus, at the South Jetty mussels probably made only a small contribution to *Pisaster*'s total caloric intake. Interestingly, the pyloric ceca from SH sea stars were consistently much darker in color than those from the South Jetty, perhaps reflecting the higher proportion of mussels vs. barnacles in the diet of these sea stars.

At Strawberry Hill, prey cover changed dramatically during the four years of this study (Fig. 3.14, Table 3.5). In 1995, I did not sample prey cover using the transect-quadrat method. However, photographs of large plots (Chapter 4) and personal observations indicated that there was a high density of *Mytilus trossulus* in the low intertidal zone during Spring 1995. During the following years (1996-98) there was a trend of decreasing cover of *M. trossulus*, increasing cover of *Pollicipes polymerus*, and declining bare space (Fig. 3.14, Table 3.5). The increase in gooseneck barnacle abundance in Spring 1998 followed a massive recruitment event during winter 1997-98

(E. Sanford, *personal observation*). Cover of other sessile invertebrates and macroalgal species changed little over the course of this study (Fig. 3.14).

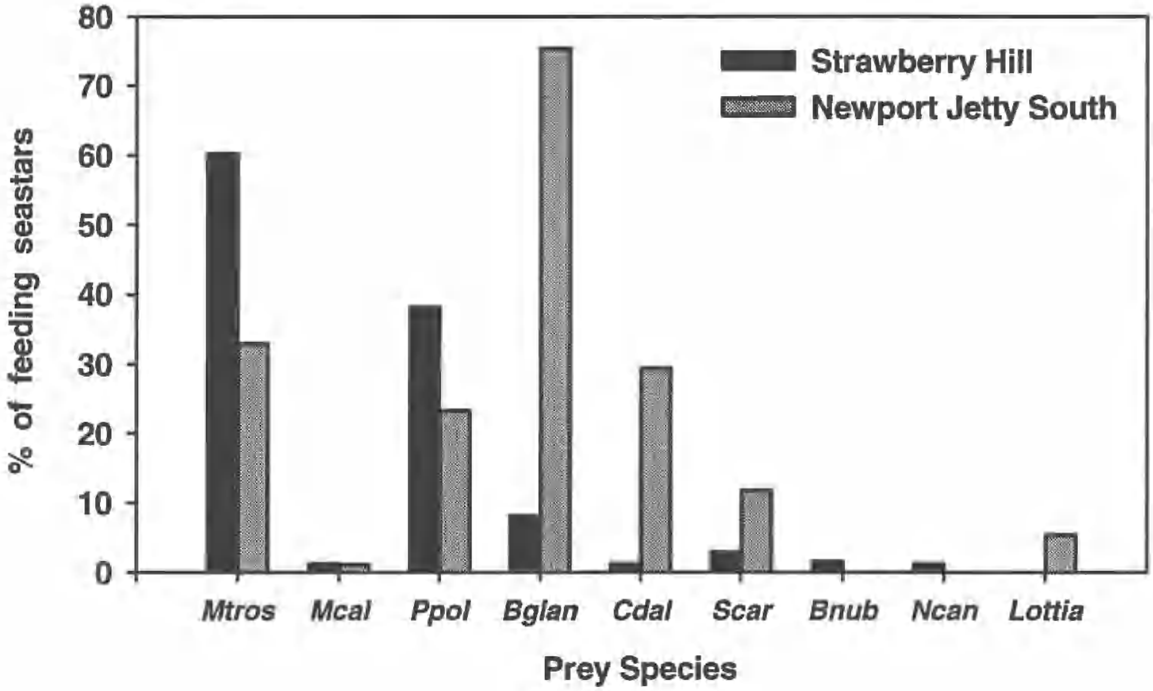


Figure 3.13 Diet of *Pisaster ochraceus* at Strawberry Hill and the Newport South Jetty during Summer 1995 and 1996. The % of feeding sea stars is the percent of actively feeding individuals observed feeding on prey species coded as follows: M.tros = *Mytilus trossulus*; M.cal = *M. californianus*; P.pol = *Pollicipes polymerus*; B.glan = *Balanus glandula*; C.dal = *Chthamalus dalli*; S.car = *Semibalanus cariosus*; B.nub = *Balanus nubilus*; N.can = *Nucella canaliculata*; Lottia = *Lottia* spp. Diets are based on 349 feeding sea stars at SH, and 392 feeding sea stars at NJS. The cumulative % at each site exceeds 100% because *Pisaster* often feeds on more than one prey species at a time.

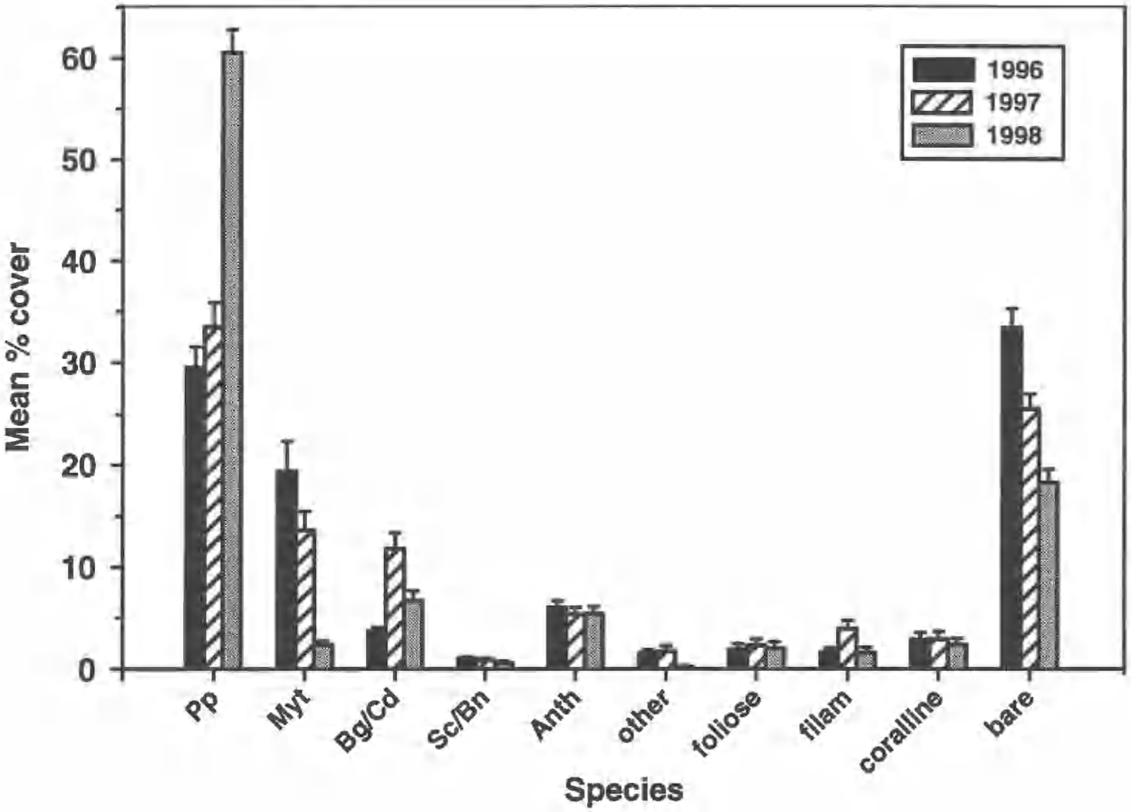


Figure 3.14 Changes in the cover of prey species and other space-holders at Strawberry Hill, Spring 1996-1998. Quadrats positioned along low intertidal transects were photographed on 5 May 1996 (n = 64), 6 May 1996 (n = 62), and 27 April 1998 (n = 61). Bars are estimated mean percent cover (+SEM) of invertebrate and macroalgal groups coded as follows: Pp = *Pollicipes polymerus*; Myt = *Mytilus trossulus* and *M. californianus*; Bg/Cd = *Balanus glandula* and *Chthamalus dalli*; Sc/Bn = *Semibalanus cariosus* and *Balanus nubilus*; Anth = *Anothopleura xanthogrammica and A. elegantissima*; other = other sessile invertebrates including *Eudistylia vancouveri* and colonial hydroids; foliose = foliose red algae including *Dilsea* and *Mazzaella* spp.; filam = fleshy filamentous red algae; coralline = erect coralline and coralline crusts; bare = bare rock.

Table 3.5 Variation in prey cover among years at Strawberry Hill. **(A)** Multivariate analysis of variance of the effect of year on the percent cover of prey types and bare space within the *Pisaster* collection area at Strawberry Hill, Spring 1996, 1997, and 1998. **(B)** Univariate F-tests of whether the cover of individual prey types and bare space varied among years. Bold face p-values indicate that the factor is significant with a Bonferroni adjusted $\alpha = 0.0083$. Analyses were conducted on arcsine-square root transformed data. df: degrees of freedom; MS: mean squares..

A. MULTIVARIATE ANALYSIS

SOURCE	Wilks' λ	num df	den df	F	p-value
YEAR	0.353	12	358	20.35	**<0.0001**

B. UNIVARIATE F TESTS

SOURCE	num df	den df	MS	F	p-value
Pollicipes	2	184	2.15	54.11	**<0.0001**
Mytilus spp.	2	184	1.07	20.80	**<0.0001**
Balanus glandula/ Chthamalus dalli	2	184	0.27	12.94	**<0.0001**
Semibalanus cariosus/ Balanus nubilis	2	184	0.02	3.58	0.0299
Other sessile inverts	2	184	0.06	7.09	**0.0011**
Bare rock	2	184	0.48	22.55	**<0.0001**

Pyloric Ceca and Gonad Cycles

At both sites, changes in pyloric ceca and gonad size were cyclical and inversely related (Fig. 3.15). The pyloric ceca index generally peaked in autumn, and then shrank in size over winter as gonads were produced. The gonad index peaked in early May and most individuals spawned during May or early June. Of the sea stars sampled, 96% had spawned by 10 June 1996, and roughly 75% had spawned by 10 June 1997 and 10 June 1998. Small numbers of sea stars (2-30) were observed spawning in the field at Strawberry Hill or Bob Creek Wayside on 17 May 1995, 4 May 1996, and 1 June 1996.

To my knowledge, these are the first data to document the timing of *Pisaster* spawning on the Oregon coast. During a five year span in central California, *Pisaster* spawned mostly in April and May (Feder 1956, Farmanfarmaian et al. 1958, Greenfield 1959). In a four year study in the San Juan Islands, WA, *Pisaster* typically spawned during mid-June (Mauzey 1966, 1967). Therefore, these results are consistent with spawning occurring progressively later at higher latitudes, a pattern that has been documented in a variety of marine invertebrates (Strathmann 1987). In 1998, *Pisaster* had already spawned by 11 July in Sitka Sound, Alaska (n = 8 sea stars at each of two sites)(E. Sanford, *unpublished data*).

Since energy stored in the pyloric ceca is thought to be converted into the production of gonads (Mauzey 1966, Lawrence & Lane 1982), interannual variation in the fall pyloric ceca was predicted to produce corresponding variation in the gonad index during the following spring. Similarly, variation between sites in the amount of energy stored in the pyloric ceca was expected to translate into between-site variation in gonad production.

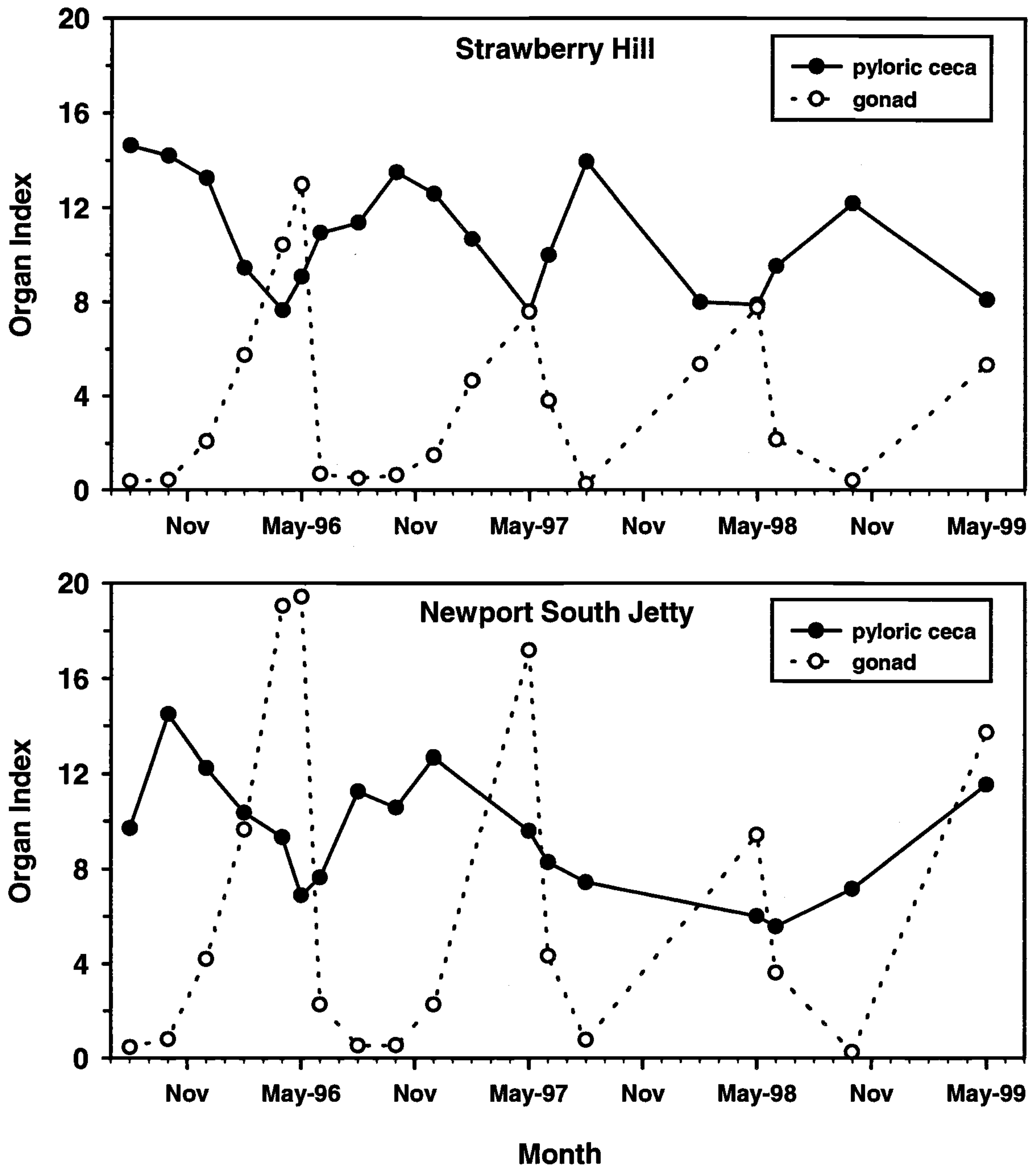


Figure 3.15 Cycles in pyloric ceca and gonad indices of *Pisaster ochraceus* at Strawberry Hill and the Newport South Jetty, August 1995 - May 1999. Organ indices are defined as the volume of the organ divided by the eviscerated wet weight of the individual. Each point is the mean of 12 sea stars collected at each site. Error bars are shown in Fig 3.16, and are omitted here for clarity.

The peak size of the pyloric ceca was dependent upon a combination of both site and year (Fig. 3.16A)(Two-Way ANOVA: “year” $F_{3,94} = 11.61$, $p < 0.001$; “site” $F_{1,94} = 21.91$, $p < 0.001$; “site*year” $F_{3,94} = 5.59$, $p = 0.0014$). In both 1997 and 1998, the pyloric ceca index reached a larger value at SH than at the South Jetty (Fig. 3.16A). Peak pyloric ceca values did not vary significantly among different years at SH (Tukey-Kramer, $p > 0.05$), but at the South Jetty, peak values were higher in 1995 and 1996 than in 1997 and 1998 (Tukey-Kramer, $p < 0.05$).

Gonad production also varied significantly among years and between sites (Fig. 3.16B)(Two-Way ANOVA: “year” $F_{3,86} = 7.93$, $p < 0.001$; “site” $F_{1,86} = 28.62$, $p < 0.001$; “site*year” $F_{3,86} = 2.08$, $p = 0.11$). In contrast to some earlier studies (see Lawrence & Lane 1982), there was no evidence that the size of the gonads varied between the sexes (Three-Way ANOVA, neither “sex” nor the interactions “site*sex”, “year*sex”, “site*year*sex” were significant, $p > 0.15$). There was suggestive but inconclusive evidence that gonad production was related to the peak size of the pyloric ceca [Fig. 3.17, $p = 0.11$ (SH), $p = 0.10$ (NJS)]. As predicted, when fall pyloric ceca values were high, gonad production during the following spring also tended to be high. Surprisingly, despite having equal or smaller pyloric ceca than SH sea stars (Fig. 3.16A), individuals at the South Jetty had about twice the gonad production in all years except 1998 (Fig. 3.16B). Thus, it appeared that South Jetty sea stars had higher gonad production for any given level of energy stored in the pyloric ceca (Fig. 3.17).

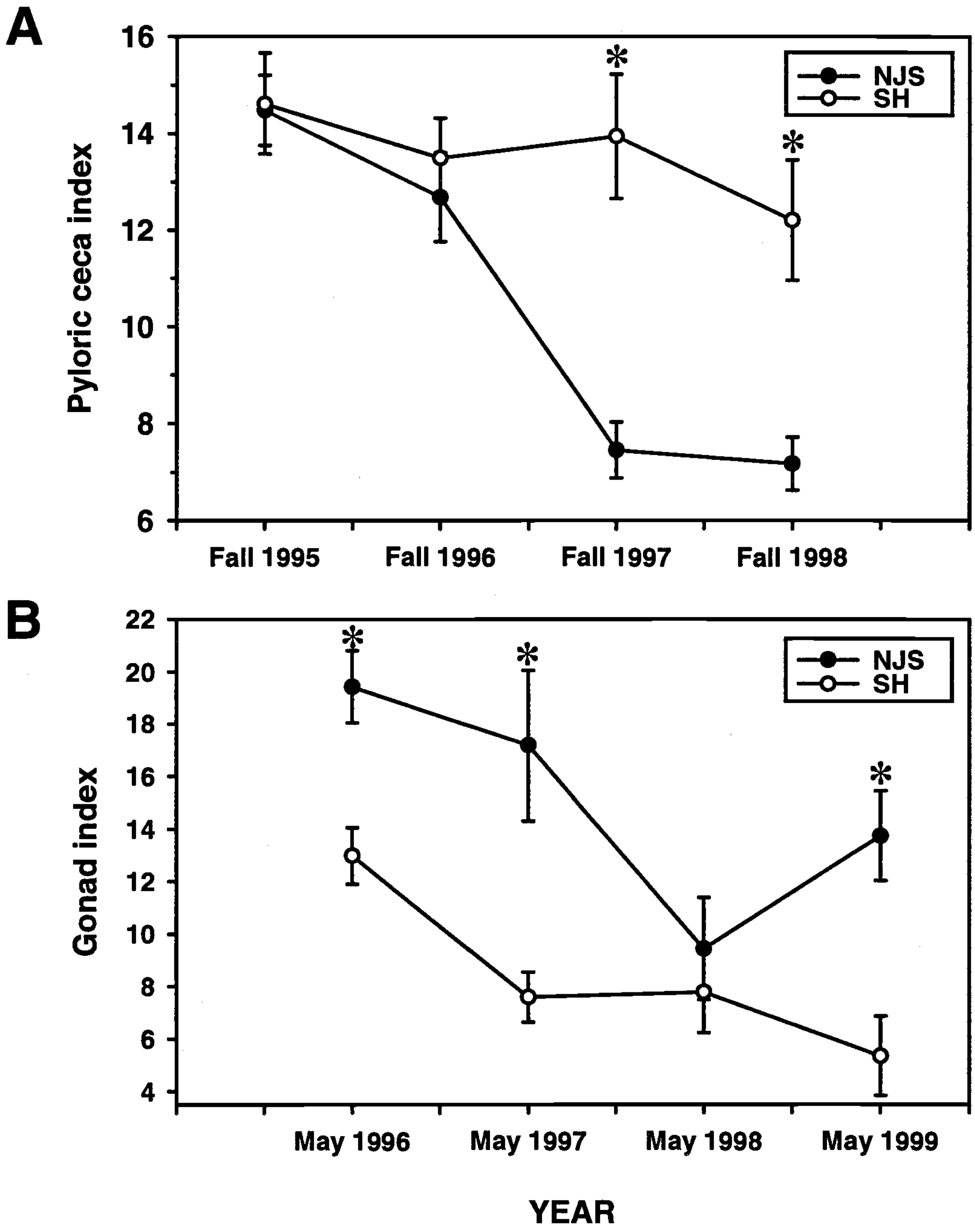


Figure 3.16 Variation in *Pisaster* condition between the Newport South Jetty (NJS) and Strawberry Hill (SH). Data are means (±SEM) for 12 sea stars per site; "*" indicates a significant difference between sites (Tukey-Kramer, $p < 0.05$). (**A**) Peak pyloric ceca index recorded during each year (month varies). (**B**) Peak gonad index recorded in May of each year.

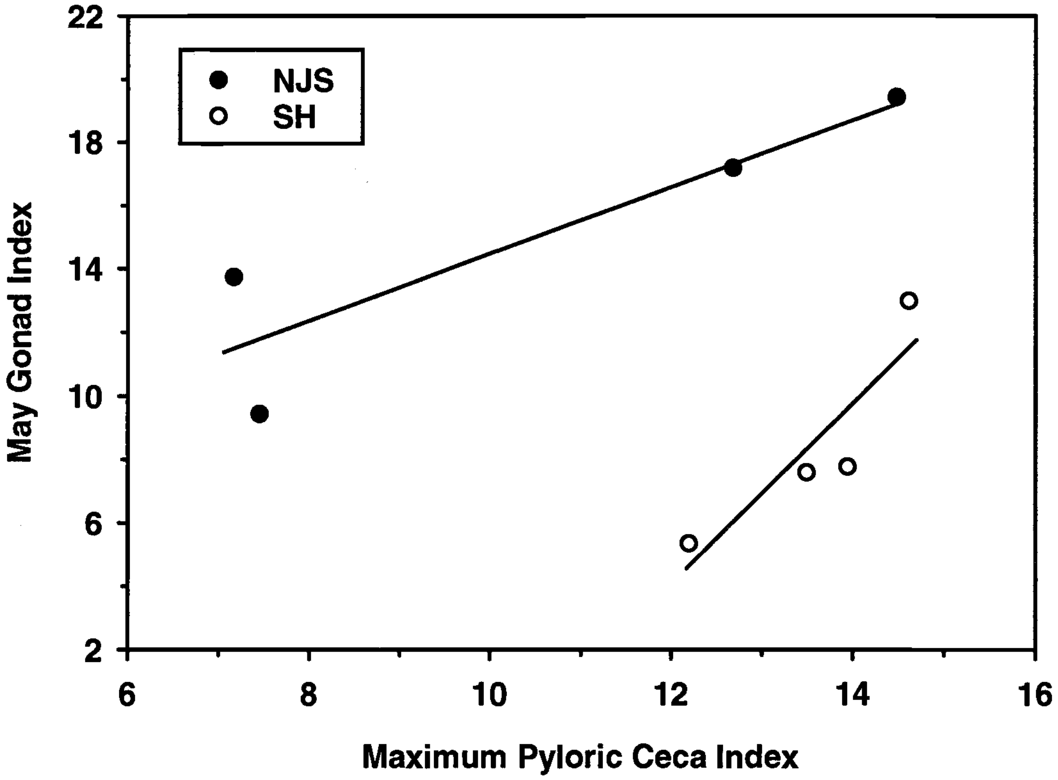


Figure 3.17 Relationship between energy stored in the pyloric ceca during the fall and gonad production during the following spring. Each point represents one year at Strawberry Hill (SH, open circles) and Newport Jetty South (NJS, closed circles). Separate regressions lines are plotted for SH ($p = 0.11$, $R^2 = 0.79$) and NJS ($p = 0.10$, $R^2 = 0.81$) .

DISCUSSION

Effect of Water Temperature on Feeding Rates

In the laboratory, small changes in water temperature had large effects on the feeding rates of sea stars and whelks. Very few studies have examined sea star feeding rates under controlled temperatures in the laboratory (see Mackenzie 1969 for an exception). Previous authors have suggested that water temperature may influence rates of sea star predation (Feder & Christensen 1966), but the supporting evidence has been largely anecdotal field observations of seasonal decreases in feeding (reviewed by Sloan 1980, Table VI). A number of factors other than water temperature could drive seasonal shifts in predation intensity. For example, reduced winter feeding may result from increased wave forces, freezing temperatures during aerial exposure, reduced prey abundance, or the occurrence of a pre-spawning quiescent phase (Mauzey 1966). This study demonstrates a causative link between water temperature and *Pisaster* feeding rates. Early in the experiment, sea stars that were either held continuously at 9°C, or exposed to 9°C for two weeks, consumed on average 29% fewer mussels than individuals in 12°C tanks (Fig. 3.4).

Small temperature differences also had strong effects on rates of whelk predation. After the first four periods of the experiment, whelks in 9°C tanks had drilled 35% fewer mussels than those in 12°C tanks (Fig. 3.8). These results are consistent with other laboratory studies that have tested the effects of temperature on the feeding rate of Atlantic species of muricid gastropods including *Nucella lapillus* (Largen 1967, Stickle et al. 1985), *Thais haemastoma* (Garton & Stickle 1980), and *Urosalpinx cinerea* (Hanks

1957). When the results of these studies are standardized to changes per 3°C, feeding rates are typically reduced by 26-44% for 3°C declines within these organisms' normal thermal ranges.

These laboratory results suggest that spatial and temporal variation in patterns of upwelling may play a previously unrecognized role in regulating the strength of predation in intertidal communities (Sanford 1999). In Oregon, the upwelling season coincides with the months when *Pisaster* and *Nucella canaliculata* attain the highest intertidal densities and most strongly affect prey abundance. Therefore, variation in the frequency and intensity of cold-water intrusions may modify the impact of predators in these communities. This potential link between upwelling and community dynamics is explored in detail in the next chapter.

Patterns of Consumption and Growth: ***Pisaster ochraceus***

In the *Pisaster* experiment, the effect of temperature on feeding rate became less clear as the study progressed (Figs. 3.4, 3.5). It appeared that sea stars became temporarily satiated on the *ad libitum* diet, and that this point was reached more quickly in the warmer tanks where sea stars had consumed more mussels. Once satiated, sea stars fed little for about one month.

Several lines of evidence suggest that satiation is unlikely to occur in the field. Sea stars added weight rapidly in the laboratory; many individuals doubled their weight in 8 weeks and had very thick arms suggesting rapid expansion of the pyloric ceca. A similar rate of growth has been reported for *Pisaster* in another laboratory study where mussels were supplied *ad libitum* (Feder 1970). In contrast, growth rates in the field appear much slower. In Central California, marked *Pisaster* that began at 100-200g wet weight generally added <50g over the course of an entire year (Feder 1970). When I terminated the laboratory experiment in October, sea stars in all treatments had very large pyloric ceca (Fig. 3.6D, mean index in the three treatments ranged from 23.6 to 28.0). By comparison, field sea stars sampled during that month had pyloric ceca that were 40-60% smaller in size (Fig. 3.15, mean index = 10.6 and 13.5 for the South Jetty and SH, respectively).

The rapid growth and large pyloric ceca of laboratory sea stars suggests that they had a much greater feeding rate than is typical of field sea stars. Feeding rates may be reduced in the field because of wave forces, greater time spent locating prey, and periods of low tide emersion during which sea stars are unable to forage. Since *Pisaster* are often found in dense aggregations around mussel patches, intraspecific interactions may also slow access to prey in the field (Palumbi & Freed 1988). The energetic costs of foraging are also probably greater in the field because sea stars often move over much greater distances than they did in laboratory tanks (Johnson 1976, Robles et al. 1995). Finally, the *M. trossulus* available to sea stars at SH were generally smaller than those consumed in the laboratory experiment (mean shell length ± SEM = 22.4 ± 0.44mm vs. 35.4 ± 0.11mm). These smaller mussels may have provided lower caloric input per unit of feeding time.

Thus, under normal field conditions, sea stars may never reach the point of satiation. If this is true, then the early part of the experiment (with sea stars recently collected from the field) best reflects the effects of temperature on *Pisaster* with natural levels of energy reserves. These results indicate that sea stars in fluctuating water temperatures may continually alternate between higher and lower feeding rates, as was seen in the upwelling treatment during the first three periods (Fig. 3.4). Based on the limited data from these periods, there was no evidence that upwelling sea stars compensated for reduced feeding in cold phases (e.g., period 2) by eating *more* than constant 12°C sea stars during the following warm phase (e.g., period 3).

There are at least two reasons why such compensation may not occur. First, if sea stars at 12°C were feeding at a maximum rate, then increased feeding after a cold phase may not have been possible. Alternatively, if sea stars have lower metabolic rates at 9°C than at 12°C, then reduced feeding during cold phases may not have produced an energetic deficit. Metabolic rate is expected to decline with temperature (Newell & Branch 1980, Cossins & Bowler 1987) and unpublished data suggest that this is the case for *Pisaster* (Paine, personal communication in Mauzey 1966). Thus, net energy gain may have been similar in 9°C and 12°C tanks because decreased consumption in cold tanks was balanced by decreased metabolic costs.

My results generally support this hypothesis. At the conclusion of the experiment, both cold and upwelling sea stars had significantly higher conversion efficiencies than warmer sea stars (Fig. 3.6C). This results suggests that sea stars benefited from cold water phases (or continuous cold water) which presumably reduced their metabolic costs and allowed greater growth per unit of tissue consumed.

Patterns of Consumption and Growth: Nucella canaliculata

The results from the whelk experiment were similar to those from the sea star experiment. Whelks grew rapidly in size in all treatments (Fig. 3.9), and appeared to grow at faster rates than did whelks in the field. Navarrete and Menge (1996) measured the shell length of *N. canaliculata* within marked plots at Strawberry Hill. Based on changes in size frequency distributions, it appears that most whelks grew only about 3-4 mm in length between 7 June 1993 and 23 September 1993 (Navarrete & Menge 1996). In contrast, whelks grew 9-11mm over a similar period in this laboratory experiment (Fig. 3.9).

As whelks grew in the lab, feeding rates also increased (Fig. 3.8), presumably because larger snails were able to drill and consume prey more quickly. After the first month, whelks in warmer and upwelling tanks were significantly larger than those in constant 9°C tanks (Fig. 3.9). Thus, the initial difference between warmer and cold tanks increased during periods two and three (Fig. 3.8), because the size advantage of warmer snails was super-imposed on the temperature effect.

Interestingly, after 8 weeks the growth rate of warmer snails slowed (Fig. 3.9). At the conclusion of the experiment, whelks in 9°C tanks had consumed 26% fewer mussels, yet had reached the same size and added as much new shell as whelks in constant 12°C tanks (Fig. 3.10). Thus, cold whelks consumed fewer mussels, but this decrease in intake was presumably balanced by a decrease in metabolic costs, leading to similar growth rates in the two treatments.

An Energetic Hypothesis: Advantage of Upwelling Conditions

The results of both the sea star and whelk lab experiments suggest that there may be an energetic advantage to living in the fluctuating temperature regime characteristic of upwelling sites. This hypothesis is illustrated by a graphical model based upon energy budgets (Fig. 3.18, modified from Levinton 1983). In this model, energy available for

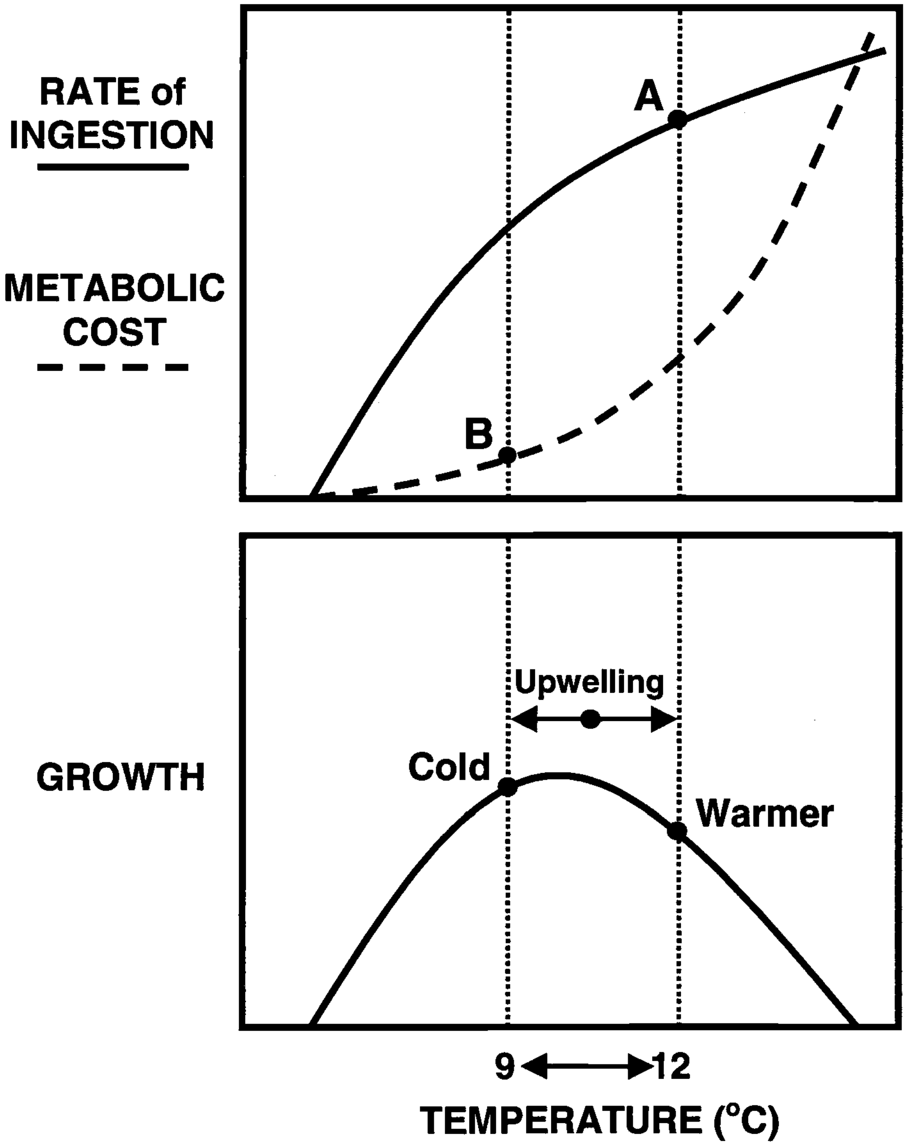


Figure 3.18 A graphical model relating growth to temperature-dependent rates of consumption and metabolism (modified from Levinton 1983). Growth (lower panel) is the difference between the curves for ingestion (solid line, top panel) and metabolic costs (dashed line, top panel). In the case shown, animals held at a constant 9°C (cold) have a similar rate of growth as those held at a constant 12°C (warmer). Animals in a fluctuating environment may benefit energetically by having high feeding rates (point A) followed by low metabolic costs (point B), producing a greater rate of growth as indicated by the position of the upwelling point in the lower panel.

growth and reproduction is a function of net energy absorbed from food minus metabolic costs (Newell & Branch 1980). Rates of ingestion typically accelerate with temperature as warmer conditions facilitate faster capture and handling of prey. Prey capture and processing are ultimately limited by functional constraints, causing the rate of ingestion to reach an asymptote at higher temperatures. On the other hand, oxygen consumption is typically an exponential function of temperature (Cossins & Bowler 1987). Energy reserves available are simply the difference between the curves for rate of ingestion and metabolic cost (Fig. 3.18). In the sea star experiment, all reserves were diverted to either growth or storage in the pyloric ceca, since gonad production had just begun when the experiment was terminated. Similarly, no egg capsules were produced during the whelk experiment, so surplus energy was presumably converted into shell and tissue growth or stored reserves.

The predictions of this model are dependent on the temperature at which optimal growth occurs. This value can be estimated from energy budgets (e.g., Vernberg 1981, Stickle & Bayne 1987), but unfortunately the physiological data required for such an analysis are not available for these species. However, if we assume that optimal growth occurs at <12°C, then predators in the cold treatment are predicted to have similar or slightly greater growth and energy storage relative to those in warmer tanks (Fig. 3.18) because reduced consumption is offset by reduced metabolic costs. This pattern was observed in both the sea star and whelk studies (Figs. 3.6, 3.10).

On the other hand, consumers experiencing fluctuating water temperatures should have the greatest rate of growth because they have a high rate of ingestion during warmer phases (Fig. 3.18, point A), but enjoy reduced metabolic costs during cold phases (Fig. 3.18, point B). The results of the *Pisaster* experiment are consistent with this prediction.

Despite equivalent intake, upwelling sea stars had a significantly greater conversion efficiency, growth, and pyloric ceca index than warmer sea stars (Fig. 3.6). Similarly, whelks in the fluctuating temperature treatment consumed the same number of mussels as those in the warmer tanks, but tended to grow larger than whelks held at either of the two constant temperatures (Fig. 3.10).

The energetic advantages of an upwelling regime may be analagous to those that select for diel vertical migration in many fish and zooplankton. It is hypothesized that these animals benefit from feeding in warmer surface waters where uptake of food is more efficient, and resting and digesting in deeper, cooler waters where energy can be more efficiently directed to growth (McLaren 1963, Brett 1971, Clark & Green 1991). In a laboratory experiment, Biette and Geen (1980) demonstrated that at all but the lowest and highest food rations, young Sockeye salmon grew at a faster rate under a daily temperature regime that was cyclic rather than constant 6 °C, 11°C, or 15 °C.

In order for a similar benefit to occur in upwelling regions, where the period of temperature fluctuations are longer (i.e., days to weeks, rather than daily), organisms would need the capacity to store energy from periods of intensive feeding so that it later could be converted into somatic growth. In *Pisaster*, the pyloric ceca store nutrient reserves in the form of lipids, proteins, and glycogen that are presumably translated into gonad development and growth (Greenfield et al. 1958, Mauzey 1966, Lawrence & Lane 1982). Gastropods also possess large, glandular digestive ceca which could serve a similar purpose (Brusca & Brusca 1990). Thus, it is possible that under a fluctuating temperature regime sea stars and whelks feed intensely during warmer phases and transfer stored energy into somatic growth during colder phases when activity and metabolic costs are reduced.

For *Pisaster*, the advantage of this strategy may be even greater under natural field conditions than in the laboratory. Sea stars in cold tanks required little movement to contact prey. However, in the field, foraging *Pisaster* can migrate >10m during a single high tide (Robles et al. 1995). It may be that the rate of movement is so slowed during cold water events, that foraging becomes inefficient. Field observations suggest that during upwelling events sea stars generally remain inactive in low zone surge channels or the shallow subtidal (Chapter 4). During these periods, I often observed clusters of individuals whose position remained unchanged on many consecutive days. Individuals that were removed from the rock showed little activity, and movement of tube feet was noticeably slower than during periods of warmer water.

The short-term duration of most upwelling events (days to weeks, Fig. 3.11) may preclude acclimatory responses to colder water, such as occur seasonally in some invertebrates and fish (Hazel & Prosser 1974, Clarke 1987). Under these circumstances, inactivity during upwelling may be advantageous, and the results of my laboratory experiments suggest that these conditions may confer an energetic bonus to consumers.

Reproductive Output: Linking Climatic Variation and Population Change?

Laboratory Studies

The laboratory results demonstrate significant effects of subtle temperature changes on patterns of growth and energy storage, and thus suggests a mechanism through which environmental change might influence the abundance of these consumers. This study focused on the season when *Pisaster* and *N. canaliculata* accumulate surplus resources for reproduction. Although not directly assessed, variation in fecundity can be inferred from the results of these experiments and previous studies relating body size and energy storage to reproductive output.

In the *Nucella* experiment, whelks in the upwelling treatment tended to reach a larger final shell length than those in the warmer tanks (Fig. 3.10B, mean shell length ± SEM = 25.44 ± 0.56mm vs. 23.80 ± 0.49mm). Thus, snails held in the fluctuating temperature treatment were about 1.6mm larger than those in the constant 12°C tanks. This may appear to be a small difference. However, a careful study of *Nucella* spp. in the San Juan Islands, WA, demonstrated that reproductive output was directly proportional to shell length (Spight 1976); larger snails laid a greater number of larger capsules containing more embryos per capsule. For *Nucella emarginata*, a difference of just 2mm (25 vs. 23mm) translated into production of over twice as many embryos. Limited observations suggested that a similar pattern held for *N. canaliculata* (Spight 1976). Thus, if seasonal upwelling is suppressed by warm water conditions, embryo production should decline because of the effects on adult snail growth. Reduced upwelling typifies El Niño events and may also accompany global warming or interdecadal regime shifts in the North Pacific (Bakun 1990, Peterson et al. 1993, Roemmich & McGowan 1995)

Whether declines in embryo production would translate directly into reduced population abundance is uncertain. A study of *Nucella lamellosa* in the San Juan Islands found that over 40% of the capsules failed to produce live embryos (Spight 1977). Mortality was attributed to both predation and physical stress. Furthermore, only 1-10% of the hatchlings survived their first year on the shore. Most importantly, the size of the yearling population was not correlated with embryo production at this site; the largest and smallest yearling classes were produced by a similar number of hatchlings. Additional studies are needed to determine if this result holds true for other *Nucella* species and other sites.

In the *Pisaster* experiment, both upwelling and cold sea stars had significantly larger pyloric ceca than warmer sea stars (Fig. 3.6D, E). The peak size of the pyloric ceca is thought to be somewhat proportional to annual gonad production. An inverse, cyclical relationship between the size of the pyloric ceca and the gonads has been noted in about a dozen asteroid species (Lawrence & Lane 1982, Table V) including *Pisaster ochraceus* (Farmanfarmaian et al. 1958, Greenfield 1959, Mauzey 1966; see this chapter, Fig. 3.15). There is little direct evidence for the transfer of resources from the pyloric ceca to the developing gonads (Lawrence & Lane 1982). Indirect evidence comes from several studies documenting decreases in the concentrations of various nutrients in the pyloric ceca during gametogenesis (reviewed by Harrold & Pearse 1980). In addition, a study of *Luidia clathrata* documented the highest annual RNA:DNA ratio in the pyloric ceca during gametogenesis, perhaps suggesting active synthesis of proteins for transport to the gonads (Watts & Lawrence 1990).

Although conclusive physiological or biochemical evidence has not been obtained, the pyloric ceca do appear to contribute to gonad production in *Pisaster* (Mauzey 1966, 1967; Nimitz 1971, Harrold & Pearse 1980). To the extent that larger pyloric ceca represent a greater pool of stored energy, the results of my laboratory experiment suggest that sea stars experiencing upwelling conditions should have greater reproductive output than those experiencing constant warm conditions. Thus, a reduction of upwelling should generally reduce *Pisaster* fecundity.

Whether such changes would translate into changes in population abundance is less clear. Virtually nothing is known about the planktonic life and early life history of *Pisaster*. All things being equal, a reduction in larval production within a region should generate reduced settlement. Based on very limited data from several sites in Nootka Sound, British Columbia, fewer than 3% of newly settled *Pisaster* survive to one year of age (Sewell & Watson 1993). As with *Nucella*, rate of recruitment appears poorly correlated with the number of year old individuals incorporated into the adult population at these sites. However, this conclusion is based on limited data from a single region and additional studies are needed.

Field Monitoring of Sea Star Condition

By monitoring field populations of *Pisaster*, I tested whether pyloric ceca and gonad indices varied with water temperature in a manner consistent with the laboratory results. During the course of this study, there was considerable interannual variation in the frequency and intensity of upwelling on the central Oregon coast. The intensity of upwelling was markedly decreased during the summer of 1997 because of the major 1997-98 El Niño event (Fig. 3.11). Upwelling favorable winds still occurred, but it appeared that upwelled waters were drawn from shallower, warmer layers, presumably because of a depressed thermocline (Peterson et al. 1993, Roemmich & McGowan 1995). As a result, water temperatures during summer 1997 only fell below 10 °C during a single upwelling event in July (Fig. 3.11), and were regularly >13 °C throughout much of the summer. In contrast, during the previous summer (1996), upwelling occurred regularly, water temperatures rarely exceeded 13 °C, and organisms experienced fluctuating temperatures similar to the upwelling treatment maintained in the laboratory.

The results of the laboratory experiment and energetic model presented above suggest that sea stars should attain smaller pyloric ceca during years of reduced upwelling relative to years with consistent upwelling (i.e., 1997 vs. 1996). At the South Jetty, interannual variation in the pyloric ceca was consistent with this expectation; the peak pyloric ceca attained was significantly smaller in 1997 than in 1996 (Fig. 3.16A). However, at SH there was no significant difference in the pyloric ceca among years (Fig. 3.16A). Thus, the field data do not offer strong support for the idea that interannual variation in upwelling patterns regulate the size of the pyloric ceca. Other factors which may alter the size of the pyloric ceca are discussed below.

Within a site, there was a tendency for year to year variation in the peak pyloric ceca index to be reflected in gonad production during the following spring (Fig. 3.17). However, this relationship was somewhat inconsistent. For example, gonad production at SH decreased significantly between the first two years of this study (Fig. 3.16B), despite a relatively consistent pyloric ceca (Fig. 3.16A). Similar patterns have been documented in the two other studies that have monitored *Pisaster* condition over intervals of four or more years (Greenfield 1959, Mauzey 1967). In both studies, the year with greatest gonad production did not follow an unusually large pyloric ceca index in the fall. It is uncertain what other factors might drive year-to-year variation in gonad production. In this study there was no obvious correlation between peak gonad size (Fig. 3.16B) and water temperature during gametogenesis (November through April, Fig. 3.12).

Additional evidence suggests that gonad production is not isometrically related to the peak size of the pyloric ceca. Sea stars at the South Jetty had dramatically greater gonad production than SH sea stars in 3 of 4 years (Fig. 3.16B), despite having equivalent or significantly *smaller* pyloric ceca in all years (Fig. 3.16A). This pattern implies that there may have been differences in resource allocation between the two sites; for example, sea stars at SH may devote more stored energy to growth at the expense of reproduction. It is uncertain what might cause such differences in allocation, although unknown differences in age-structure between these sites could be important.

Differences in resource quantity and quality might also influence energy storage in the pyloric ceca. I predicted that sea stars at the South Jetty would have lower peak pyloric ceca values because of the greater proportion of barnacles in their diet (Fig. 3.13). Barnacle tissue is generally of lower caloric value than mussel tissue; *Balanus glandula* has 30.1% fewer kcal/g dry weight than does *Mytilus trossulus* (Menge 1972). In addition, because of their larger size, mussels typically have considerably more tissue per individual than do acorn barnacles. However, in 1995 and 1996 (the years when mussels were most abundant at SH, Fig. 3.14), pyloric ceca from SH sea stars were not larger than those from South Jetty sea stars (Fig. 3.16A). Sea stars at the South Jetty often remove patches of densely packed acorn barnacles and feed on many individuals at one time. It is possible that the large number of barnacles consumed using this method compensates for barnacle's smaller size and lower caloric content.

Alternatively, assuming that mussels are in fact a more productive food source, sea stars at SH may devote a greater proportion of their energy to immediate growth. If this were the case, sea stars at SH may grow at much faster rates than at the South Jetty while storing similar amounts of energy in the pyloric ceca. This could also explain why the pyloric ceca of sea stars at Strawberry Hill changed little over the four years of this study (Fig. 3.16A) despite a substantial decline in the cover of *Pisaster*'s preferred prey (*Mytilus trossulus*)(Fig. 3.14). Sea stars may attain relatively consistent annual peaks in the pyloric ceca by regulating the amount of energy devoted to growth. Although sea stars are difficult to tag or mark (Paine 1976), growth studies at these sites would be very informative.

To summarize the results of this field monitoring, the dramatic reduction in upwelling during the 1997-98 El Niño was marked by a sharp decline in the pyloric ceca and gonad production at the South Jetty, but not at SH. There appeared to be a general correspondence between the size of the pyloric ceca and annual gonad production within a site. However, sea stars at the South Jetty produced much larger gonads than SH sea stars despite having pyloric ceca that were equal or smaller in size. Unknown variation in allocation of energy to growth may have obscured the predicted effects of variable prey and water temperature on the size of the pyloric ceca.

Conclusions

The results of this study emphasize the need for greater integration of environmental physiology and ecology (Kingsolver 1989). Variation in water temperature on the order of 3°C has largely been viewed as inconsequential by marine ecologists. In part, this may be due to the fact that intertidal organisms can experience much greater temperature fluctuations (often 10-20°C) during shifts between periods of immersion and emersion. Therefore ecologists who have addressed the influence of temperature on intertidal populations have typically focused on aerial temperature as a potential source of "environmental stress", defined as conditions that weaken or kill an organism (Menge & Sutherland 1987, Bertness & Leonard 1997). Two points are worth emphasizing. First, the fact that intertidal invertebrates can tolerate larger temperature changes does not mean that small changes are not having important, sub-lethal impacts on biological processes. Secondly, although intertidal organisms often experience the greatest thermal changes during periods of aerial exposure, many low intertidal organisms on the Oregon coast spend greater than 90% of their life submerged. Exposure to extreme air temperatures may induce stress-related responses with cellular effects that persist well after organisms are re-submerged (Somero 1995, Hofmann & Somero 1995, 1996a, b). However, exposure to less severe air temperatures may merely elevate body temperatures temporarily whereas changes in water temperature will set the temperature at which most cellular and physiological processes occur.

This study suggests a pathway through which upwelling-associated variation in water temperature might influence the abundance of *Pisaster* and *Nucella*. It has been suggested that changes in population abundance may be driven largely by short-term impacts on critical phases of an organism's life cycle (Bhaud et al. 1995). These impacts are more likely to occur if such critical phases coincide with periods characterized by strong environmental variation. This may be the case for sea stars and whelks along the Oregon coast. The fecundity of these consumers is driven largely by their ability to accumulate surplus energy during a relatively short window of seasonal feeding. This period of intensive feeding coincides with the upwelling season, which is by far the season of greatest variability in water temperature. Year-to-year variation in the relative proportion of upwelling and relaxation periods may impact the abundance of these consumers through the effects of water temperature on energetics, growth, and perhaps fecundity.

This study underscores the need for incorporating greater mechanistic understanding into efforts aimed at predicting and mediating the impacts of climatic change on natural populations. To date, most work has been based on classic principles of biogeography that are poorly defined and largely untested. It is generally assumed that individual growth and fecundity vary as a simple function of temperature or other climatic variables (Fig. 3.1A). The results of this study imply that this model may not accurately describe the effect of environmental change on an organism's performance. In the laboratory, sea stars and whelks appeared to grow at a faster rate under a fluctuating temperature regime than at either a constant 9°C or 12°C. Hence it would be inappropriate to model whelk or sea star growth as a simple function of temperature; the relationship is more complex and must incorporate temperature variability. The results of this study suggest that changes in the frequency of episodic or seasonal events like coastal upwelling may often have greater impacts on natural populations than changes in mean temperature.

CHAPTER 4

Community Responses to Climate Change: Links Between Temperature and Keystone Predation in a Rocky Intertidal System

ABSTRACT

It is widely predicted that increasing global temperatures will shift the geographic ranges of species to higher latitudes or altitudes. Although range shifts may have important long-term consequences, few studies have addressed the possibility that climatic change may disrupt communities and ecosystems more immediately and dramatically by altering species interactions. In particular, key species interactions that are sensitive to temperature may act as leverage points through which small changes in climate could generate large changes in natural communities.

I examined the effect of small changes in water temperature on the interaction between a keystone predator, the sea star *Pisaster ochraceus*, and its prey, the rocky intertidal mussel *Mytilus californianus.* Experiments were conducted to quantify rates of predation at three sites on the central Oregon coast during five consecutive 14-day periods. Variation in predation intensity was significantly related to variation in water temperature, but unrelated to potential aerial heat stress, maximum wave forces, or precipitation. Per capita effects of sea stars on mussels were sharply reduced when water temperatures dropped 3°C during a persistent upwelling event. The collective or population impact of sea stars declined even more dramatically during upwelling as a result of two effects: (1) individual sea stars consumed less, and (2) the density of

foraging sea stars was reduced. This reduction in local density presumably occurred because sea stars typically remained in the low zone (< +0.7m) or shallow subtidal waters during cold water events.

These results suggest that interannual variation in the frequency and intensity of coastal upwelling could alter the dynamics of these communities through strong effects on keystone predation. In recent decades, upwelling patterns in the California Current have changed substantially in response to more frequent and intense El Niño events, interdecadal regime shifts in the North Pacific, and perhaps global warming. Attempts to predict future changes in rocky intertidal communities are hampered by uncertainty about the influence of global warming on upwelling patterns and the potentially enormous number of cascading indirect effects. Nevertheless, the sensitivity of this keystone interaction to small changes in water temperature implies that substantial changes could arise. Experimentally testing the influence of environmental factors on key species interactions thus represents a useful approach for evaluating the sensitivity of natural systems to climatic change.

INTRODUCTION

A large body of evidence suggests that human activities are dramatically increasing the concentration of greenhouse gases in the atmosphere and warming the planet (IPCC Report 1996, Mann et al. 1998, Pollack et al. 1998). During this century average global surface temperatures have increased by about 0.5°C, and atmospheric models predict that global warming will cause average surface temperatures to rise another 1-3.5°C during the next century. Faced with these changes, there is a growing need to evaluate the potential effects of climatic change on natural systems. In this chapter, I review our understanding of how temperature changes may impact species ranges, species interactions, and natural communities. I suggest that experimentally testing the response of key species interactions to changes in environmental variables may be a useful way to evaluate the sensitivity of biotic communities to climatic change. This approach is illustrated using field experiments conducted in a rocky intertidal community on the central Oregon coast. This study underscores the importance of considering the effects of climate change on species interactions and highlights the value, as well as the limitations, of using experimental approaches to predict community-level responses.

Temperature and Species Range

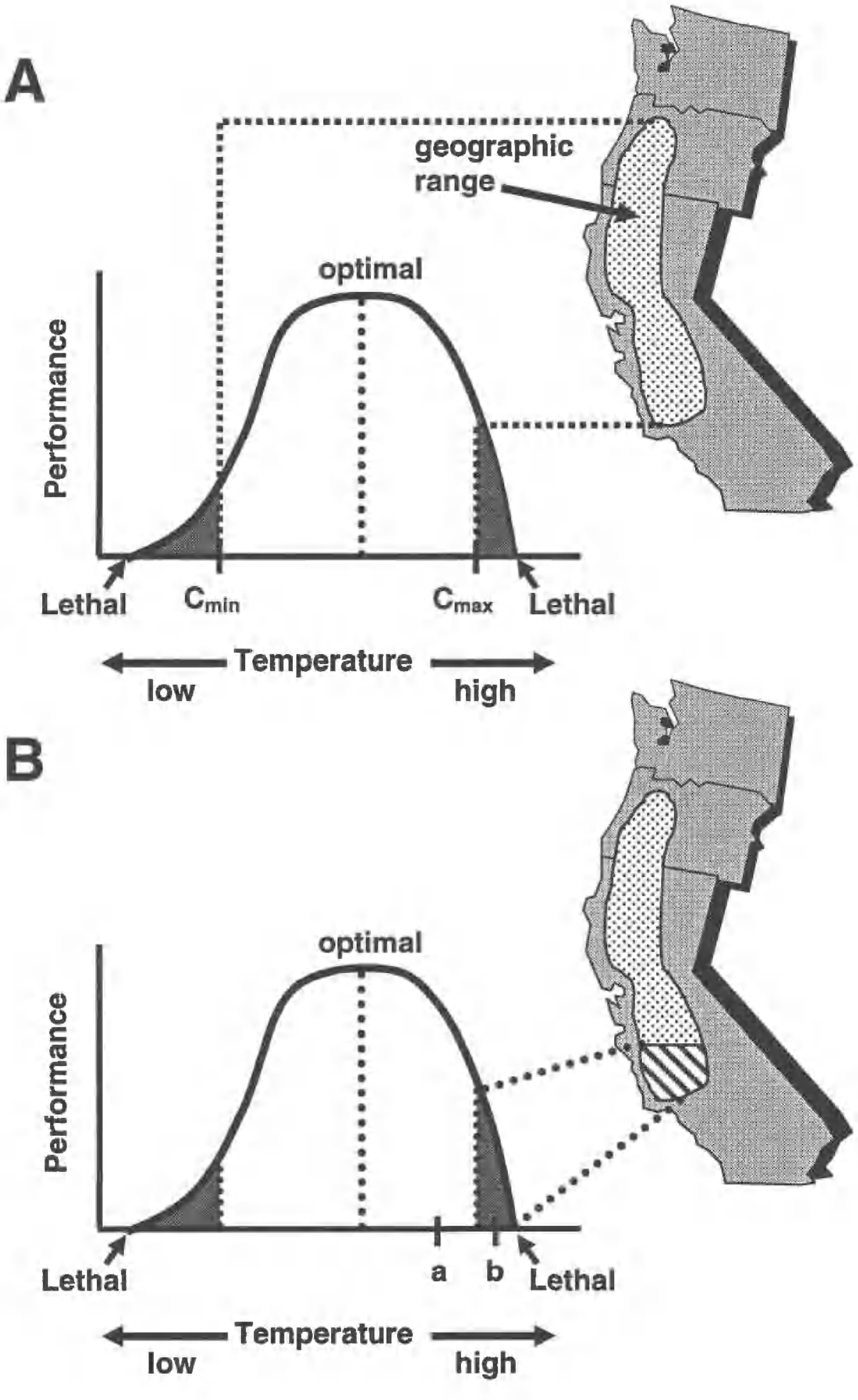
To date, most predictions regarding the potential effects of climate change on natural communities have focused on shifts in the geographic ranges of species. Species are expected to respond to warming temperatures by gradually shifting to higher latitudes or altitudes to remain within their thermal tolerance ranges (Breeman 1990, Davis & Zabinski 1992, Fields et al. 1993, Lubchenco et al. 1993, Gates 1993). Several recent studies in marine and terrestrial systems report long-term changes in species distributions that are consistent with these predictions (Barry et al. 1995, Parmesan 1995, Sagarin et al. 1999, Pounds et al. 1999, Thomas & Lennon 1999, Parmesan et al. 1999).

Projected range shifts are based on the long-standing hypothesis that temperature sets the geographic range limits of most species (e.g., Orton 1920, Hutchins 1947). Although there are only a handful of studies that establish a direct physiological or experimental connection between temperature and geographic range boundaries (Nobel 1980, Sundene 1962, references in Breeman 1990), there are many strong correlations between temperature isotherms and species range limits that suggest such links may be common (e.g., Woodward 1987, Root 1988).

These patterns imply a general model of range limits based on the relationship between temperature and physiological tolerance. An organism's "performance" (i.e., growth or efficiency of operation) is expected to vary as a roughly bell-shaped function of temperature (Fig. 4.1A), driven by the relationship between temperature and the efficiency of underlying physiological processes (Shelford 1913, Huey & Stevenson 1979, Cossins & Bowler 1987, Huey & Kingsolver 1993). Optimal performance occurs in the middle of this temperature range. At high and low temperatures there are critical limits, beyond which an organism is no longer able to reproduce successfully (i.e., the organism may be unable to produce offspring, or alternatively, the organism's offspring may be unable to survive; Orton 1920, Hutchins 1947, Bhaud et al. 1995). These upper and lower critical limits are thought to set the geographic boundaries of a species range (Fig. 4.1A).

Given this model, a species range contracts when temperature change eliminates populations living at the margin of the range. For example, a population living near its southern boundary may disappear when a small temperature increase pushes individuals beyond their upper critical limit (Fig. 4.1B). This model implies that populations living near their range limits are most vulnerable to a slight temperature change (Davis & Zabinski 1992), whereas populations living near the middle of their geographic range (i.e., close to their physiological optimum) should be less strongly affected by a slight temperature change.

Figure 4.1 A simple model relating temperature and the geographic range of a hypothetical sedentary species in California and Oregon. (**A**) Individual performance varies as a species-specific function of temperature. Geographic range limits are set by a critical minimum (C_{min}) and critical maximum (C_{max}) temperature, beyond which the organism is unable to successfully reproduce (shaded regions under curve). (**B**) Dynamics of a hypothetical range contraction. A small temperature increase occurs throughout the geographic range. Individuals near their southern range limit formerly experienced temperature "a", but now experience a higher temperature "b" within the species' upper critical range. Individuals are unable to successfully reproduce and southern populations ultimately disappear (cross-hatched region of geographic range). Analogous processes may expand the northern range limit, leading to a northward shift of the entire range.


A
geographic
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C_{min}
C_{max}
Lethal
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low
high
B
optimal
Performance
Lethal
a
b
Lethal
Temperature
low
high

Figure 4.1

Considerable evidence suggests that physiological optima and critical limits are likely to vary among species within the same community. For example, different species of plants living within the same habitat frequently vary in their physiological responses to temperature and other environmental factors (such as light, CO_2, and soil nutrients; Pacala & Hurtt 1993). A similar pattern may apply to animals. For example, in a study conducted in a short-grass prairie in Colorado, seven congeneric species of darkling beetles showed peak activity at different ambient temperatures (Whicker & Tracy 1987). In the laboratory, beetles selected these same, species-specific temperatures from a thermal gradient. These and similar studies (e.g., Lévêque 1997) suggest that species within a community are likely to respond differentially to temperature change.

This idea is also supported by the fossil record in North America which indicates that species ranges shifted independently from one another in response to past changes in climate (Foster et al. 1990). For example, during the last North American glacial cycle (14,000-10,000 yrs ago), individual species of small mammals showed shifts in geographic range marked by different directions and rates (Graham 1992). Similarly, pollen records suggest that the distributions of tree species responded individualistically to climatic changes over the past 18,000 years (Webb 1992). To the extent that species ranges reflect thermal tolerances, these individualistic responses suggest that communities are impermanent associations of species with different underlying physiologies.

Assuming these individualistic responses apply broadly to most species, ongoing climatic warming is likely to shift species ranges independently of one another, and perhaps disassemble present-day communities, leading to the formation of new species associations. As a result, scientists considering climatic impacts have generally treated species as isolated units, rather than considering the influence of temperature on communities and community processes. Most studies have focused on single species, using some combination of climate-space analysis (Porter & Gates 1969) and climate mapping to predict range shifts. This prevailing strategy has three main parts (summarized by Harte et al. 1992): (1) field-derived correlations and physiological information from laboratory studies are used to estimate a species' thermal tolerance, (2) atmospheric models are used to predict temperature changes, and (3) these data are combined to determine whether a species would need to move in order to remain in a suitable climate. This approach has been used to project range shifts for a variety of species of macroalgae, trees, insects, fish, and mammals (e.g., Breeman 1990, Scott & Poynter 1991, Davis & Zabinski 1992, Rogers & Randolph 1993, Johnston & Schmitz 1997).

This approach is conceptually simple and appealing, and predicting range shifts is a useful first step in evaluating potential impacts of climate change. However, the near exclusive focus on range shifts implies that: (1) impacts on communities can be evaluated solely by assessing the response of isolated species to the direct effects of temperature change, (2) changes will be manifested mainly through lethal effects on individuals, and (3) populations near geographic range limits will be most vulnerable to temperature change, whereas those near the central portion of a range will be relatively unaffected.

Temperature and Species Interactions

I suggest that in many cases, a focus on the direct, lethal effects of temperature has caused ecologists to underestimate the potential effects of climate change on natural communities. Many studies have concluded that, at least in the short-term, anticipated warming will have little impact on the ability of a species to survive within its current range (e.g., Johnston & Schmitz 1997, Sætersdal & Birks 1997). This conclusion is based on the likelihood that available behavioral and physiological plasticity will minimize the risk of extinction to most species (Dawson 1992). Although range shifts may have important long-term effects, changes in species distributions (in and of themselves) may not significantly disrupt communities during the next century (Paine 1993).

However, an emphasis on range shifts neglects other important, and potentially more immediate effects. In particular, few studies have addressed the possibility that climatic changes may impact local populations more rapidly and dramatically by altering the strength of interactions between a species and its competitors, mutualists, predators, prey, or pathogens (Lubchenco et al. 1991). This hypothesis follows logically from the idea that performance varies as a species-specific function of temperature. For example, following a slight temperature increase, an individual that was previously living near its physiological optimum may be forced to spend more time operating at a reduced level of performance (Fig. 4.2). Such sub-lethal effects may change the way that one species interacts with another, for example by changing competitive ability, rates of consumption, or susceptibility to predators or pathogens. Moreover, these effects may occur throughout a species range, not just in populations living near range boundaries.

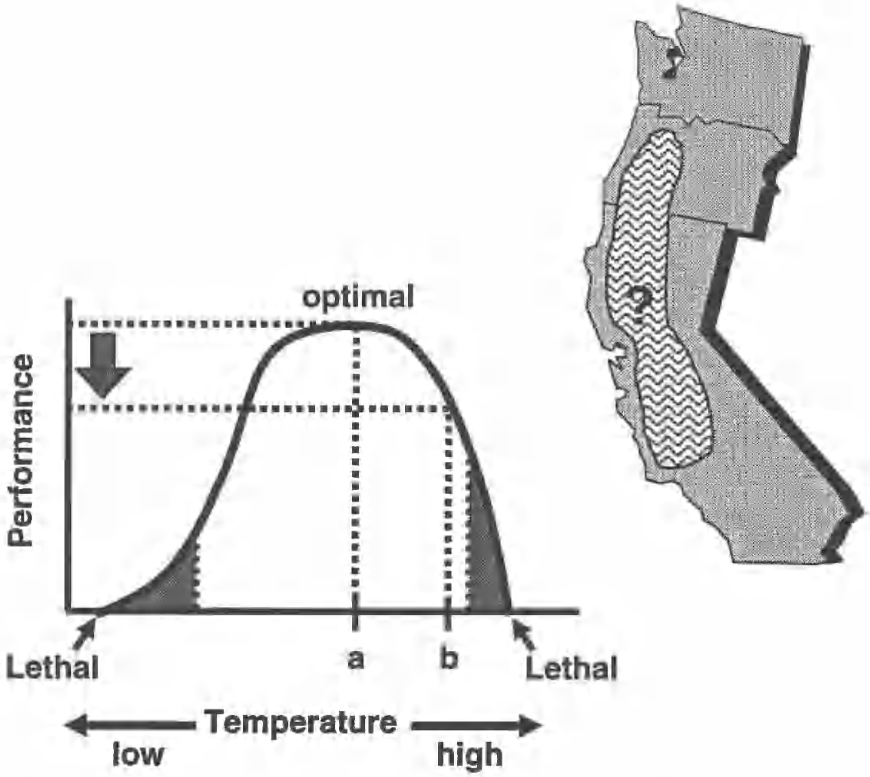


Figure 4.2 Potential effects of temperature change on species interactions. A small temperature increase occurs throughout the geographic range. Individuals near the middle of their range formerly experienced temperature "a", but now experience temperature "b" , and a resulting decrease in performance. Reduced performance may change the interaction between individuals and their competitors, predators, prey, etc. Such sub-lethal effects may affect individuals throughout a species range (indicated by the "?").

The recognition that physical conditions may mediate the strength or outcome of species interactions is not a new idea. This concept was the focus of several foundational papers in modern experimental ecology. For example, Tansley (1917) determined that the outcome between two competing plant species was dependent on soil type. Similarly, Park's (1954) classic flour beetle studies demonstrated that competition between different species of *Tribolium* was mediated by temperature and humidity. Although these and other early experiments clearly suggested that biotic processes could be modified by abiotic factors, community ecology has passed through phases emphasizing the primary importance of either abiotic (e.g., Andrewartha & Birch 1954) or biotic factors (e.g., Paine 1966) in determining patterns of abundance and distribution.

However, in recent years there has been a strong movement toward integrating the roles of biotic and abiotic factors into an understanding of community dynamics (Menge & Sutherland 1976, 1987, Tilman 1980, Kingsolver 1989, Dunson & Travis 1991, Hunter & Price 1992, Bertness & Callaway 1994). These models of community regulation are all based on the idea that species are imbedded in a complex web of interacting species, and that the strength of these biotic interactions may be influenced by environmental conditions. Species are linked by trophic interactions to species that are above and below them in a food web. Competitive and facilitative interactions may link species within the same trophic level. Changes in temperature or other environmental factors may alter the strength of any of these links, with effects that ripple throughout a food web via species interactions (Hunter & Price 1992).

This community perspective has led some ecologists to caution that climatic change may impact communities by altering species interactions (Lubchenco et al. 1991, Harte et al. 1992, Castilla et al. 1993, Carpenter et al. 1993, Lubchenco et al. 1993, Ayres 1993, Root & Schneider 1993, Brown et al. 1997, Davis et al. 1998). If such alterations change the relative abundance of a given species, effects may then be transmitted through chains of species interactions. These sorts of cascading effects could theoretically arise anywhere in a food web (Hunter & Price 1992).

Evaluating Community-Level Impacts

Is there any empirical evidence that climatic changes can disrupt communities through altered species interactions? In fact, some long-term studies have observed interdecadal variation in community structure and have inferred that altered species interactions played a role. For example, a recent study reported that krill abundance in the Antarctic tended to be much lower during the period 1984-1996 than during 1976-1984 (Loeb et al. 1997). Declining krill abundance was associated with a decrease in the frequency of winters with extensive sea-ice cover. In contrast to krill, the abundance of filter-feeding salps (pelagic tunicates) increased with decreasing sea-ice. The authors suggested that open-water conditions support rapid growth of salp populations, and that krill abundance is reduced by strong competition with salps for food (phytoplankton). Krill, in turn, are the major food source for higher trophic levels, such as Adelie penguins, which also appear to be in decline. Thus, recent decreases in sea-ice cover may alter competition between salps and krill, leading to changes throughout the Antarctic food web.

In a similar long-term observational study, recent climatic changes appear to have sparked major changes in a Chihuahuan Desert ecosystem during the period 1977-1995 (Brown et al. 1997). In this ecosystem, winter precipitation over this period has increased significantly, apparently triggering large increases in shrub cover. These changes in vegetation may be linked to substantial changes in the abundance of many species of rodents, seed-harvesting ants, and lizards. The authors attribute the wholesale reorganization of this ecosystem to both the direct effects of increased winter moisture and the indirect effects of altered biotic interactions (Brown et al. 1997).

Long-term ecological data sets like those from the Chihuahuan Desert and Antartica are uncommon, but may be necessary to observe effects that reverberate through food webs (Brown & Heske 1990). These studies suggest a link between climatic changes, species interactions, and community-level changes. However, since these studies were observational, these links can at present only be inferred. Furthermore, in these studies, community changes were observed *first*, and researchers then tried to trace these changes back to specific interactions which may have been altered by climatic changes.

These studies point to important challenges in evaluating community-level impacts of climatic changes. For example, is it possible to obtain direct, experimental evidence of how species interactions are affected by environmental changes? If so, which interactions should be the focus of attention? Can pathways likely to generate community change be identified *a priori*? To what extent can ecologists hope to predict the likely effects of climate change on natural communities?

Experimentally testing the response of species interactions to environmental change may be tractable in many systems, and is likely to provide valuable mechanistic insight. Plant and ecosystem ecologists have pioneered the approach of using experimental field studies to test how small changes in climatic conditions may affect species interactions. Plastic enclosures or heating lamps have been used to manipulate light, soil temperature, and moisture in the field (Chapin et al. 1995, Harte & Shaw 1995, Henry & Molau 1997). For example, in a recent study of a subalpine meadow in the Rocky Mountains, Colorado, heating lamps were used to reduce soil moisture and increase soil temperature by ~1°C in experimental plots (Harte & Shaw 1995). These small changes in environmental factors altered the competitive ability and the relative abundance of plant species within this community. Similar responses have been documented in other climate warming experiments, such as those by Chapin and colleagues in tussock tundra near Toolik Lake, Alaska (Chapin & Shaver 1985, Chapin et al. 1995, Chapin & Shaver 1996). To date, this experimental approach has been predominantly used to assess changes in plant populations, rather than changes within whole communities or ecosystems.

Addressing changes at the community or ecosystem-level obviously introduces substantial complexity. It is often logistically difficult or even impossible to manipulate environmental factors at large scales in the field. Moreover, even relatively simple communities contain dozens of species and hundreds, if not thousands, of species interactions. Investigating all possible links in the field would be an enormous and impractical task (Davis et al. 1995). Thus, there is a clear need to identify species interactions that are both highly sensitive to environmental changes *and* particularly likely to effect changes in communities.

A large body of experimental work suggests that the composition and diversity of many communities are maintained by a few critical interactions (Paine 1966, 1969, 1992, Power et al. 1996). These interactions frequently involve “keystone species”; i.e., a species whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance (Power et al. 1996). Keystone species have been identified in marine, freshwater, and terrestrial ecosystems (Menge et al. 1994, Power et al. 1996). Although these species often exert their effects through consumption, keystone interactions can also include competition, mutualism, dispersal, pollination, and disease (Power et al. 1996).

In this chapter, I suggest that if key species interactions are sensitive to temperature, they may act as leverage points in natural systems, through which relatively small temperature changes can generate surprisingly large changes in community structure or ecosystem function (Sanford 1999). Identifying key species interactions in under-studied systems remains a significant challenge, but one that can be addressed by experimental and comparative approaches (Power et al. 1996). Although not all communities contain keystone species, community and ecosystem processes may often be dominated by a few strong interactions against a background of many weak interactions (Paine 1992, Carpenter et al. 1993, Fagan & Hurd 1994).

Quantifying the response of strong interactions to slight changes in temperature is thus a logical starting point in evaluating the potential effects of climate change on communities. The remainder of this chapter demonstrates how experimental and observational approaches can be combined to provide mechanistic insight into how climate change may impact communities. I focus on the interaction between a keystone predator, the sea star *Pisaster ochraceus*, and its prey, the rocky intertidal mussel *Mytilus californianus*. I use my results to suggest how climate change might impact these rocky intertidal communities, and in so doing highlight some of the limitations and challenges of global change research.

METHODS

Study System

I conducted studies at wave-exposed rocky intertidal sites within Neptune State Park (44°15'N, 124°07'W), just south of Cape Perpetua on the central Oregon coast. This 4 km stretch of coastline is composed of extensive rocky benches, outcrops, pools, and surge channels. The communities here are similar to those of many other wave-exposed regions along the northern Pacific coast of North America (Dayton 1971, Paine 1980, Menge et al. 1994). The high intertidal zone is characterized by fucoid algae and barnacles, the mid zone by dense beds of the California mussel (*Mytilus californianus*), and the low zone by a diverse mixture of algae, seagrass, and invertebrates, including the sea star *Pisaster ochraceus.*

Intertidal communities in the Pacific Northwest are diverse, accessible, and easy to observe and manipulate. As a result, these communities are extremely well-described and have long served as model systems to develop and test general ecological theories about disturbance, succession, and biotic interactions (reviewed by Paine 1994). Numerous experimental studies during the past 30 years have identified a subset of strong interactions which maintain the composition and diversity of many of these communities (Paine 1966, 1969, 1992, Connell 1970, Dayton 1971, Menge 1992, Menge et al. 1994, Navarrete & Menge 1996). In particular, Paine's classic experiments (Paine 1966, 1969) in Washington State demonstrated that predation by the sea star *Pisaster ochraceus* prevents the mussel *Mytilus californianus* from dominating the low intertidal zone. When sea stars were removed from experimental areas, the low intertidal zone shifted from a diverse assemblage of invertebrates and algae to a monoculture of *M. californianus*. Paine coined the term "keystone predator" to describe a single predator species (like *Pisaster*) that determines most patterns of community structure. Experimental studies have confirmed that *Pisaster* plays a similar keystone role in wave-swept communities on the central Oregon coast (Menge et al. 1994).

This keystone interaction occurs in a system that is ideally suited to testing the influence of slight temperature change on trophic dynamics. In many terrestrial and aquatic systems, there is a high degree of spatial heterogeneity in the thermal environment (e.g., shaded microhabitats, stratified lakes, above vs. below-ground habitats, etc.). Many poikilothermic consumers (e.g., lizards, fishes, insects) may thus be able to mediate the effects of minor temperature change by selecting preferred microhabitats or limiting activity to certain times (Caulton 1982, Christian et al. 1983, Cossins & Bowler 1987, Whicker & Tracy 1987, Gates 1993). These changes in behavior could have important ecological effects, for example by changing where and when consumers are foraging (Rubenstein 1992, Dunham 1993). In addition, changes in behavior complicate attempts to predict the body temperature of consumers, since it is difficult to assess if (or how much) behavioral thermoregulation might offset changes in ambient temperature.

In contrast, most marine benthic consumers (e.g., sea stars, whelks, herbivorous gastropods, sea urchins, etc.) have little opportunity for behavioral thermoregulation when submerged. Sea temperatures typically vary little over several hundred meters, which is a scale far larger than these organisms' daily movement. Thus, changes in water temperature are experienced as direct changes in the body temperatures of these consumers.

Water temperatures along the Pacific coast vary seasonally, but also vary over shorter time scales in response to coastal upwelling. Episodes of upwelling lasting from several days to 3 or more weeks are common along the Oregon coast from May through September (Menge et al. 1997b). Persistent, strong southward winds combine with the Coriolis effect to push surface waters offshore (Fig. 4.3), and water temperatures typically drop 3-5°C as cold, nutrient-rich water rises from below.

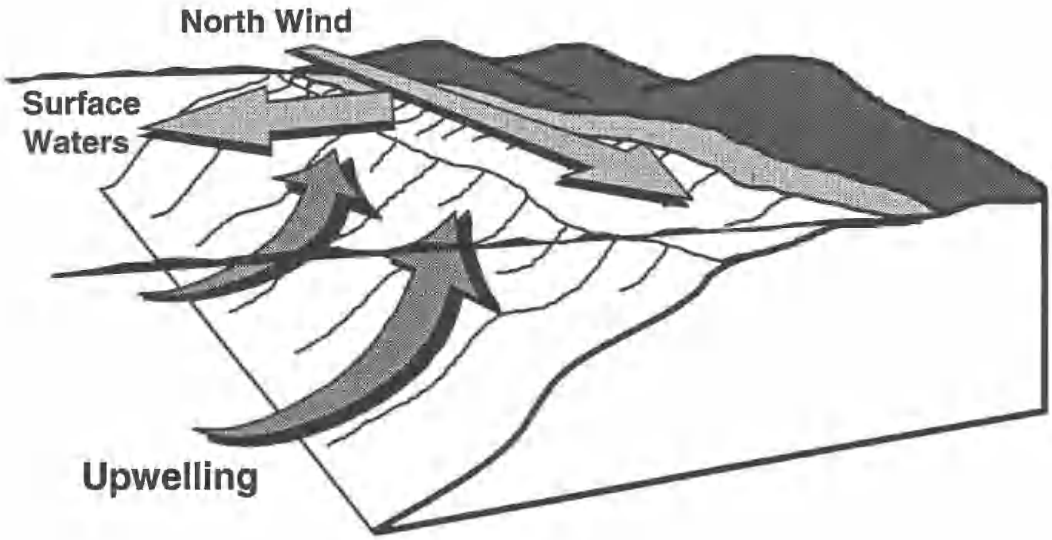


Figure 4.3 Mechanics of coastal upwelling. Strong northerly winds and the Coriolis effect cause surface waters to flow offshore, drawing up cold, nutrient-rich waters from depth (after Bakun 1990).

In the Pacific Northwest, densities of *Pisaster* and its impact in the intertidal zone are highest between May and October (Mauzey 1966, Paine 1974, Robles et al. 1995). However, preliminary observations in Oregon suggested that intertidal sea star activity within this season underwent marked fluctuations associated with oceanographic conditions. During periods of cold water upwelling, many sea stars appeared to become inactive in low zone channels or shallow subtidal waters. In this study, I quantified changes in *Pisaster* abundance, distribution, and predation intensity to test the hypothesis that the impact of sea stars is reduced during upwelling events.

***Pisaster* Abundance, Distribution, and Feeding Observations**

At two sites within Neptune State Park, I quantified temporal changes in sea star abundance, distribution, and activity in relation to variation in water temperature. In April 1995, I established permanently marked rectangular plots (mean area ± SEM = 3.49 ± 0.30 m^2) at Strawberry Hill (n = 11), and Bob Creek Wayside (n = 15)(see site map below). Plots were positioned on horizontal surfaces in the upper portion of the low intertidal zone (approximately +0.7 to +1.2m above MLLW) within the tidal range where *Pisaster* were most commonly observed foraging. In most cases, the landward side of plots was located just below an adjacent *Mytilus californianus* bed. In 1995 these plots contained high densities of the bay mussel (*Mytilus trossulus*) and gooseneck barnacles (*Pollicipes polymerus*). In 1996-1998, *M. trossulus* recruitment was low and the plots were dominated by *P. polymerus* (Chapter 3, and E. Sanford, *unpublished data*). I recorded the density of sea stars within these plots every two weeks during the spring and summer, and every four to six weeks during the remainder of the year. Densities were examined in relation to changes in water temperature recorded by intertidal data-loggers (see "Quantification of Environmental Conditions" below).

Since these plots were all located at approximately the same tidal height, they provided only indirect evidence regarding the vertical movements of sea stars. I therefore also quantified vertical distribution of sea stars along a permanently marked 30m section of intertidal wall at Bob Creek Wayside. This steeply sloping to nearly vertical wall ran in the east to west direction, roughly perpendicular to the breaking waves. Sea stars on this wall were either fully exposed to wave action or partially sheltered by several rocky outcrops. There was an extensive mid-zone *Mytilus californianus* bed along the entire length of the wall. I routinely recorded the abundance of all *Pisaster* within three vertical zones on the wall: (1) above or within 15 cm of the lower limit of the *M. californianus* bed (approximately +1.2m), (2) within the zone just below the mussel bed, characterized by *M. trossulus* and *P. polymerus* (approximately +0.7 to +1.2 m), and (3) the low intertidal zone below +0.7m, characterized by coralline algae and sea anemones (*Anthopleura xanthogrammica*). This lowest zone included the bottom portion of the wall which ranged into the shallow subtidal. During several upwelling events, I examined all individuals along this wall and recorded whether or not individuals were feeding (defined by observation of an everted stomach and/or remains of recently consumed prey held at the oral disk).

Finally, I quantified the diet of actively feeding *Pisaster* in wave-exposed habitats at Bob Creek and Strawberry Hill on 14 dates during the summer of 1995 and 1996. Individuals were carefully removed from the rock with a screwdriver, and the identity of all prey species being consumed was recorded. On several dates I sampled all individuals along the 30m wall transect described above. On other occasions, a 30m transect was laid parallel to the water in the low intertidal zone and I examined the first 100 sea stars encountered within 1m of the transect.

Experimental Quantification of Predation Intensity

I quantified rates of *Pisaster* predation to explicitly test the hypothesis that the strength of the sea star-mussel interaction is reduced during periods of cold water upwelling. Experiments were conducted at three wave-exposed sites separated by several hundred meters: Strawberry Hill, Pigeon Reef, and Bob Creek Wayside (Fig. 4.4). Experiments were replicated at this spatial scale because water temperatures varied little (generally < 0.2°C) over these distances, yet the sites were far enough apart that foraging sea stars were unlikely to move among them. At each site, I identified two large rocky reefs (mean area ± SEM = 132.5 ± 49.7 m^2) that were in close proximity to one another, yet isolated by surge channels and sand. All sea stars were routinely removed from one reef in each pair and allowed to remain at natural densities on the other (Fig. 4.4).

In April and May 1997, I transplanted 20 clumps of 50 mussels to the low intertidal zone on each of these reefs. *Mytilus californianus* were used in these experiments to gauge the influence of *Pisaster* on the competitively dominant space-holder (Paine 1992). Mussels (shell length, 4.5 to 5.5 cm) were placed in overlapping rows under Vexar™ mesh cages that were screwed into the rock. Cages held mussels in place, allowed them to reattach firmly to the rock with byssal threads, and protected them from being eaten by sea stars until cages were removed. This technique has been used successfully by other researchers in Washington and Oregon (Paine 1976, Menge et al. 1994, Navarrete & Menge 1996).

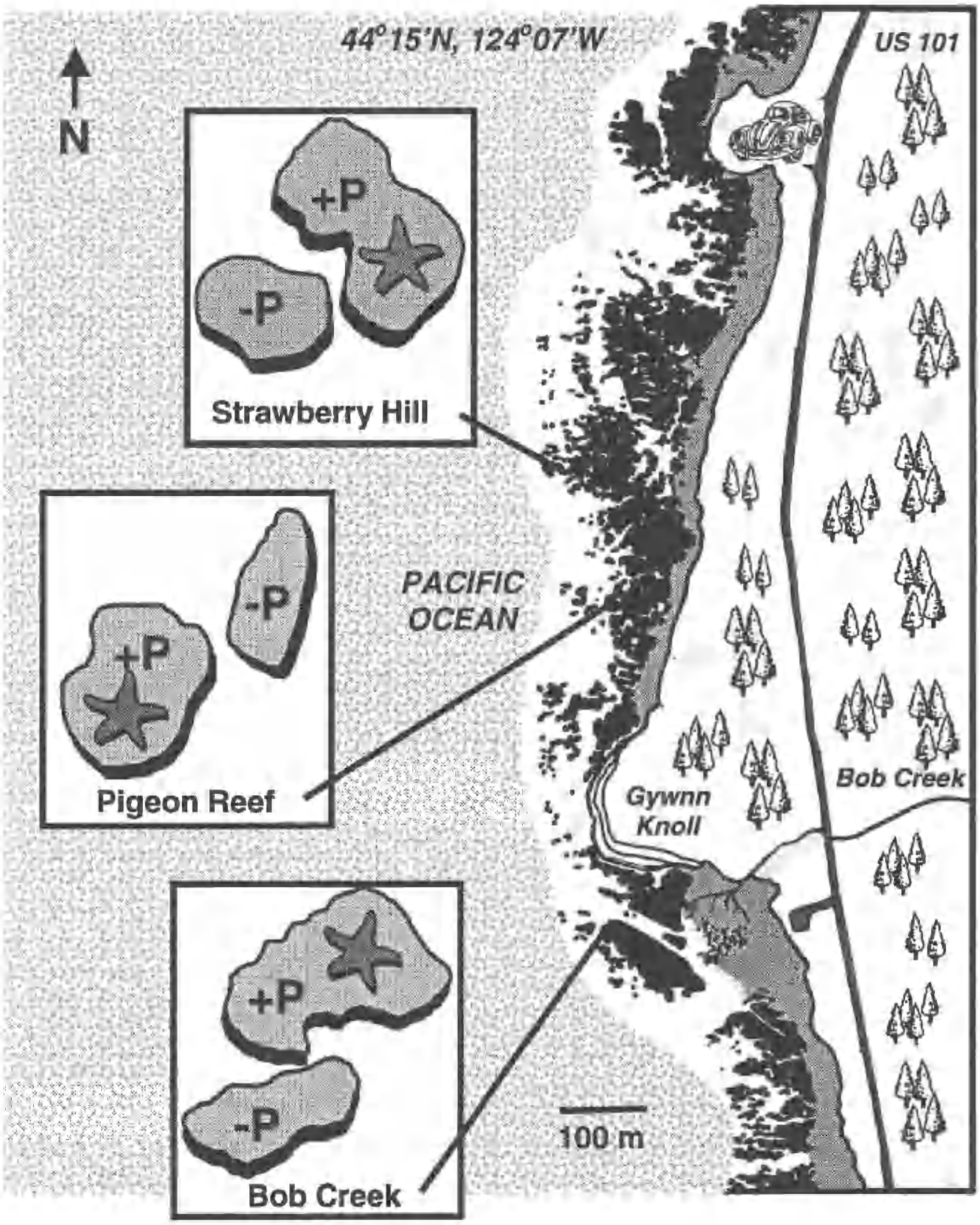


Figure 4.4 Map of study sites within Neptune State Park, OR. Rocky benches are shown in black, sand and cobble beach in dark gray. At each site, mussels were transplanted to reefs where *Pisaster* were either routinely removed (-P) or allowed to remain at natural densities (+P).

Beginning in mid June, I conducted five consecutive experiments to measure the intensity of sea star predation during periods lasting 14 days each. Starting dates were set *a priori* as the first day of each spring tide series, so that each experiment consisted of a similar 14-day tidal cycle. At the start of each experiment, I randomly selected four mussel transplants on each reef and removed their cages, thereby exposing these mussels to sources of mortality. I then recorded mussel survivorship daily for the first 6-7 days, and again on day 14 (study sites were inaccessible during neap tides, days 8-13). On each of these days, I also recorded the local sea star density (defined as the number of sea stars in a 1m radius around each clump). Uncaged mussels that remained on day 14 were counted and then removed.

Quantification of Environmental Conditions

I tested whether variation in predation intensity on transplanted mussels was associated with changes in water temperature and other environmental factors. In the low intertidal at each site, a data-logger (Optic StowAway™, Onset Computer Corp., Pocasset, MA) was installed to record water temperature (during high tide) or air temperature (during low tide) every 30 minutes. Data-loggers were positioned on horizontal surfaces that were exposed to full sunlight during daylight periods of aerial exposure. From these records at each site, I calculated High Tide Water Temperatures, defined as the mean of all readings during a period from two hours before to two hours after each high tide. I also extracted the maximum temperature recorded during each low tide period of aerial exposure. The time of low and high tides was estimated using NOAA tide charts.

I tested whether temperatures recorded by data-loggers during periods of aerial exposure could be used to predict sea star body temperatures (and thus potential heat stress during low tide). Since sea star body temperatures generally peaked at the end of the low tide (just prior to being re-submerged; E. Sanford, *unpublished data*) it was only possible to record maximum body temperatures at one site per day. I therefore decided to record all measurements at the same site, Strawberry Hill. On 20 dates during these experiments (2-5 dates per period), I laid a 30m transect parallel to the water on the reef where the mussel transplants and data-logger were located. I randomly selected 10 sea stars and used a digital thermometer and hypodermic probe (Thermometer Model HH-21; Probe Model HYP-1, Omega Engineering, Inc, Stamford, CT) to measure their body temperature 20-30 minutes before they were re-submerged by the incoming tide. I compared these body temperatures to the maximum temperature recorded by the data-logger during that low tide.

Since consumer efficiency may be reduced during periods of increased wave stress (see references in Menge & Olson 1990), five wave force dynamometers (Bell & Denny 1994) were deployed in the low zone at each site to record variation in maximum wave forces. Dynamometers were read and reset every 24 hours for the first 5-7 days of each period.

Finally, because sea stars are very sensitive to osmotic changes (Feder & Christensen 1966), predation intensity could hypothetically be reduced by low tide exposure to precipitation. I therefore inspected rainfall records from the nearest coastal weather station, located about 34 km north of Neptune State Park at Hatfield Marine Science Center in Newport, OR. This station at Guin Library records precipitation ($\pm$ 0.25mm) every 15 minutes (Rain Collector Model 7852, Davis Instruments, Hayward, CA). From these records, I calculated total precipitation during each of the five 14-day periods. Records from this weather station were consistent with my field notes and suggested that precipitation patterns were qualitatively similar at Neptune State Park and Guin Library.

Calculation of Interaction Strength

Interaction strengths were calculated according to the method of Navarrete and Menge (1996)(see also Paine 1992, Laska & Wooton 1998). I used the discrete time version of the Lotka-Volterra equation: $M_t = M_o e^{(\gamma-\alpha P)t}$, where M_t is the number of mussels at time t, M_o is the number of mussels when the transplant was first uncaged, e is the base of the natural logarithm, γ describes the per capita rate of change for mussels in the absence of *Pisaster*, α is the per capita interaction strength of *Pisaster* on the per capita rate of change of mussels, and P is local sea star density. I estimated survival rates for each mussel transplant from the slope of the linear regression of $\ln(M_t / M_o)$ over time (days 1-14). Population interaction strengths (αP) were estimated by subtracting the mean mussel survival rate (slope of log regression) on reefs without *Pisaster*, from the survival rate observed in mussel transplants on reefs with *Pisaster*. Dividing by the mean local sea star density for that transplant and time period gave per capita interaction strength (α). This procedure gave four independent estimates of interaction strength per site x time period combination. Because densities could not be measured during neap tides (days 8-13), I estimated mean local density for each transplant as: [mean density (days 1-7) + mean density (days 7+14)] * 1/2.

Statistical Analysis

Observational Data

I used multiple linear regressions (MLR) to examine changes among sampling dates in the vertical distribution of sea stars along the 30m wall transect. I used the total number of sea stars *above* +0.7m and the total number of sea stars *below* +0.7m as dependent variables in two separate MLR's. I tested whether sea star abundance in the two zones was a function of (i) recent water temperature (the mean of the four High Tide Water Temperatures preceding sampling), (ii) tidal amplitude (the height of the high tide immediately before sampling), (iii) potential heat stress (the maximum data-logger temperature during the most recent period of aerial exposure), and (iv) season [using an indicator variable to designate winter (1November-15April) vs. the remainder of the year]. Assumptions of normality and homogeneity of variance were checked by visual inspection of residual plots and normal probability plots. These assumptions were satisfied reasonably well and therefore analyses were conducted on untransformed sea star abundances.

I also tested whether the peak *Pisaster* density in permanently marked plots varied among years. For each year, I examined all sampling dates during May through September and extracted the maximum sea star density recorded in each plot. I analyzed these peak densities in a One-Way ANOVA with year as the main effect.

Experimental Data

Per-capita interaction strength (IS), population IS, and sea star density were analyzed using Two-Way Analyses of Variance (ANOVA) with site and period as fixed factors (JMP Version 3.2.2, SAS Institue, 1997). A repeated measures analysis was not necessary because predation and sea star density during each period were assessed using independent sets of mussel transplants. Assumptions of normality and homogeneity of variance were checked by visual inspection of residual plots and normal probability plots, and by using the Brown-Forsythe (1974) and O'Brien's (O'Brien 1979) tests for unequal variances. For both per capita and population IS, log transformed data exhibited more normal distributions and homoscedasticity than untransformed data. *A priori* planned contrasts were performed to test whether per capita IS, per population IS, and density were significantly lower during upwelling periods vs. non-upwelling periods. Upwelling periods were designated as 14-day periods with an overall mean High Tide Water Temperature $\leq 10.0^{o}$C.

I used separate multiple linear regressions (MLR) to test whether variation in per capita and per population IS was associated with environmental factors. The dependent variables were untransformed mean per capita or mean per population IS (i.e., the mean of the four measures per site and time period). Independent variables included (i) water temperature (the mean of the 27 High Tide Water Temperatures per period), (ii) potential aerial heat stress (the mean of maximum low tide air temperature on the five warmest days per period), (iii) wave stress (the mean of maximum force per day on the 5-7 days per period when measurements were taken), and (iv) study sites (included using indicator variables). The significance of study site was evaluated using extra-sum-of-square F-tests to compare the full regression models (with indicator variables for study sites) vs. the reduced models (without site variables) (Ramsey & Schafer 1997).

RESULTS

Abundance, Distribution, and Feeding Observations

The abundance of *Pisaster* within permanently marked plots was highly seasonal. Sea stars occurred at high, but variable, densities from May through October (Fig. 4.5). During November through April, sea star densities were consistently low. The onset of this seasonal decline in October or November did not appear to be triggered by a coincident drop in water temperature; densities declined despite the fact that water temperatures remained around 11-12°C during November 1995, 1996, and 1997 (Chapter 3).

The peak density of sea stars in marked plots differed among summers (Fig. 4.5; ANOVA, $F_{2,63} = 18.52$, $p < 0.001$) and was significantly greater in 1995 than in either 1996 or 1997 [Tukey-Kramer, $p < 0.05$; mean maximum density ± SEM = 20.14 ± 1.90 sea stars/m^2 (1995), vs. 9.11 ± 0.93 (1996) and 11.12 ± 1.06 (1997)]. Higher densities were presumably recorded in 1995 because of the greater cover of *M. trossulus* relative to the following two years (Chapter 3 and E. Sanford, *unpublished data*). *Pisaster* form large feeding aggregations around patches of juvenile mussels (Robles et al. 1995), but not around less preferred prey such as gooseneck barnacles (E. Sanford, *personal observation*).

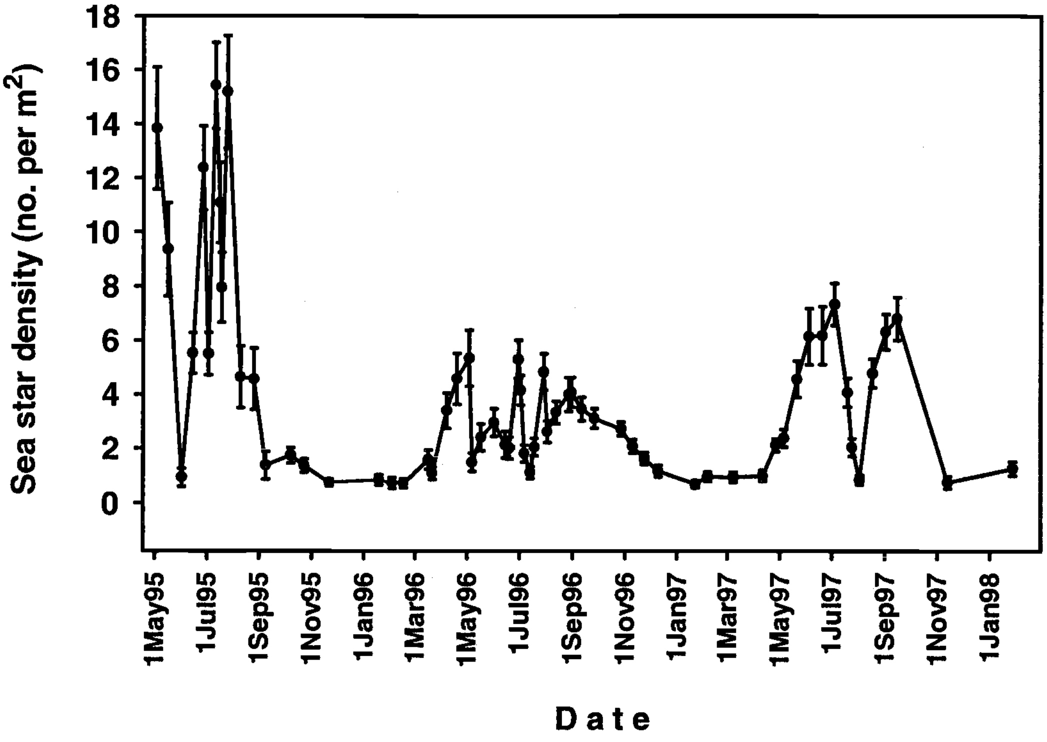


Figure 4.5 Temporal variation in the density of *Pisaster* within permanently marked plots at Bob Creek Wayside and Strawberry Hill. Data are mean densities (±SEM) in 20-26 low intertidal plots within the zone (+0.7 m to +1.2 m) dominated by *Mytilus trossulus* and *Pollicipes polymerus*.

Within the season of highest *Pisaster* densities (May-September), sea star densities within plots often dropped sharply on sampling dates that followed or fell within cold water upwelling events (< 10°C)(Fig. 4.6). In contrast, peak densities were often recorded following upwelling relaxation periods when water temperatures exceeded 12°C (Fig. 4.6). These changes in density appeared to reflect variation in the vertical distribution of sea stars. Along the intertidal wall transect, the total number of sea stars remained fairly consistent from May through September (Fig. 4.7). However, the vertical distribution of these sea stars often changed substantially over short time scales (i.e, days to weeks).

During upwelling events, the majority of individuals were typically in the low zone (Fig. 4.7), often clustered in crevices or among anemones. The multiple linear regression (MLR) analysis indicated that there was a significant negative relationship between recent water temperature and the number of sea stars in this zone (Fig. 4.8A; Table 4.1, "water temp", $p < 0.05$). During cold water events, sea stars in low zone clusters appeared to move little, if it all, from day to day. Consistent with this observation was the fact that 72-98% of those sea stars in the low intertidal zone were not feeding during upwelling (Table 4.2). Those individuals that occupied higher zones during upwelling were frequently feeding (40-84%), but the collective impact was presumably low since few sea stars were present in these zones during upwelling periods (Table 4.2, Fig. 4.8B).

In contrast, during periods of warmer water most sea stars moved up into the *Mytilus trossulus* and *Pollicipes polymerus* zone to feed (Fig. 4.7). The total number of sea stars in this zone or above (i.e., along the *Mytilus californianus* border) was positively related to water temperature (Table 4.3; "water temp", $p < 0.05$, Fig. 4.8).

Figure 4.6 Temporal variation in the density of *Pisaster* in relation to changes in water temperature during 1May-1September 1995, 1996, and 1997. Sea star data (dotted lines) are mean densities (±SEM) recorded in 20-26 permanently marked plots at Bob Creek Wayside and Strawberry Hill. Water temperatures (solid lines) are High Tide Water Temperatures (the mean of all readings from 2 hours before to two hours after each high tide) recorded by intertidal data-loggers (n = 1-3) located near the plots. Horizontal reference line represents 12°C.

Figure 4.7 Temporal variation in the vertical distribution and abundance of *Pisaster* along a 30m wall transect at Bob Creek Wayside. The total number of sea stars was recorded within each of three intertidal zones: ***Mytilus californianus*** **border** (black bar; above or within 15 cm of the lower limit of the mussel bed), ***M. trossulus-Pollicipes*** **zone** (cross hatched bar; the zone characterized by *M. trossulus* and *Pollicipes polymerus*, from approx. +0.7 m to +1.2 m), **Low zone** (gray bar; the zone < +0.7 m). To examine the influence of water temperature on vertical distribution, recent water temperatures were calculated as the mean water temperature during the four high tides preceding each sampling date. The letter **"c"** above a bar indicates recent cold water upwelling (with a mean water temperature ≤ 10°C over the previous four high tides), whereas the letter **"w"** indicates warmer conditions (≥ 12°C).

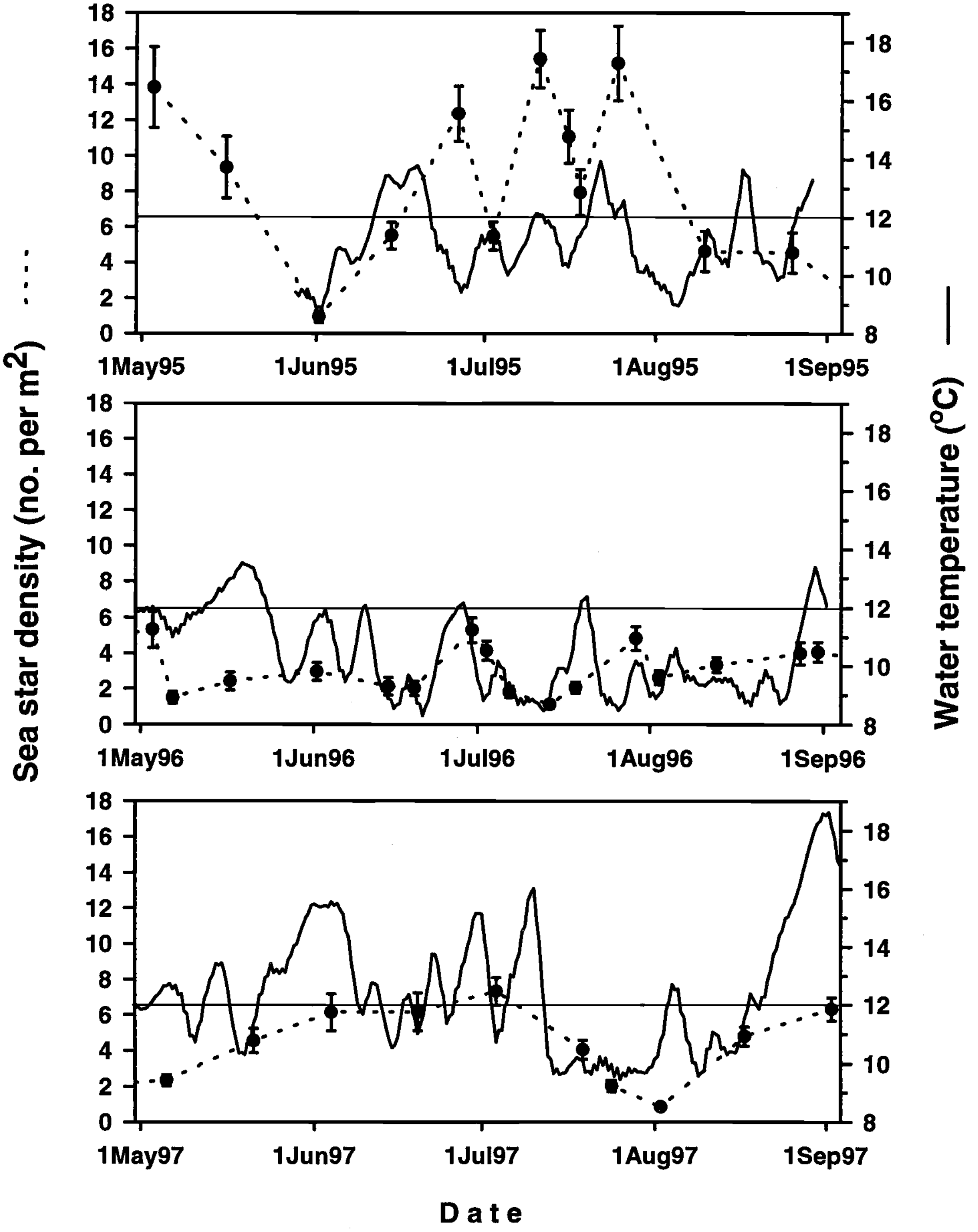
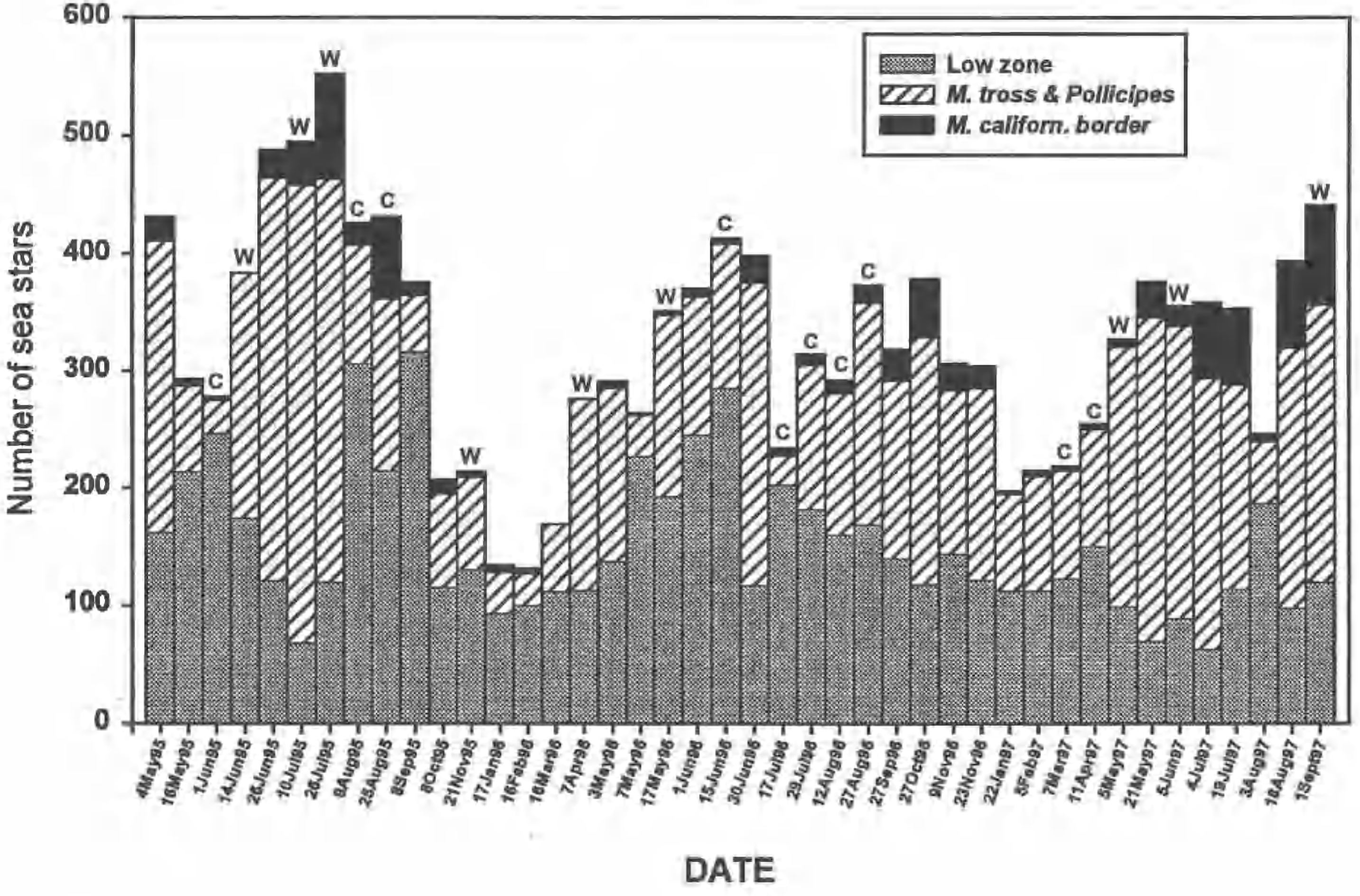

Sea star density (no. per m^2) · · · ·
Water temperature (°C) ——
18
16
14
12
10
8
6
4
2
0
1May95
1Jun95
1Jul95
1Aug95
1Sep95
1May96
1Jun96
1Jul96
1Aug96
1Sep96
1May97
1Jun97
1Jul97
1Aug97
1Sep97
Date

Figure 4.6

Figure 4.7


600
500
400
300
200
100
0
Number of sea stars
Low zone
M. tross & Pollicipes
M. californ. border
C
W
W
W
C
C
W
W
W
C
C
C
C
C
C
C
W
W
W
4May95
16May95
1Jun95
14Jun95
26Jun95
10Jul95
26Jul95
8Aug95
25Aug95
8Sep95
8Oct95
21Nov95
17Jan96
16Feb96
16Mar96
7Apr96
3May96
7May96
17May96
1Jun96
15Jun96
30Jun96
17Jul96
29Jul96
12Aug96
27Aug96
27Sep96
27Oct96
9Nov96
23Nov96
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18Aug97
1Sept97
DATE

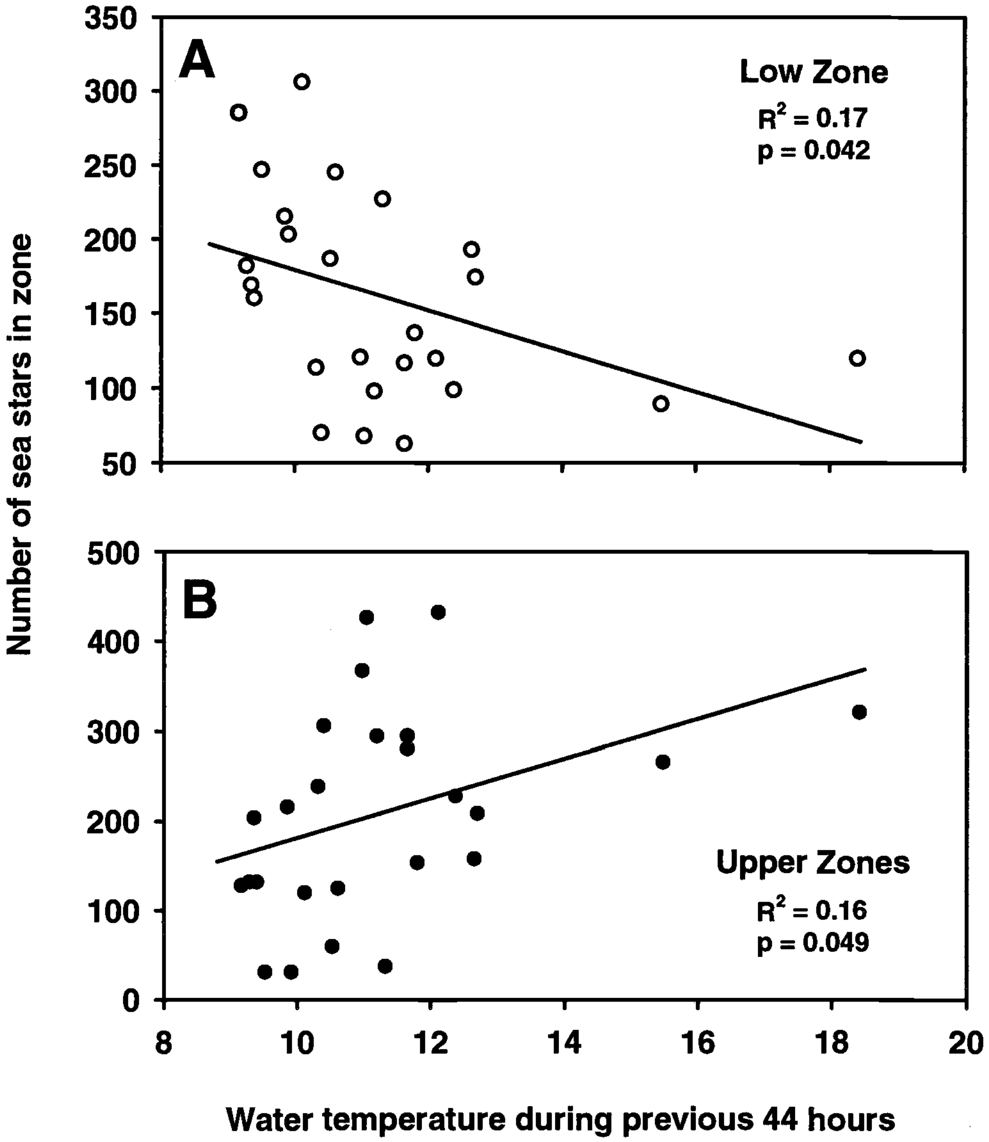

Figure 4.8 Regressions of sea star abundance along the 30m wall transect vs. recent water temperature during the four high tides preceding sampling. Each point represents one sampling date, and only non-winter dates (from 15April-1November) are plotted in order to focus on the influence of seasonal upwelling. Data are the total number of individuals in (**A**) the low zone (< +0.7 m), and (**B**) upper zones (> +0.7 m, including the *M. trossulus* and *Pollicipes* zone as well as the *M. californianus* border). Exclusion of the two warm water points (>15°C, during late summer 1997) did not dramatically alter the results for either the low zone ($R^2 = 0.15$, $p = 0.038$) or the upper zones ($R^2 = 0.15$, $p = 0.064$), so these points were included in the analyses.

Table 4.1 Multiple linear regression analysis of sea star abundance in the low zone (< +0.7 m) as a function of season and recent water temperature. All sea stars in this tidal zone were counted along a 30m intertidal wall at Bob Creek Wayside (n = 37 dates). Water temperature is the mean of the four High Tide Water Temperatures prior to sampling (i.e., the water temperature during the preceding 44 hours). Season is an indicator variable representing winter (1November-15April) vs. the remainder of the year. Tidal amplitude (p = 0.78), potential heat stress (p = 0.69), and all interaction terms were non-significant and were dropped from the model. SE: standard error; df: degrees of freedom; MS: mean squares; Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

$R^2 = 0.253$ n = 37

EFFECT	Coefficient	SE	t	2-sided p-value
INTERCEPT	266.16	59.02	4.51	**0.0001**
WATER TEMP	-13.06	5.07	-2.58	**0.0145**
SEASON	41.39	8.63	2.22	**0.0331**

ANALYSIS OF VARIANCE

SOURCE	df	MS	F	p-value
Regression	2	16200.0	5.76	**0.0070**
Residual	34	2814.6		

Table 4.2 Vertical distribution and feeding activity of sea stars during four upwelling events. The abundance of sea stars was sampled along a 30m wall at Bob Creek Wayside within three intertidal zones (listed from highest to lowest): ***M. calif* border** (above or within 15cm of the lower limit of the *M. californianus* bed), ***M. tross-Pollic*** (the zone characterized by *M. trossulus* and *Pollicipes polymerus*, from approx. +0.7 m to +1.2 m above MLLW), **Low zone** (the zone < +0.7 m). Water temp = the mean water temperature during the high tide immediately preceding sampling; # of sea stars = total number of individuals along the 30m wall; % of sea stars feeding = the percent of individuals within each zone that were actively feeding or held the remains of prey at the oral disk.

DATE:	**25-Aug-95**	**16-Jun-96**	**1-Jul-96**	**17-Jul-96**
Water temp (^oC):	9.65	8.32	8.86	8.94
# of sea stars:	414	313	391	234
<u>% of sea star total in each zone:</u>				
M. calif border	16.9	1.6	8.4	2.1
M. tross-Pollic	32.4	33.9	57.3	9.4
Low zone	50.7	64.5	34.3	88.5
<u>% of sea stars feeding:</u>				
M. calif border	48.6	40.0	78.8	40.0
M. tross-Pollic	73.9	67.9	83.9	40.9
Low zone	28.1	6.4	23.9	1.9

Several authors have suggested that the height of *Pisaster* on the shore may be dictated by the upper water levels reached at the higher high tide of the day (Feder 1956, Feder & Christensen 1966). However, in this study the abundance of sea stars in the upper zones was not related to the height of the most recent higher high tide (Table 4.3, $p = 0.62$). Nor was the number of sea stars in either the low zone or the upper zones related to potential heat stress (i.e., the maximum data-logger temperature during the most recent period of aerial exposure) (Tables 4.1, 4.3, $p > 0.60$). During spring and summer the wall transect was generally censused on the first or second day after a neap tide series. Thus, low tides prior to sampling were very early in the morning, and maximum air temperatures were cool (mean maximum temperature ± SEM = 13.4 ± 0.59°C, n = 25 dates between 1May-1September).

As in the marked plots, the total number of sea stars along the 30m wall transect declined by 50-70% during November through April (Fig. 4.7), presumably because a large portion of the local population moved into subtidal waters (Mauzey 1966). As a result, the abundance of sea stars within both zones was also significantly associated with season (Tables 4.1, 4.3; "season", $p < 0.05$).

Observations along at least 1 km of shore suggested that the trends observed along the wall transect and within the marked plots generally reflected *Pisaster* behavior over a much broader area. Taken together, these observations indicate that during periods of upwelling the majority of sea stars remained in the low intertidal zone and exhibited low feeding activity. During periods of warmer water, sea stars moved into higher zones to feed. As a result, the diet of *Pisaster* in wave-exposed habitats at Bob Creek and Strawberry Hill consisted predominantly of *M. trossulus* and *P. polymerus* (Fig. 4.9). Low numbers of *Pisaster* were typically observed along the lower border of the mussel bed (Fig. 4.7), and consequently *M. californianus* was a minor component of the diet (Fig. 4.9).

Table 4.3 Multiple linear regression analysis of sea star abundance above +0.7m as a function of season and recent water temperature. This tidal range included the *Mytilus trossulus* and *Pollicipes* zone and the lower border of the *M. californianus* bed. All sea stars within this tidal range were counted along a 30m intertidal wall at Bob Creek Wayside (n = 37 dates). Water temperature is the mean of the four High Tide Water Temperatures prior to sampling (i.e., the water temperature during the preceding 44 hours). Season is an indicator variable representing winter (1November-15April) vs. the remainder of the year. Tidal amplitude (p = 0.62), potential heat stress (p = 0.82), and all interaction terms were non-significant and were dropped from the model. SE: standard error; df: degrees of freedom; MS: mean squares; Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

$R^2 = 0.277$ n = 37

EFFECT	Coefficient	SE	t	2-sided p-value
INTERCEPT	-129.49	107.98	-1.20	0.2387
WATER TEMP	21.64	9.27	2.33	**0.0256**
SEASON	93.34	34.09	2.74	**0.0098**

ANALYSIS OF VARIANCE

SOURCE	df	MS	F	p-value
Regression	2	61335.5	6.51	**0.0040**
Residual	34	9420.5		

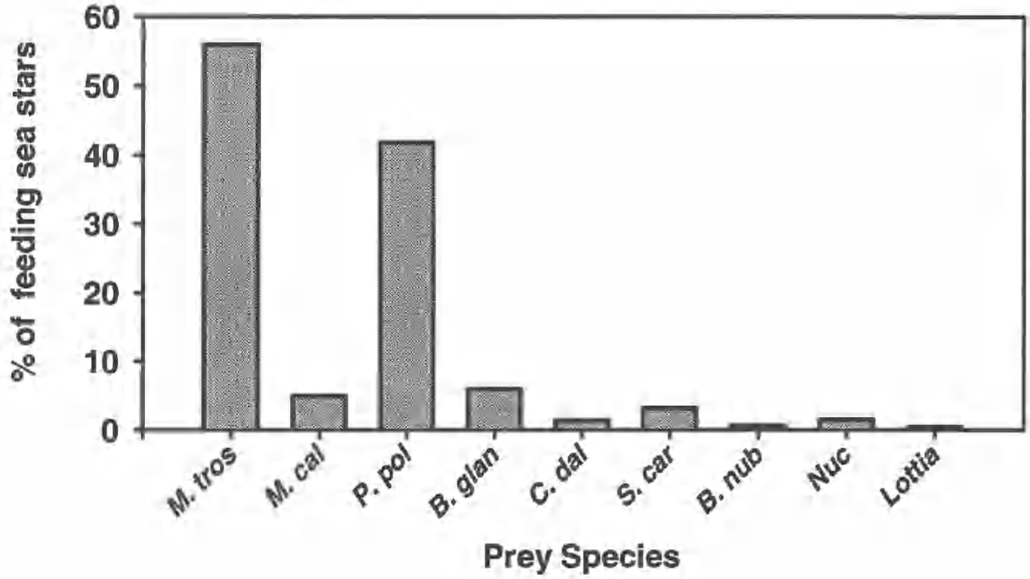

Figure 4.9 Diet of *Pisaster ochraceus* in wave-exposed habitats at Bob Creek Wayside and Strawberry Hill during Summer 1995 and 1996 (n = 14 dates). The % of feeding sea stars is the percent of actively feeding individuals (n = 1664) observed feeding on prey species coded as follows: M.tros = *Mytilus trossulus*; M.cal = *M. californianus*; P.pol = *Pollicipes polymerus*; B.glan = *Balanus glandula*; C.dal = *Chthamalus dalli*; S.car = *Semibalanus cariosus*; B.nub = *Balanus nubilus*; Nuc = *Nucella canaliculata* or *N. emarginata*; Lottia = *Lottia* spp. The cumulative % exceeds 100% because *Pisaster* often feeds on more than one prey species at a time.

Predation Intensity Experiments

Measures of predation on transplanted mussels confirmed that the intensity of *Pisaster* predation was reduced during upwelling. On reefs without sea stars, mean percent survivorship (± SEM) 14 days after cages were removed was 97.4 ± 0.45% (n = 60 transplants). This suggests that (1) mussels transplanted under Vexar™ mesh reattached securely to the rock, (2) the sand and surge channels surrounding sea star removal reefs effectively slowed the rate of sea star re-invasion, and (3) sources of mortality other than predation by sea stars (e.g., dislodgement by waves, consumption by crabs or river otters, etc.) had little effect during these experiments.

On reefs with sea stars, feeding individuals were regularly observed at low tide hunched over the mussel transplants. Occasionally sea stars removed a mussel from the clump and then started moving away from the transplant. However, I never found these individuals >1m from the transplant despite periodically inspecting individuals at greater distances. These observations suggest that a 1m radius around each transplant was an appropriate area for the assessment of sea star densities.

Measurements of predation intensity suggested that the strength of the sea star-mussel interaction was regulated by water temperature. During the third experiment (17July-1August) there was a persistent cold water upwelling event during which water temperature dropped about 3°C (Fig. 4.10A). The per capita interaction strength of *Pisaster* on *Mytilus* (i.e., the difference in rates of mussel mortality on reefs with and without sea stars divided by local sea star density) was sharply reduced during this period (Fig. 4.11A, ANOVA, contrast the third period with the other four; $F_{1,53} = 5.73$, $p = 0.020$). During upwelling there was an even greater proportional drop in the collective (i.e., per population) impact of *Pisaster* (Fig. 4.11C, ANOVA, contrast the third period with the other four; $F_{1,53} = 7.20$, $p = 0.0097$). This occurred as a result of two effects: individual sea stars consumed less (lower per capita effects) and the local density of sea stars was reduced during upwelling (Fig. 4.11B, ANOVA, contrast the third period with the other four; $F_{1,53} = 5.33$, $p = 0.025$), presumably as a result of more sea stars remaining inactive in low zone channels or shallow subtidal waters.

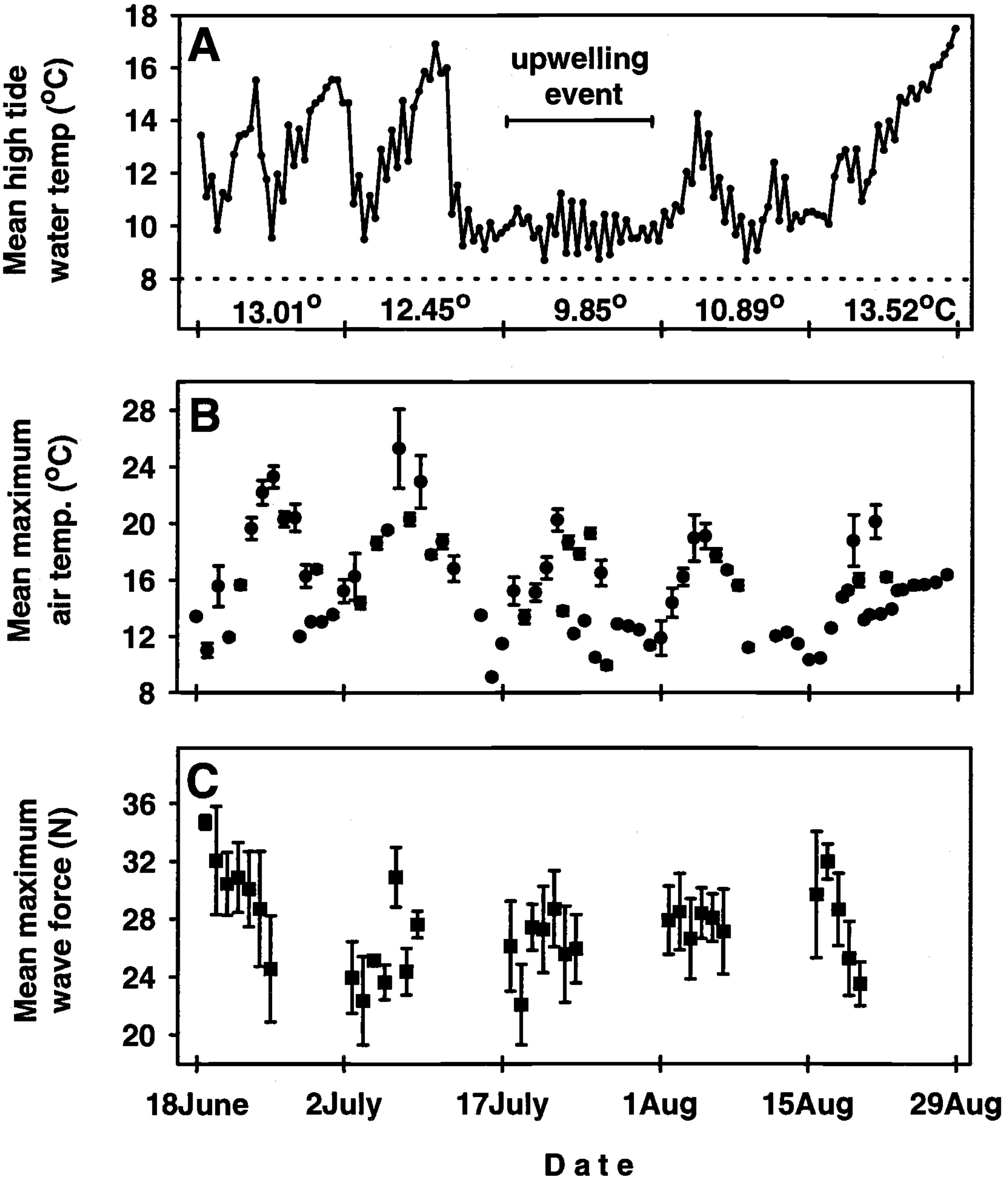

Figure 4.10 Environmental conditions during experiments measuring rates of predation by sea stars on mussels. The five, consecutive 14-day periods are noted on the x-axis. All data are means ± SEM for three study sites. **(A)** High Tide Water Temperature (mean from two hours before to two hours after each high tide). Temperatures above the x-axis are the overall means for the 27 high tides of each period. **(B)** Maximum air temperature recorded during each low tide exposure. The periodicity in air temperature reflects the tidal cycle, with peak temperatures generally occurring on days when low tide occurred in the late morning. **(C)** Maximum wave force recorded during 24 hour intervals, on 5-7 days/period.

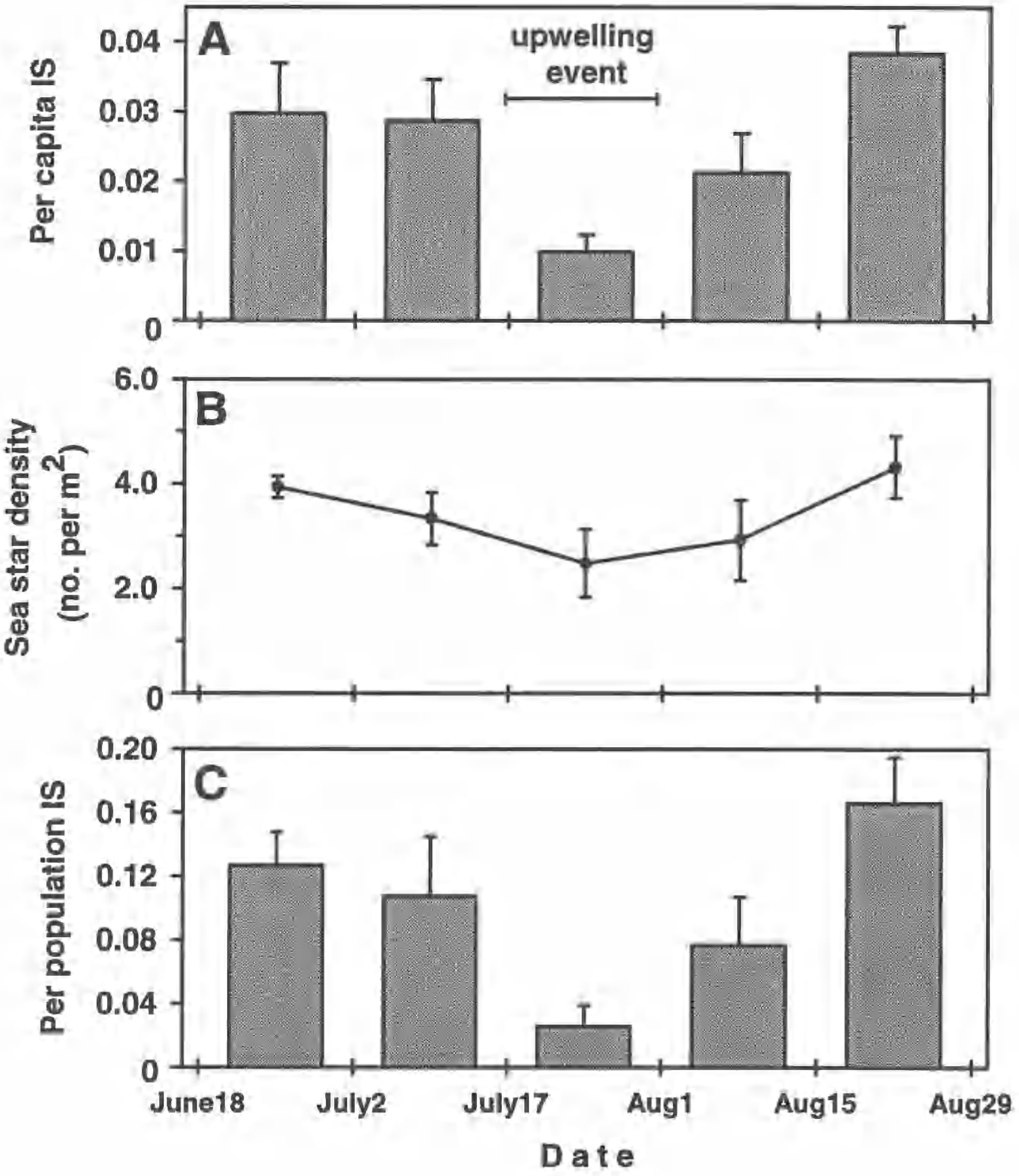

Figure 4.11 Results of field experiments quantifying rates of sea star predation. The five, consecutive 14-day periods are noted on x-axis. Persistent upwelling occurred during the 3rd period (17July-1Aug). All data are means ± SEM for three study sites. **(A)** Mean per capita interaction strength (IS) of sea stars on transplanted mussels during each 14 day period **(B)** Mean local sea star density around mussel clumps **(C)** Mean per population IS of sea stars during each period. Per capita IS, sea star density, and population IS were all significantly reduced during the upwelling event (ANOVA planned contrasts, middle period vs. the other four, $p \leq 0.025$).

Moreover, across all five experiments, both per capita and population IS were linearly related to the mean water temperature during the 14-day periods (Fig. 4.12A and B). The multiple linear regression (MLR) analysis indicated that per capita IS was associated with water temperature (Table 4.4, $p < 0.001$), but not with maximum air temperatures ($p = 0.18$) or wave forces ($p = 0.53$). Similarly, population IS was correlated with water temperature (Table 4.5, $p < 0.001$) but not with maximum air temperatures ($p = 0.13$) or wave forces ($p = 0.74$).

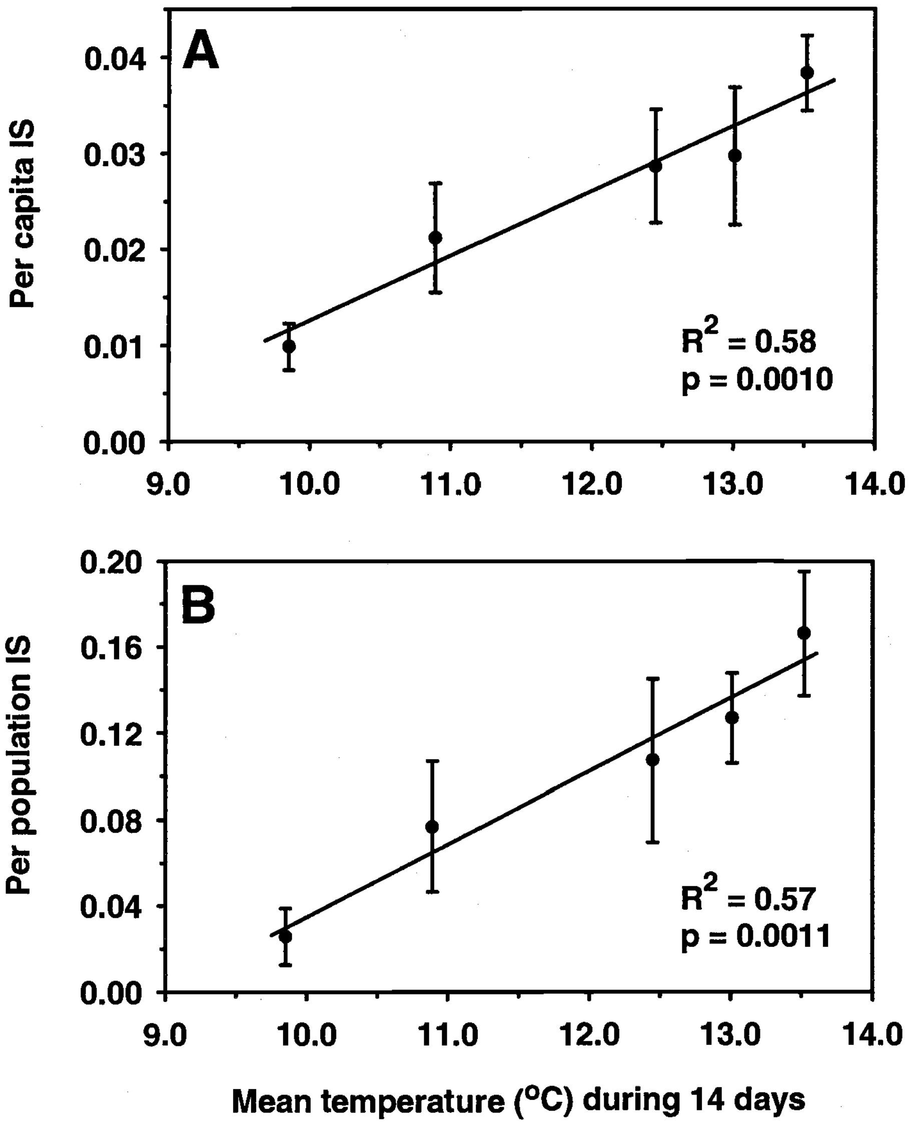

Figure 4.12 Relationship between water temperature and interaction strength (IS). Lines are linear regressions of (A) per capita IS and (B) population IS on water temperature. Interaction strengths are means (± SEM) from the three study sites. Water temperatures are the overall mean High Tide Water Temperature during the 27 high tides of each of the five 14-day experiments.

Table 4.4 Multiple linear regression analysis of mean per capita interaction strength as a function of environmental factors and study sites. Indicator variables for study sites were retained in the model if the extra-sum-of-squares F-test indicated joint significance ($p < 0.05$) for the set of study site variables. Factors or interaction terms that were non-significant ($p > 0.05$) were dropped from the model. SE: standard error; df: degrees of freedom; MS: mean squares; PR = Pigeon Reef, SH = Strawberry Hill. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

$R^2 = 0.809$ n =15

EFFECT	Coefficient	SE	t	2-sided p-value
INTERCEPT	-0.064	0.014	-4.47	**0.0010**
WATER TEMP	0.007	0.001	5.81	**0.0001**
SITE (PR)	0.013	0.004	3.33	**0.0068**
SITE (SH)	0.012	0.004	2.99	**0.0122**

ANALYSIS OF VARIANCE

SOURCE	df	MS	F	p-value
Regression	3	0.00059	15.57	**0.0003**
Residual	11	0.00004		

Table 4.5 Multiple linear regression analysis of mean population interaction strength as a function of environmental factors and study sites. Indicator variables for study sites were retained in the model if the extra-sum-of-squares F-test indicated joint significance ($p < 0.05$) for the set of study site variables. Other factors or interaction terms that were non-significant ($p > 0.05$) were dropped from the model. SE: standard error; df: degrees of freedom; MS: mean squares; PR = Pigeon Reef, SH = Strawberry Hill. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

$R^2 = 0.824$ n =15

EFFECT	Coefficient	SE	t	2-sided p-value
INTERCEPT	-0.336	0.069	-4.86	**0.0005**
WATER TEMP	0.034	0.006	5.96	**0.0001**
SITE (PR)	0.074	0.019	3.89	**0.0025**
SITE (SH)	0.026	0.019	1.35	0.2047

ANALYSIS OF VARIANCE

SOURCE	df	MS	F	p-value
Regression	3	0.0155	17.14	**0.0002**
Residual	11	0.0009		

Throughout these experiments, maximum air temperatures were relatively mild, seldom exceeding 21°C (Fig. 4.10B). Data collected at Strawberry Hill confirmed that temperatures recorded by data-loggers during periods of aerial exposure were an accurate predictor of sea star body temperature (Fig. 4.13; maximum body temperature = 1.02 * maximum logger temp - 0.18, $p < 0.0001$, $R^2 = 0.819$, $n = 197$). Note that the temperature sensor of the data-logger was sealed in air within a hard plastic casing that absorbed solar radiation and therefore did not record air temperature *per se*. These properties of the data-logger may roughly mimic those of a sea star that has large spaces within each arm and an aboral surface that absorbs solar radiation. Using maximum data-logger temperatures as an indicator of sea star body temperature (and thus potential heat stress), there was no suggestion that the upwelling period was more thermally stressful than the other periods (Fig. 4.10B).

Similarly, maximum wave forces recorded at the three sites suggested that the upwelling period was not characterized by high wave stress (Fig. 4.10C). There were no storms during these experiments and maximum wave forces were relatively consistent and low. Finally, there was no evidence that upwelling was associated with increased precipitation that might have reduced sea star predation via osmotic stress. Total precipitation (mm) during periods one through five was 57.15, 1.22, 0, 1.01, and 55.37, respectively. Thus, there was no precipitation recorded during the upwelling event (period 3).

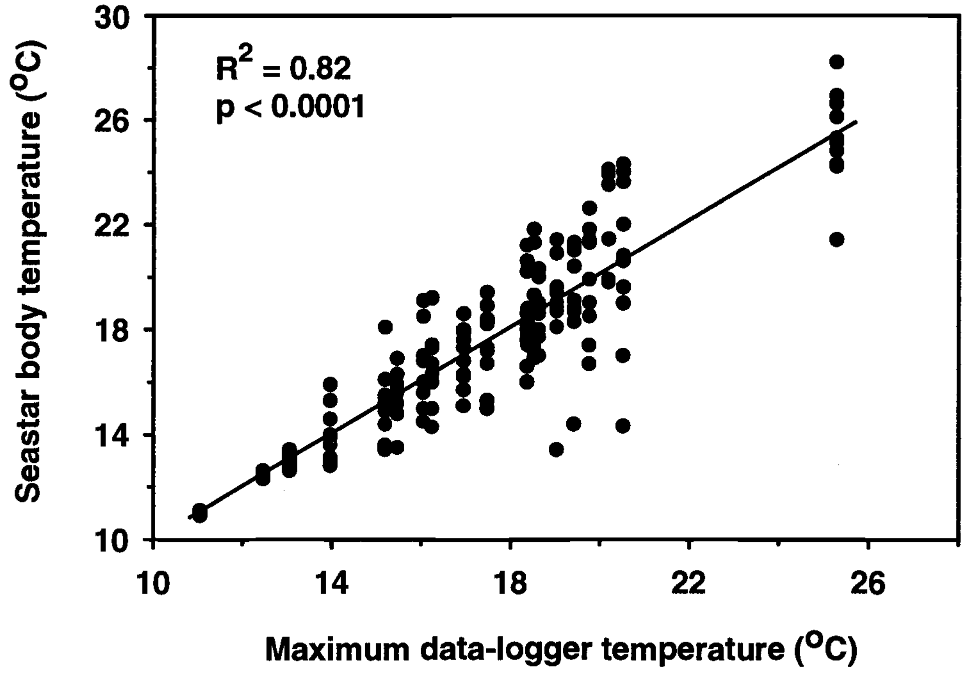

Figure 4.13 Relationship between maximum recorded data-logger temperature and the body temperature of nearby sea stars during low tide at Strawberry Hill. Body temperatures of 10 sea stars were measured just prior to being re-submerged on 20 dates. Linear regression line is shown ($y = 1.02x - 0.18$, $n = 197$). Note that on overcast, cool mornings (i.e., <14°C) there was little variation in body temperature among sea stars. On clear, warmer mornings (i.e., >18°C) sea star body temperatures were more heterogeneous and dependent upon microhabitat.

Sea star density varied significantly among sites (Table 4.6; "site", $p = 0.0024$) and was consistently higher at Pigeon Reef than at the other two sites (mean density ± SEM = 4.36 + 0.38 sea stars/m^2, n = 20 vs. 2.92 = 0.25 sea stars/m^2, n = 40). As expected, more sea stars translated into a greater collective impact; population IS varied significantly among sites (Table 4.7; "site", $p = 0.027$) and was consistently higher at Pigeon Reef. In accordance with this ANOVA result, the MLR analysis also indicated that study site explained a significant portion of the variation in population IS (Table 4.5). Indicator variables for study sites were significant in the regression model (Extra-sum-of-squares F-test, $F_{2,11} = 7.80$, $p < 0.010$), and together water temperature and study sites explained 82.4% of the variation in mean population interaction strength.

Table 4.6 Two-way Analysis of Variance of the effects of site and 14-day period on sea star density. The interaction term SITE*PERIOD was not significant ($p = 0.95$) and was dropped from the model. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

SOURCE	df	MS	F	p-value
SITE	2	16.07	6.79	**0.002**
PERIOD	4	6.63	2.80	**0.035**
ERROR	53	2.37		

Table 4.7 Two-way Analysis of Variance of the effects of site and 14-day period on log-transformed population interaction strengths. The interaction term SITE*PERIOD was not significant ($p = 0.92$) and was dropped from the model. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

SOURCE	df	MS	F	p-value
SITE	2	8.52	3.87	**0.027**
PERIOD	4	7.91	3.59	**0.012**
ERROR	53	2.21		

There was conflicting evidence that per capita IS also varied among sites. Indicator variables for study sites were significant in the MLR analysis for per capita IS (Extra-sum-of-squares F-test, $F_{2,11} = 6.74$, $p < 0.025$). Together, water temperature and sites explained 80.9% of the variation in mean per capita interaction strength (Table 4.4). However, the ANOVA results did not suggest significant variation among sites (Table 4.8; "site", $p = 0.20$). In four of the five experiments, Pigeon Reef had the highest mean per capita IS of the three study sites although these differences were not statistically significant (Tukey-Kramer, $p > 0.05$). The weak trend for the site with the highest sea star density to have the highest per capita effects may suggest that the per capita effects of *Pisaster* are a nonlinear function of density (e.g., Ruesink 1998).

Table 4.8 Two-way Analysis of Variance of the effects of site and 14-day period on log-transformed per capita interaction strengths. The interaction term SITE*PERIOD was not significant ($p = 0.99$) and was dropped from the model. df: degrees of freedom; MS: mean squares. Bold face p-values indicate that the factor is significant at $\alpha = 0.05$.

SOURCE	df	MS	F	p-value
SITE	2	2.53	1.67	0.197
PERIOD	4	3.89	2.58	**0.048**
ERROR	53	1.51		

DISCUSSION

Linking Predation and Temperature

These field observations and experiments suggest that the strength of the interaction between this keystone predator and its prey is directly regulated by slight changes in water temperature. This conclusion is strengthened by laboratory experiments reported in the previous chapter (Chapter 3). In temperature controlled tanks, *Pisaster* maintained at a constant 9°C consumed, on average, 29% fewer mussels (*Mytilus trossulus*) than sea stars maintained at a constant 12°C. Sea stars alternately exposed to 14 days at 12°C and 14 days at 9°C, fed intensely at 12°C, more slowly at 9°C, then faster again at 12°C.

The sensitivity of *Pisaster* predation to small changes in water temperature is surprising since changes of a few degrees, in the middle of a species' tolerance range, have traditionally been viewed as inconsequential by marine ecologists. *Pisaster ochraceus* ranges from at least Punta Baja, Baja California, Mexico to Prince William Sound, Alaska. Populations of *Pisaster* living near these range limits regularly experience water temperatures > 20°C and < 4°C, respectively. The changes in predation in this study were observed over the range of 9-13°C, in the middle of *Pisaster*'s thermal tolerance range.

Although generally overlooked by marine ecologists, some decrease in predation rate with declining temperature is expected from a physiological perspective. The direct effects of colder temperatures on rates of movement, metabolism, and digestion should slow feeding rates (Cossins & Bowler 1987, Birkeland & Lucas 1990). *Pisaster* shows a lowered metabolic rate at lower temperatures (Paine, *personal communication* in Mauzey 1966) and feeding has been observed to decline or stop completely at low temperatures in several other species of sea stars (Feder & Christensen 1966).

Field observations suggested that sea stars remained in the low intertidal and shallow subtidal during upwelling (Figs. 4.7, 4.8), and that most of these individuals were not feeding (Table 4.2). Similarly, *Pisaster* predation on transplanted mussels was sharply reduced during upwelling (Fig. 4.12C), not only because each sea star consumed less (Fig. 4.12A), but also because densities of foraging sea stars were locally reduced (Fig. 4.12B). This two-fold effect may be a common response of poikilothermic consumers to temperature change. Not only should colder temperatures slow feeding rates, but a greater proportion of individuals should become inactive and seek shelter as temperature declines to some species-specific level (e.g., Aleksiuk 1976, Frazer & Gilbert 1976, Hunt 1977, Whicker & Tracy 1987). For example, the rate of predation of ladybird beetles on aphids was found to decrease exponentially as temperature decreased, since both mean walking speed and the proportion of ladybirds that were actively foraging decreased linearly with temperature (Frazer & Gilbert 1976, Kingsolver 1989).

Interestingly, the seasonal decline in *Pisaster* abundance in the intertidal zone did not appear related to water temperature. In the San Juan Islands, WA, Mauzey (1966, 1967) observed a 50% seasonal decline in the intertidal abundance of sea stars that coincided with a plateau of minimum winter water temperatures from November through March or April. In contrast, in Oregon, water temperatures typically remained at 11-12°C during November (Chapter 3) and then generally declined 1-2 °C in mid-December, well after intertidal sea star abundances had already declined (Fig. 4.5). Thus, it appears that seasonal changes in *Pisaster* distribution in Oregon were not triggered by decreases in water temperature. Other factors such as increased wave action, decreased aerial temperatures, reduced prey abundance, changes in photoperiod, or the onset of gametogenesis might drive the seasonal change in sea star distribution (Mauzey 1966).

There was no evidence in this study that sea star predation was altered by variation in potential heat stress or wave stress. Maximum air temperatures and wave forces were both relatively low and consistent throughout the predation experiments (Fig. 4.10B, C). Desiccation and heat stress are presumed to set *Pisaster*'s upper foraging limit, and consequently the lower limit of the mid-zone *Mytilus californianus* bed (Paine 1974). Surprisingly, the connection between desiccation and *Pisaster*'s vertical foraging range has not been rigorously explored. The little evidence that is available suggests that *Pisaster* may be fairly resistant to aerial exposure; individuals can apparently tolerate at least 55 hours of exposure with no detectable signs of damage (Feder 1956, Feder & Christensen 1966, Landenberger 1969). Further research is needed to identify possible sub-lethal effects of aerial exposure on *Pisaster*.

My study indicates a direct link between water temperature and the strength of keystone predation in these rocky intertidal communities. These data provide mechanistic insight into how temperature change impacts an important species interaction. Such information lies at the heart of individual-based and physiologically structured models (Dunham 1993, Kingsolver et al. 1993, Murdoch 1993). These models seek to predict how the influence of environmental change on the physiology of individual organisms translates into population or community level effects. Knowledge of how temperature changes influence the *Pisaster-Mytilus* interaction should thus facilitate specific predictions about how anticipated climatic changes would impact these rocky intertidal communities.

There is, however, a major obstacle to this and similar global change studies; physical models used to predict climatic changes are resolved to a scale far broader than the relatively local scale of ecological studies (Root & Schneider 1993). General circulation models (GCMs) represent the globe as a grid of boxes and use laws of atmospheric physics to predict average conditions in each box. Although improvements have been made, computational limits still restrict GCMs to using boxes that are about 160 x 160 km. This scale is too coarse to accurately predict changes in regional climate (Root & Schneider 1993).

Even more uncertain are changes in the frequency, timing, and intensity of seasonal or episodic events such as coastal upwelling, storms, frosts, heat waves, or fire (Root & Schneider 1993). Many researchers have suggested that it is changes in extreme or seasonal events, rather than changes in mean conditions, which may have the greatest effects on individuals, populations, and communities (Cossins & Bowler 1987, Dobson et al. 1989, Kingsolver et al. 1993, Root & Schneider 1993, Bhaud et al. 1995; see also Chapter 3). It is possible to generate some estimates of climatic variability from physical models, yet these data are rarely considered by climatic modelers (Root & Schneider 1993). There is thus little information available regarding the sort of variability that may be central to predicting the responses of ecosystems to climatic change. For example, in the Pacific Northwest, the density and impact of *Pisaster* in the rocky intertidal zone are highest during the summer (the upwelling season). It is thus changes in the frequency and intensity of upwelling, rather than changes in annual sea surface temperature, that should play the greater role in regulating sea star predation.

Predicting Changes in Upwelling Intensity

To what extent can we predict how global warming will alter patterns of upwelling along the Pacific coast of North America? Coastal upwelling is a complex process affected by atmospheric and oceanic conditions at local, regional, and hemispheric scales (Barber 1988). The intensity of upwelling (i.e., the temperature of upwelled waters) and its frequency (i.e., the duration of events and number of events per season) varies naturally from year to year and among different sites along the coast (Table 4.9). Variation in upwelling is driven primarily by two factors: strength of alongshore winds and the depth of the thermocline. Understanding how global warming may influence these two factors is the key to understanding how upwelling patterns may be changed.

Table 4.9 Interannual variation in upwelling intensity at Neptune State Park, OR, 1995-98. Values are the percent of High Tide Water Temperatures from 1 May to 1 September in each of three temperature ranges (<10°C, 10-12°C, and >12°C). Water temperatures were recorded by data-loggers (n = 1-3) in the low intertidal zone. High Tide Water Temperatures were calculated as the mean of all readings from 2 hours before to two hours after each high tide. On the Oregon coast, upwelling is generally marked by water temperatures below 10°C. The reduction of upwelling in 1997 was associated with the 1997-98 El Niño event.

YEAR	<10°C	10 – 12°C	>12°C
1995	23.46	46.37	30.17
1996	48.54	31.38	20.08
1997	13.81	33.47	52.72
1998	29.58	48.33	22.08

Alongshore Wind Stress

Unfortunately, current GCM's lack the resolution to accurately estimate regional winds. Present estimates of wind fields generally underestimate historical upwelling indices by 10-20 times (Harte et al. 1992). Nevertheless, an understanding of the forces that drive coastal winds suggests that global warming may increase alongshore wind stress. Bakun (1990) argued that global warming may intensify the daytime heating of continental land masses, which should accentuate the atmospheric pressure gradient between the continental low-pressure cell and the higher pressure cell over the cooler ocean. As this gradient strengthens, alongshore wind stress, and consequently coastal upwelling, should intensify. Wind observations from ships at sea suggested that alongshore wind stress off the Northern California coast increased over the period from 1946-1988 (Bakun 1990). A more detailed analysis of wind data during this period indicated that a trend of increasing seasonal wind stress was apparent from the US-Mexico border to Cape Mendocino (32-40°N), and also along the central Oregon coast (45°N) (Schwing & Mendelssohn 1997).

Depth of the Thermocline

Coastal upwelling is also strongly influenced by the depth of the thermocline. As the depth of the thermocline increases, a given wind stress draws upwelled waters from shallower, warmer layers which are typically nutrient depleted (Roemmich & McGowan 1995). In recent decades, there is evidence of a deepened thermocline along at least some regions of the Pacific coast of North America. During the period from 1951 to

1993, surface waters off of Southern California warmed about 1.5°C and the depth of the thermocline increased. During this same period, the biomass of macrozooplankton in this region decreased by an astonishing 70%, presumably because of damped upwelling that reduced nutrient input and primary productivity (Roemmich & McGowan 1995).

The depth of the thermocline is influenced by processes operating at the scale of the entire Pacific basin (Barber 1988). Under normal conditions, the trade winds blow westward across the tropical Pacific and pile up warm surface water in the west Pacific. As a result, the depth of the thermocline is tilted across the Pacific basin, being deep in the western Pacific and shallow in the eastern Pacific, along the margin of North and South America. During El Niño-Southern Oscillation (ENSO) events, the trade winds relax, and the warm water pool expands eastward. This has the effect of reducing the basin-wide tilt in the thermocline, and deepening the thermocline in the eastern Pacific (Barber 1988).

As a result of the deeper thermocline, the frequency and intensity of cold water upwelling are generally reduced during ENSO years. These changes were apparent along the central Oregon coast during the recent 1997-98 El Niño. During 1997, only 13.8% of May-August high tides fell below 10.0°C, compared to 48.5% of high tides during this same period in 1996 (a non-ENSO year) (Table 4.9). Nutrient input into the euphotic zone (and resultant primary productivity) are also typically reduced during El Niño years, leading to well-documented disruptions of marine food webs in upwelling regions (Glynn 1988).

The depth of the thermocline may also be influenced by poorly understood regime shifts in the northeastern Pacific (Lange et al. 1990, Roemmich & McGowan 1995, McGowan et al. 1998). There appears to be a cyclic warming of the California

Current and deepening of the thermocline that occurs on an interdecadal scale, with alternating states lasting roughly 20-50 years. A warm phase has persisted in the California Current since 1976 and appears to be associated with a southward shift and intensification of the Aleutian Low. Earlier explanations hypothesizing switches in the relative strength of currents flowing into the California Current vs. the Gulf of Alaska do not appear to have physical support (McGowan et al. 1998). Thus, it remains unclear what factors trigger these interdecadal regime shifts or whether they are related to ENSO events (Trenberth & Hurrell 1994, McGowan et al. 1998).

Upwelling and Climate Change

Some models indicate that global warming may produce persistent El Niño-like conditions (Meehl & Washington 1996), which would depress the thermocline in the eastern Pacific, and weaken coastal upwelling (Peterson et al. 1993). El Niño events have become more frequent and intense in recent decades, perhaps as a result of global climatic change (Trenberth & Hoar 1996, 1997). However, since GCMs are currently unable to accurately reproduce ENSO events, it is not yet possible to definitively link changes in ENSO behavior to global climatic change (Trenberth & Hoar 1997).

It is possible that increased daytime heating of the interior valleys along the Pacific coast may increase alongshore wind stress (Bakun 1990), whereas changes in the Pacific Ocean basin may depress the thermocline. The net effect of such changes would be an increase in the *volume* of upwelled water, but the water would be drawn from shallower, warmer layers (Peterson et al. 1993). Available physical data are consistent with this prediction. Seasonal wind stress (April-July) during the period 1946-1990 increased over the region 32-40°N. However, since at least 1970 sea surface temperatures during the upwelling season (April-July) have generally *increased* over the entire region from 23-47°N (Schwing & Mendelssohn 1997).

Although upwelling patterns in the California Current appear to be undergoing dramatic changes, it is uncertain whether these changes are the result of a natural regime shift, changing patterns of ENSO events, anthropogenic global warming, or some combination of these phenomena. At present, it is difficult to predict how climatic change will alter patterns of coastal upwelling. However, since the physical mechanics of upwelling are sensitive to atmospheric and oceanic conditions, it is likely that climatic disruptions will generate significant changes in upwelling patterns. These changes will probably be complex and vary among regions. Although greater wind stress may increase upwelling circulation, it is likely that this water will be drawn from shallower layers leading to a general reduction in cold water upwelling.

Potential Changes in Rocky Intertidal Communities

How might rocky intertidal communities along the central Oregon coast be impacted by a reduction in the frequency and intensity of cold water upwelling? My results suggest that a long-term damping of upwelling should increase the strength of the *Pisaster-Mytilus* interaction in these communities by shortening the amount of time when sea star feeding is reduced. This change would not be expected to directly impact species diversity in the low zone; sea stars would continue to hold the competitively dominant *M. californianus* in check. However, increased *Pisaster* predation might diminish the vertical extent of the mid-zone mussel beds. Since mussel beds provide habitat and shelter for diverse taxa (e.g., crabs, worms, sea cucumbers, and other invertebrates; Suchanek 1979), reducing the areal extent of mussel beds may reduce the abundance of these infaunal species.

In addition, increased rates of *Pisaster* predation in the low zone at these study sites should decrease the abundance of preferred mussel prey, which might increase sea star effects on prey that are currently a minor part of *Pisaster*'s diet (such as acorn barnacles, limpets, chitons, and whelks, Fig. 4.9; see also Navarrete & Menge 1996). These changes might, in turn, trigger other indirect effects in the community. For example, decreases in the abundance of herbivorous grazers like limpets and chitons, along with a reduction in the density of sessile space-holders such as barnacles, might increase the abundance of low zone algae. However, a reduction in the upwelling of deep water would also reduce the input of nutrients, which could trigger opposing changes in the abundance and composition of macroalgae (Nielsen 1998). Although these changes are plausible, it is telling that even in this well-studied community, it is difficult to make detailed predictions about community-level changes.

This coarse level of resolution may be typical of attempts to predict community-level responses to climatic change. The surprising sensitivity of *Pisaster* predation to water temperature suggests that substantial community changes will occur, but provides only general ideas about the specifics of these changes. Nevertheless, examining the response of key species interactions to temperature change should help identify ecosystems that are particularly vulnerable to climatic change. If key species interactions are sensitive to temperature, they may act as leverage points through which even small climatic changes can effect surprisingly large community changes. In contrast, systems with key interactions that are relatively insensitive to temperature change may have patterns of species composition and diversity that are more stable in the face of climatic changes.

Conclusions

There is a strong need to incorporate the potential impacts of altered species interactions into evaluations of how climatic change may affect biotic communities. To date, potential effects on species interactions have been overshadowed by a disproportionate emphasis on shifts in species' ranges. The possibility that natural systems may be disrupted more immediately and dramatically by changes in species interactions has been acknowledged, but little progress has been made in testing this hypothesis.

The sheer number of species links within even relatively simple communities complicates attempts to address this problem. A reasonable strategy is to focus on key species interactions as pathways with a high capacity to effect changes in natural systems. Community ecology offers experimental approaches which can quantify the strength of these interactions and their sensitivity to changes in environmental factors. I have illustrated the value of these approaches using experiments in a well-described, model system. These experiments are the first to document a direct mechanistic link between small temperature changes and the strength of a keystone interaction.

This study underscores the importance of evaluating physiological and behavioral effects beyond those associated with a species' thermal limits. These studies were carried out on the central Oregon coast, in the middle of the geographic range of *Pisaster ochraceus*, which ranges from Baja California, Mexico to Alaska. Nevertheless, small changes in water temperature, well within this species thermal tolerance range, were sufficient to dramatically alter the impact of this predator.

Variation in predation intensity in this study was linked to the frequency and intensity of seasonal upwelling, a process which is highly variable among years and extremely sensitive to atmospheric and oceanographic conditions. The coupling of a temperature-sensitive keystone interaction and a climatically-sensitive seasonal process may represent a potent recipe for community change. Systematic changes in upwelling may generate rapid changes in these communities through strong effects on a keystone predator.

Despite this insight, it is difficult to predict specific changes that may arise in this community as a result of global warming. In part, this is because of uncertainty in modeling changes in upwelling patterns. However, predicting exactly how changes in one species may be transmitted directly and indirectly through species networks may ultimately be the greater obstacle. Nevertheless, testing the response of key species interactions to environmental change should help identify ecosystems that are particularly vulnerable to climate change. Whether key species interactions in other systems are equally sensitive to temperature is unknown. The results of this study suggest that impacts of climate change on communities and ecosystems may be more immediate and complex than generally realized.

CHAPTER 5

General Conclusions

The studies presented in this dissertation suggest that upwelling-related variation in nearshore conditions can profoundly influence intertidal systems at the organismal, population, and community level. Rates of invertebrate growth and feeding, as well as community processes such as keystone predation, appear tightly linked to subtle variation in oceanographic conditions. In Chapter 2, I presented findings on the short-term growth of two barnacle species in relation to spatial and temporal variation in water-column Chl-a concentration. Several recent papers have suggested that the growth of barnacles and other suspension feeders may be positively related to phytoplankton abundance (Bertness et al. 1991, Menge 1992, Bustamante et al. 1995). In my study, barnacle growth rates were low during a persistent upwelling event and increased two to three-fold during the subsequent relaxation. Although this increase coincided with a large phytoplankton bloom at one site, growth rates also increased at a second site where no bloom was recorded. The data presented suggest that barnacle growth may be enhanced by multiple factors associated with the relaxation of upwelling, including warmer water temperatures and an increase in the concentrations of both phytoplankton and zooplankton.

In Chapter 3, I reported controlled laboratory experiments used to test the effect of small changes in water temperature on the feeding, growth, and energetics of two important intertidal predators, the sea star *Pisaster ochraceus* and the whelk *Nucella canaliculata*. I am aware of no previous studies that have examined how the temperature fluctuations characteristic of episodic upwelling might affect benthic organisms. Rather, laboratory studies investigating thermal effects on feeding have generally held animals at constant temperatures in treatments that differed by at least 5°C. In my study, feeding rates of both sea stars and whelks were sharply reduced by a decrease in water temperature of only 3°C. Moreover, there appeared to be an energetic advantage to living under the cyclic temperatures characteristic of upwelling systems. Benthic predators may thus feed intensely during periods of warmer water while benefiting from reduced metabolic costs during periods of cold-water upwelling. By altering the amount of surplus energy available for reproduction, subtle variation in upwelling patterns could alter the fitness of individuals and ultimately impact the size of local populations.

In Chapter 4, I presented results of field manipulations to quantify the association between small changes in water temperature and the strength of the keystone interaction between *Pisaster ochraceus* and *Mytilus californianus*. Both per capita and per population effects of sea stars on transplanted mussels were sharply reduced during upwelling. These results suggest that changes in the frequency and intensity of upwelling may alter the dynamics of intertidal communities through effects on keystone predation. More broadly, this study implies that key species interactions that are sensitive to temperature may act as leverage points through which small changes in climate could generate large changes in natural communities.

The results presented in this dissertation contribute to the growing recognition that local communities are often shaped by processes operating at larger scales than those that have traditionally been investigated in experimental field studies (Menge 1992, Brown 1995). In many ways, analogous developments have characterized research on the mechanics of coastal upwelling. Oceanographers initially focused on the physical processes occurring in the limited region where upwelling occurred (Barber 1977). However, as this work progressed it became clear that coastal upwelling was embedded in the large-scale dynamics of the Pacific basin and global wind system. In particular, the 1982-83 El Niño event demonstrated the strong influence of basinwide processes on coastal upwelling (reviewed by Barber 1988, Peterson et al. 1993).

The discovery that coastal upwelling is integrally related to the Pacific basin heat budget has sparked predictions that upwelling patterns may be altered by global warming. If global warming increases the areal extent of the warm water pool in the western Pacific (as occurs during ENSO events), the cross-basin tilt of the thermocline will be reduced, thereby deepening the thermocline in the eastern Pacific (Peterson et al. 1993). As a result, upwelled water would be drawn from shallower, warmer layers (Roemmich & McGowan 1995), regardless of whether or not regional warming enhances alongshore winds (Bakun 1990). Predicting the impact of climatic change on local upwelling patterns is therefore dependent upon understanding the influence of basinwide processes.

There has thus been a trend towards "scaling-up" in the investigation of both intertidal communities and coastal upwelling systems. As a result, it is now apparent that (1) spatial and temporal variation in upwelling may leave a strong signature on intertidal communities, and (2) upwelling patterns may be altered by El Niño events and longer-term geophysical changes. This chain of effects therefore suggests pathways through which global climate change may impact the structure and dynamics of rocky intertidal systems along the Pacific coast.

Despite these advances, critical gaps remain in our understanding of how global changes may ultimately impact marine ecosystems. For example, to what extent are

ENSO events, interdecadal regime shifts, and global warming interrelated? How might coastal upwelling be altered by the interaction of regional changes in alongshore winds and basinwide changes in currents and thermal stratification? How does the sensitivity of an organism to thermal change vary through a species' geographic range? To what extent might acclimatization and local adaptation modify the response of marine organisms to changes in water temperature?

Such questions are critical to predicting the impact of climatic changes in nearshore marine ecosystems. Efforts to address these issues will rely heavily on large-scale, interdisciplinary research efforts and the incorporation of new technological advances. Significantly, much of the work in this thesis was facilitated by new technologies including affordable temperature data-loggers, electronics capable of precisely controlling laboratory temperatures, and internet access to satellite images and weather data. However, technology and promising large-scale approaches should not be a substitute for the tools that are the foundation of marine ecology. A wealth of insight will always be produced through attention to natural history and the continued use of controlled experiments to tease apart mechanisms at the local level.

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