

AN ABSTRACT OF THE DISSERTATION OF

Tess L. Freidenburg for the degree of Doctor of Philosophy in Zoology presented on May 24, 2002.

Title: Macroscale to Local Scale Variation in Rocky Intertidal Community Structure and Dynamics in Relation to Coastal Upwelling.

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Understanding how large-scale processes (>100 kms) influence ecological communities is currently a major focus in ecology. In marine systems, coastal upwelling, a large-scale oceanographic process in which surface water pushed offshore by winds is replaced by cold, nutrient-rich water from depth, appears to cause variation in rocky intertidal communities. Along the central Oregon coast upwelling occurs intermittently during the summer while on the southern coast it begins earlier in the spring and is less variable throughout the summer.

Coastal upwelling can affect rocky intertidal communities by altering the delivery of nutrients, larvae, and phytoplankton. I conducted three studies on both the southern and central Oregon coast to understand how differences in upwelling affect rocky intertidal community structure and dynamics. In the first study, I examined the recruitment and growth rates of sessile invertebrates (mussels and

barnacles). Recruitment of both mussels and barnacles, and growth of mussels were consistently higher on the central Oregon coast than the southern coast.

Upwelled water is nutrient-rich, so differences in upwelling are likely to affect growth rates of macroalgae. In the second study, I tested this hypothesis by monitoring the growth of two species of intertidal kelp at both central and southern coast sites. During El Niño years, when upwelling is sharply reduced on the central Oregon coast, algae may fare better at sites on the southern coast where upwelling is less affected. However, during years when upwelling is strong all along the coast, nutrient limitation does not appear to differentially affect macroalgal growth rates.

Finally, in the third study, I examined the influence of upwelling on the interactions between microalgal primary producers and herbivorous limpets. I conclude that this interaction is complex and varies both within and between upwelling regions.

My research suggests that a transition in upwelling from weak and sporadic on the central Oregon coast to stronger and more persistent on the southern Oregon coast drives the striking differences in rocky intertidal community structure and dynamics between these areas.

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Macroscale to Local Scale Variation in Rocky Intertidal Community Structure and
Dynamics in Relation to Coastal Upwelling

by
Tess L. Freidenburg

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Tess L. Freidenburg, Author

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Dr. Bruce A. Menge was directly involved in the design and data collection of the studies reported in Chapters 2, 3, and 4.

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MACROSCALE TO LOCAL SCALE VARIATION IN ROCKY INTERTIDAL COMMUNITY STRUCTURE AND DYNAMICS IN RELATION TO COASTAL UPWELLING

CHAPTER ONE: GENERAL INTRODUCTION

The quest to understand ecosystem dynamics is changing as ecologists shift their focus from local to regional processes (Menge and Olson 1990, Levin 1992). Researchers are examining the roles of scale and linkages between ecosystems in their effort to achieve an integrated understanding of the causes of variation among ecological communities (Menge 1992, Bustamante et al., Polis and Hurd 1995, Bustamante and Branch 1996b, Polis and Hurd 1996). In marine ecosystems there is increasing recognition that oceanographic conditions can profoundly affect both the structure and dynamics of communities (Bustamante et al. 1995b, Menge et al. 1997a, 1997b, Connolly and Roughgarden 1999b). Oceanographic processes can be strongly affected by El Niño events, regime shifts such as the Pacific Decadal Oscillation, and potentially by global climate change (Bakun 1990, Peterson et al. 1993, Latif and Barnett 1994, Roemmich and McGowan 1995, Mann and Lazier 1996, McGowan et al. 1998). My dissertation focuses on understanding how oceanographic processes, in particular coastal upwelling, influence rocky intertidal communities.

Along the West Coast of the United States, coastal upwelling occurs when southward winds combine with the Coriolis effect to generate a net movement of surface water offshore. This water is replaced by cold, nutrient rich water from depth (Smith 1983). Upwelling can affect rocky intertidal communities in a number of ways. Offshore transport of surface water advects both planktonic larvae and phytoplankton offshore. When upwelling ceases, this water returns bringing larvae and phytoplankton back to shore. Pulses of recruitment (Farrell et al. 1991, Roughgarden et al. 1991, Wing et al. 1995b) and growth spurts of filter-feeding invertebrates (Dahlhoff and Menge 1996, Sanford and Menge 2001) often result. In addition, upwelling is likely to affect productivity and growth of phytoplankton and macroalgae through the delivery of nutrient-rich water (Small and Menzies 1981, Abbott and Zion 1985, Bosman et al. 1987, Fujita et al. 1989, Bustamante et al. 1995b).

In Oregon, the intensity and persistence of upwelling can vary substantially along the coast. In particular, the upwelling regime at Cape Blanco (hereafter CB) on the southern Oregon coast is fundamentally different from sites on the central Oregon coast (Huyer 1983, Smith 1983, Barth and Smith 1998, Barth et al. 2000). As is true for many major headlands, upwelling at CB is persistent due to stronger winds and by deflection of currents offshore (Parrish et al. 1981, Brink 1983, Smith 1983, Rosenfeld et al. 1997, Barth and Smith 1998). In contrast, upwelling at sites along the central coast is predominantly a function of seasonal weather patterns (Huyer 1983) and thus is less persistent than at CB. Within the central Oregon

coast, the width and bathymetry of the continental shelf further influence nearshore circulation patterns. At Cape Foulweather, the shelf is narrow while at Cape Perpetua the shelf is relatively wide and currents form eddies and gyres that may act to concentrate larvae and phytoplankton (Figure 1.1).

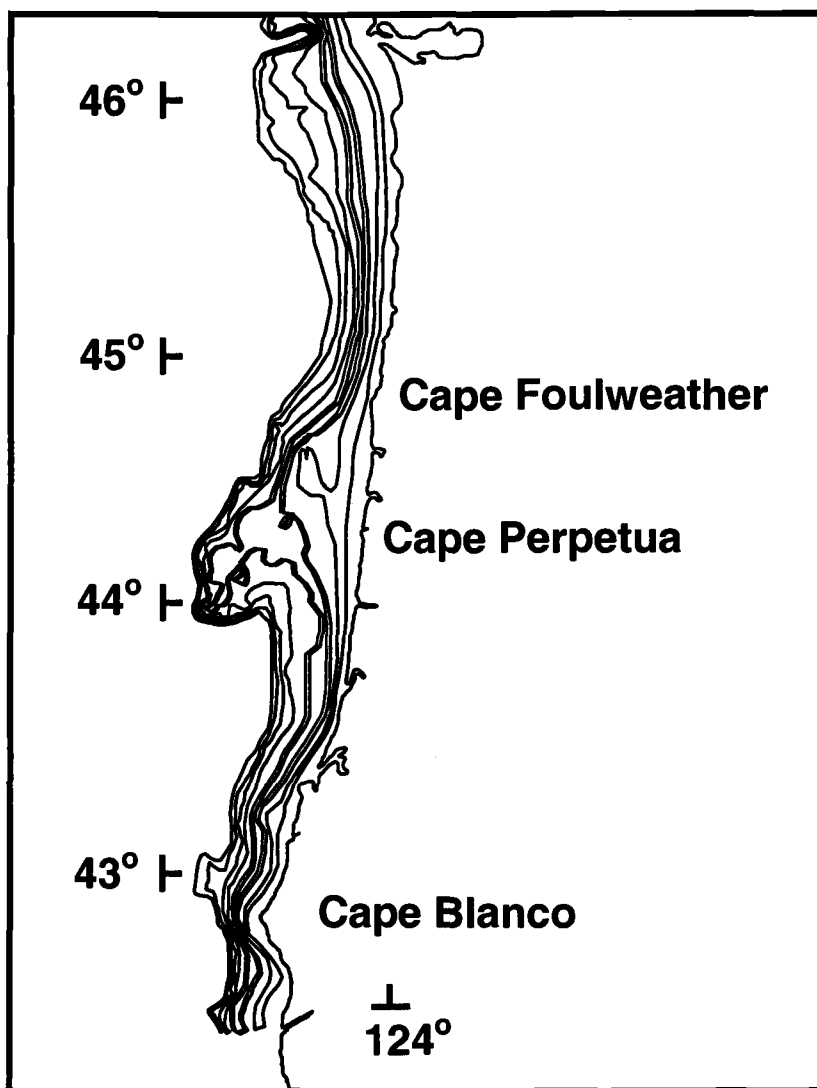


Figure 1.1. Study regions. Map of the Oregon coast showing the width and bathymetry of the continental shelf and the three regions that were the focus of our study.

My dissertation examines how these differences in nearshore oceanographic patterns affect rocky intertidal communities. We tested the hypotheses that in areas with persistent upwelling, 1) recruitment rates of sessile invertebrates would be lower due to advection of planktonic larvae offshore, 2) growth rates of filter-feeding invertebrates would be lower due to offshore advection of phytoplankton and 3) growth rates of macroalgae will be higher due to higher rates of nutrient delivery. We also investigated the degree to which variation in bottom-up processes (i.e. nutrients, phytoplankton concentration) affect the interaction between herbivorous limpets and microalgal primary producers.

In Chapter 2 we examined the influence of variation in upwelling regimes on recruitment and growth rates of invertebrates along the Oregon coast. We found that differences in upwelling patterns are likely responsible for observed variation in recruitment and growth rates between the central Oregon coast, where upwelling is relatively intermittent, and the southern Oregon coast, where upwelling is more persistent. In general, recruitment and growth rates were higher in central Oregon where more frequent relaxation events presumably led to higher rates of delivery of larvae and phytoplankton (a primary food source for filter-feeding invertebrates) to onshore communities. However, we did not observe consistent differences between sites within the central Oregon coast. Therefore, it appears likely that other factors, including variation in local coastal morphology may be more important in structuring communities at this mesoscale.

In Chapter 3 we focused on how large-scale variation in upwelling regimes affected intertidal kelp communities along the Oregon coast and how regions with persistent upwelling may modify the impact of perturbations such as those associated with El Niño events. Using both observational and experimental studies we examined the responses of intertidal kelps to large-scale changes in oceanographic conditions observed during and subsequent to the 1997-98 El Niño. We found that immediately following the El Niño kelps were more abundant at CB than at sites on the central Oregon coast. However, in the 2 years following the El Niño, kelps on the central Oregon coast recovered such that the differences between regions ended. These results indicate that in areas with persistent upwelling, the effects of El Niño can be modified such that kelps are not as strongly impacted as in areas where upwelling is typically less persistent.

In Chapter 4 we investigated how regional scale variation in upwelling patterns affected top-down and bottom-up processes along the Oregon coast. We focused on the effects of limpets on algal and barnacle cover and how this varied between zones (scales of m), among sites (scales of km) and among regions (scales of 10s to 100s of km) with different patterns of seasonal upwelling. We found that limpet effects on algal recolonization and rates of limpet grazing were highest at sites in the Cape Perpetua region, where bottom-up influences, specifically nutrients and rates of production of microalgae, tended to be weaker than at either Cape Foulweather or Cape Blanco. We conclude that limpet-algal interactions vary inversely to bottom-up (nutrient input, algal growth) processes.

This research is a large-scale study designed to understand the mechanisms underlying variation in community structure and dynamics along an extensive stretch of coastline. Understanding how different oceanographic processes affect communities tens to hundreds of kilometers apart is vital if ecologists are to predict how coastal communities may react to changes in oceanographic patterns at large spatial scales. We conclude that large-scale variation in upwelling between the central and southern coast has consistently strong effects on intertidal communities. In contrast, differences in the width of the continental shelf did not have consistent effects. Our results point to the importance of understanding the spatial scales at which underlying processes vary.

CHAPTER TWO: THE EFFECTS OF REGIONAL VARIATION IN COASTAL UPWELLING ON RECRUITMENT AND GROWTH OF INTERTIDAL INVERTEBRATES

ABSTRACT

Recent studies in marine systems have pointed to the importance of understanding how links between adjacent ecosystems can influence community structure. Along the U.S. West Coast, coastal upwelling can affect both the delivery of larvae to adult habitats and phytoplankton production. From 1998-2000, we investigated how regional variation in upwelling regimes affected recruitment rates of barnacles and mussels, growth rates of mussels, and phytoplankton concentration along the Oregon coast. The central Oregon coast is characterized by intermittent upwelling during the spring-summer upwelling season. A shift in upwelling regimes occurs at Cape Blanco, on the southern Oregon coast, where upwelling is more persistent. Within the central Oregon coast, nearshore circulation patterns are influenced by the width and bathymetry of the continental shelf. At Cape Foulweather, the shelf is narrow while at Cape Perpetua the shelf is relatively wide and currents form eddies and gyres that are believed to concentrate larvae and phytoplankton. Our results suggest that large-scale regional differences in upwelling between the central and southern coasts are likely responsible for

observed macroscale variation in recruitment and growth rates of intertidal invertebrates. However, at the mesoscale, comparisons between regions within the central Oregon coast did not reveal consistent patterns of recruitment and growth rates, although significant variation occurred among sites. We conclude that between-site sources of variability may have a greater influence on recruitment and growth rates than regional differences in ocean circulation within the central coast.

INTRODUCTION

Links between benthic and pelagic habitats have become the focus of studies seeking to understand the processes important in structuring marine communities (Gaines and Roughgarden 1985, Bosman et al. 1987, Menge 1992, Bustamante et al. 1995a, 1995b, Menge et al. 1997a, 1997b, 1999b, Connolly et al. 2001). In rocky intertidal systems, the nearshore environment can significantly affect onshore communities by influencing the delivery of nutrients, food (i.e. phytoplankton and detritus) and larvae (Fujita et al. 1989, Dahlhoff and Menge 1996, Sanford and Menge 2001). The availability of nutrients can affect growth and production of macrophytes and phytoplankton and thus affect herbivores and filter-feeding invertebrates (Bosman et al. 1987, Duggins et al. 1989, Bustamante et al. 1995a, Bustamante and Branch 1996a, Sanford and Menge 2001). For organisms with planktonic larvae, the pelagic environment can influence transport and

delivery of those larvae to suitable adult habitats (Roughgarden et al. 1988, Farrell et al. 1991, Ebert et al. 1994, Wing et al. 1995a, 1995b, Connolly and Roughgarden 1999a, Connolly et al. 2001).

Recent studies along the U.S. west coast have focused on how nearshore oceanographic processes, especially those associated with the California Current, influence onshore communities (Menge et al. 1997a, 1997b, Connolly and Roughgarden 1999b, Sanford 1999). The California Current flows southward from Washington through southern California and extends up to 100 km offshore (Mann and Lazier 1996). The speed and direction of the current can be influenced by winds. When winds blow from the north, they interact with the Coriolis effect to drive surface water offshore, a phenomenon called coastal upwelling. This surface water is replaced by cold, nutrient-rich water from depth (Parrish et al. 1981, Brink 1983, Huyer 1983).

The intensity of seasonal upwelling varies in response to both latitude and local geographic features. Upwelling varies with latitude because the Coriolis effect, and thus the magnitude of offshore water transport, weakens with distance from the equator (Mann and Lazier 1996). Upwelling is locally strengthened near major headlands where upwelling favorable winds intensify and the California Current is deflected offshore (Parrish et al. 1981, Brink 1983, Smith 1983, Rosenfeld et al. 1997). Oceanographic evidence suggests that upwelling intensity does not decrease gradually with increased latitude as predicted by the weakening of the Coriolis effect. Rather the coast is comprised of distinct upwelling regions

bounded by oceanographic discontinuities (Parrish et al. 1981). One such discontinuity is Cape Blanco on the southern Oregon coast. North of Cape Blanco, upwelling is relatively intermittent while at Cape Blanco and southward, upwelling is more persistent (Parrish et al. 1981, Barth and Smith 1998, Barth et al. 2000) (Figure 2.1).

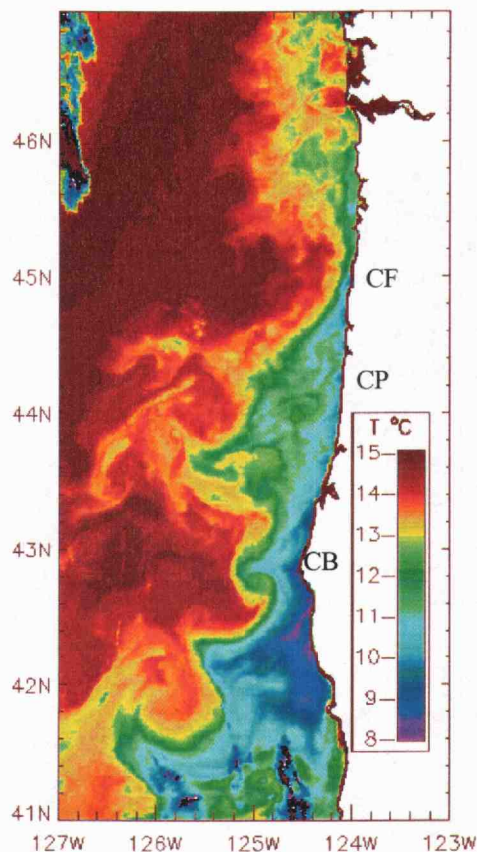


Figure 2.1. AVHRR image showing sea surface temperature (SST) along the Oregon coast on August 13, 1995. Cold upwelled water is near the coast and warm surface is water offshore. CF = Cape Foulweather, CP = Cape Perpetua, CB = Cape Blanco

During upwelling, coastal waters are characterized by a band of cold water nearshore and relatively warm water offshore. The interface between cold, upwelled water and warm surface water is referred to as an upwelling front. Larvae and phytoplankton can become entrained in the offshore moving water and accumulate in these fronts (Roughgarden et al. 1988, Farrell et al. 1991, Roughgarden et al. 1991). Cessation of upwelling-favorable winds leads first to relaxation, or slowing of both alongshore and offshore currents, and, if winds reverse, to downwelling. During downwelling, surface waters reverse direction, moving generally shoreward, delivering larvae and phytoplankton to the onshore communities.

How upwelling affects benthic communities may depend in part on the bottom topography and the width and bathymetry of the continental shelf (Figure 1). Menge and colleagues (Menge et al. 1997a, 1997b) have investigated how these physical factors affect intertidal communities in Oregon. At one site, Boiler Bay (hereafter BB), the continental shelf is narrow and the upwelling front does not extend far offshore. At another site, Strawberry Hill (hereafter SH), the shelf is wider and the upwelling front is typically farther from shore. Between the front and shore on this wider shelf region, eddies form that can concentrate phytoplankton and larvae. Surface currents off BB tend to be stronger and more persistently southward than at SH, where currents are both weaker and more variable in direction (Kosro et al. 1997). Water masses off SH appear to move

shoreward during upwelling relaxation and downwelling, enhancing local rates of recruitment and particulate food delivery. Differences in community structure and dynamics between BB and SH, have been attributed in part to this mesoscale variation in nearshore currents (Menge et al. 1997a, 1997b).

Our goal in the present study was to explore how recruitment and growth rates of filter-feeding invertebrates respond to differences both within and between upwelling regions. We examined sites in two upwelling regions, around Cape Blanco, where upwelling is relatively persistent, and on the central Oregon coast, where upwelling is relatively intermittent. As described above, within the central Oregon region, water transport patterns also vary due to differences in the width and bathymetry of the continental shelf. These differences in oceanographic conditions can be seen in AVHRR images of sea surface temperature (SST) (Figure 2.1). In the Cape Foulweather region (which includes BB), the width of the continental shelf is narrow, which is reflected in the narrow band of cool water close to shore. To the south, in the Cape Perpetua region (which includes SH), the shelf is wider as is the band of cool water – with currents beginning to form eddies. At Cape Blanco, the band of cold water extending offshore south of the headland indicates that intense upwelling is occurring. We hypothesized that these differences in nearshore oceanography would have important effects on intertidal communities. Specifically we hypothesized that (1) recruitment and growth of sessile invertebrates would be greater on the central coast than the southern coast due to more frequent upwelling relaxation, and (2) within the central coast, sites in

the Cape Foulweather region would have low recruitment and growth of sessile invertebrates relative to the Cape Perpetua region where the delivery of larvae, phytoplankton, and detritus are likely to be higher.

METHODS

Study sites

Our study sites spanned approximately 300 km of the Oregon coast from Fogarty Creek (44° 50' N, 124° 03' W) in the north to Rocky Point (42° 43' N, 124° 28' W) in the south (Figure 2.2). All sites consisted of rocky intertidal benches ranging in wave exposure from protected to exposed; our focus was on communities at the wave-exposed end of this physical gradient. Patterns of zonation were typical of sites along the Oregon coast with a high zone dominated by barnacles and fucoid algae and a mid zone dominated by the mussel *Mytilus californianus*. The low zones at these sites varied from domination by sessile and mobile invertebrates, such as at Strawberry Hill and Gull Haven (hereafter GH) to domination by algae at sites such as Boiler Bay and Cape Blanco (hereafter CB).

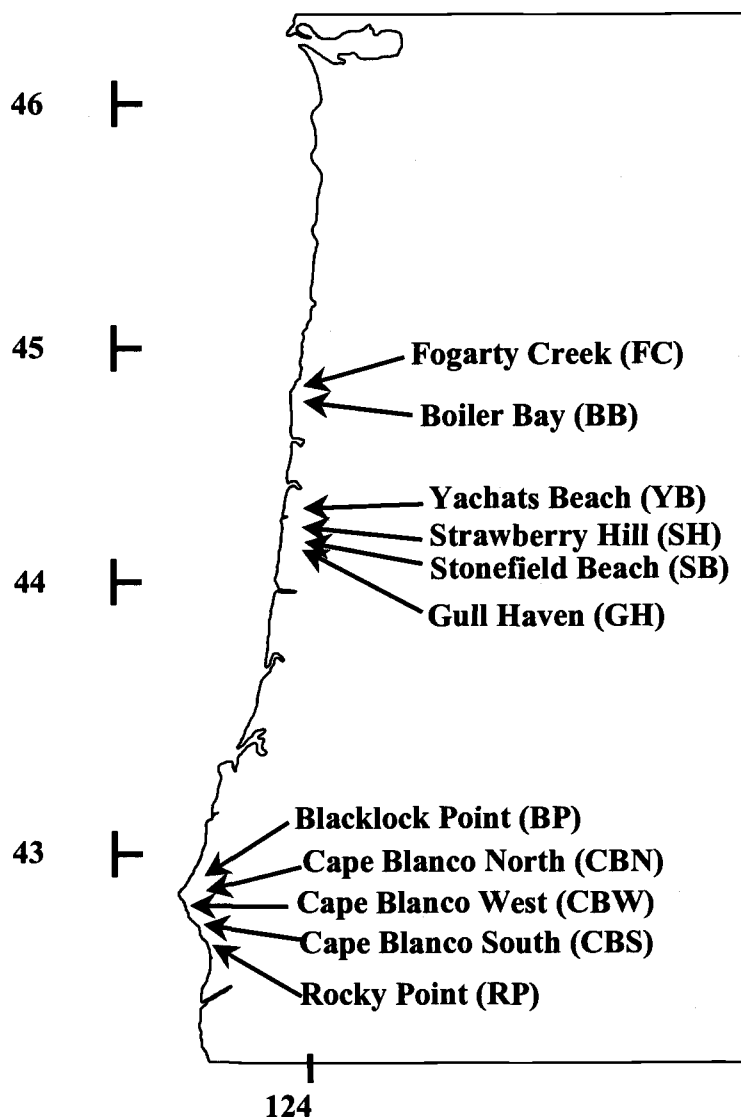


Figure 2.2. Map of study sites along the Oregon coast. FC and BB are in the Cape Foulweather region, YB, SH, SB and GH are in the Cape Perpetua region and BP, CBN, CBW, CBS and RP are in the Cape Blanco region.

Recruitment

Barnacles

We measured barnacle recruitment using by attaching 10 x 10cm plexiglass plates covered with safety-walk tape (3M Company, Saint Paul, Minnesota, USA) in the mid intertidal zone at each site (Farrell et al. 1991, Menge 2000a). Safety-walk tape has a textured surface that mimics bare rock, a preferred settlement substrate for barnacle cyprids. Plates were attached to the rock with a single stainless steel screw in a predrilled hole. Five to eight replicate collectors were placed in wave-exposed areas of the mid intertidal zone at each site. We exchanged the settlement plates monthly and counted the number of juveniles and cyprids on the plates using dissecting microscopes. Individuals were identified to species, when possible. The species most commonly present were *Balanus glandula* and *Chthamalus dalli*. In this study we analyzed total recruitment of all barnacle species.

Mussels

We measured mussel recruitment using plastic mesh scrub pads (SOS Tuffly pad, The Clorox Company, Oakland, California, USA), which provides a

standardized surface to which mussel veligers can attach (Menge et al. 1994, 1999a, Connolly et al. 2001). These pads were secured to the substrate with a stainless steel washer and screw. As with the barnacle plates, five to eight replicate collectors were placed in wave-exposed areas of the mid intertidal zone at each site and were exchanged monthly. In the laboratory, mussels were removed from the collectors by using bleach to dissolve the byssal threads attaching them. The contents of each "Tuffy" were then poured through a 250 μ m sieve and recruits were counted using a dissecting scope. The two species of mussels that we observe in these communities, *Mytilus californianus* and *Mytilus trossulus*, are visually indistinguishable when newly settled. Therefore, we analyzed the total recruitment of all mussel species.

Mussel growth

Mussel growth was measured by transplanting 6-10 groups of 50 mussels to the mid and low zone of each site, following previously established methods (Menge et al. 1994, 1999a). Mussels 4-5 cm in length were collected from each site. Individual mussels were marked by filing a notch on the posterior end of the shell. Mussels were then placed ventral side down in a clump and vexar mesh cages were used to hold them in place until they had reattached to the substrate with their byssal threads. Once they were firmly reattached, after approximately one month,

the vexar mesh was removed. Mussels grow by adding material to the edge of their shells, so we measured subsequent growth as the increase in shell length relative to the notch. Transplanted mussels were collected after approximately one year. We measured proportional daily growth as the increase in shell length divided the initial size divided by the number of days the mussel was transplanted. We conducted this experiment three times in the mid zone: from May 1998 to June 1999, from June 1999 to June 2000, and from June 2000 to June 2001. In the low zone, we conducted this experiment twice: from April 1999 to June 2000, and from April 2000 to May 2001.

Phytoplankton abundance

To evaluate variation in phytoplankton abundance we quantified Chl-a concentrations from water samples collected from the shore periodically during the spring and summer from 1998-2000. On each sampling day, five water samples were collected by attaching brown plastic bottles to a pole 3m in length and dipping them from the seaward edge of the reef to depths of approximately 30cm. Samples were processed immediately after collection by filtering 50ml of seawater through a 25mm glass fiber filter. After filtering, the filter was placed in a centrifuge tube and stored on ice until being returned to the lab. Chl-a concentrations were measured

using a Turner Quantech Digital Filter Fluorometer after extraction in 10 ml of 90% HPLC acetone for 24 hours (Menge et al. 1997b).

Temperature

We measured water temperature at each site using data-loggers that were attached to the substrate in the low intertidal zone. Measurements of temperature were taken hourly and we used tide charts to filter out all low tide water temperatures (i.e. when the instruments were measuring air, not water, temperatures). We averaged daily water temperatures among sites within each region: FC and BB in the Cape Foulweather region; YB, SH, SB and GH in the Cape Perpetua region; and BP, CB and RP in the Cape Blanco region.

Data analysis

We analyzed recruitment of mussels and barnacles and growth of mussels using a nested ANOVA with region (Cape Foulweather, Cape Perpetua, and Cape Blanco), year, site nested within region and year*region as the explanatory variables. We used linear contrasts to compare recruitment levels between regions for each year. For each analysis, we visually examined probability plots of

residuals and plots of residuals vs. estimated values to evaluate assumptions of normality and homogeneity of variance, respectively. When necessary, data were log transformed ($\ln \{y + 1\}$). For the mid zone mussel growth study we included Cape Arago (CA) as a southern coast site. Although CA is approximately 60km north of Cape Blanco, it is a site with persistent upwelling and thus is likely to experience similar oceanographic influences.

We examined interannual differences in the proportion of non-upwelling days, defined as days where water temperature was greater than 10.5°C , within each region, using Chi-square tests. For each region we pooled daily water temperature data across sites. To test for differences among years, we then calculated a Chi-square statistic, where a significant P-value indicates that the proportion of relaxation days were not equal among years (Zar 1974).

RESULTS

Barnacle recruitment

Barnacle recruitment varied among regions, years, and sites within regions and the regional effects varied among years (Table 2.1). Barnacle recruitment was higher on the central coast than the southern coast in both 1998 ($P < 0.0001$) and

Table 2.1. Summary statistics for nested ANOVA analyses of regional and annual differences in barnacle and mussel recruitment and mussel growth in the mid and low intertidal zone.

Source	df	MS	F-ratio	P-value
<i>Barnacle recruitment</i>				
Model	16	2.8441	25.47	<0.0001
Region	2	6.9108	61.89	<0.0001
Year	2	3.6949	33.09	<0.0001
Site (Region)	8	1.3307	11.92	<0.0001
Year*Region	4	1.6434	14.72	<0.0001
Error	13	0.1117		
<i>Mussel recruitment</i>				
Model	15	4.9479	13.51	<0.0001
Region	2	21.5601	58.87	<0.0001
Year	2	5.9910	16.36	0.0002
Site (Region)	7	2.0559	5.61	0.0030
Year*Region	4	0.6199	1.69	.2075
Error	14	0.3663		
<i>Mid zone mussel growth</i>				
Model	13	1.1173	14.45	0.0008
Region	2	5.3568	69.26	<0.0001
Year	2	0.2781	3.60	0.084
Site (Region)	5	0.3718	4.81	0.032
Year*Region	4	0.0236	0.31	0.8662
Error	7	0.0773		
<i>Low zone mussel growth</i>				
Model	9	0.1341	8.88	0.1052
Region	2	0.1357	8.98	0.10
Year	1	0.0274	1.82	0.31
Site (Region)	4	0.0984	6.52	0.14
Year*Region	2	0.0668	4.43	0.18
Error	2	0.0151	0.02	

1999 ($P < 0.0001$), but did not differ in 2000 ($P = 0.44$) (Table 2.2, Figure 2.3).

Recruitment did not differ between the Cape Foulweather region and the Cape Perpetua in 1998 ($P = 0.64$) and 1999 ($P = 0.26$), but was higher at sites in the Cape Foulweather region in 2000 ($P = 0.025$) (Table 2.2, Figure 2.3). Sites in the Cape Blanco region had consistently lower recruitment than either of the central coast regions in 1998 and 1999 ($P < 0.0001$ for both comparisons), but recruitment was not different from Cape Perpetua in 2000 ($P = 0.40$). Recruitment was slightly higher at Cape Foulweather than at Cape Blanco in 2000, but this difference was only marginally significant ($P = 0.058$, Table 2.2).

In each year, barnacle recruitment tended to peak in mid-late summer (July-September), with considerable variation in the magnitude of recruitment between years (Figures 2.4, 2.5, 2.6). Southern coast sites tended to be similar to each other and different from sites on the central coast in both timing and magnitude of recruitment. Recruitment patterns at central coast sites also tended to be similar. In 1998 peak recruitment occurred at most sites in June and July (Figure 2.4). In 1999 the 2 peak months were July and September (Figure 2.5). Peaks were more pronounced in September on the central coast. At virtually all sites there was little to no recruitment in August. In 2000 there was less consistency among sites on the central Oregon coast (Figure 2.6). Peaks occurred from July – October, depending on the site. Sites on the southern coast had more consistent patterns with peaks in July and August (Figure 2.6).

Table 2.2. Results of linear contrasts of differences in barnacle and mussel recruitment and mussel growth in the mid and low intertidal zone between regions. For each response we examined four contrasts: central vs. southern coast and each pairwise comparison between Cape Foulweather (CF), Cape Perpetua (CP) and Cape Blanco (CB). Non-significant comparisons are indicated with "ns". For each comparison we present the effect size, measured as the number of times higher a value was between regions, and the associated 95% confidence interval from the linear contrasts. Values greater than one indicate that the first region was greater than the second, while values less than one indicate that the second region was greater. For example, barnacle recruitment was 5.3 times higher on the central coast relative to the southern coast in 1998.

	1998		1999		2000	
	Effect Size	95% CI	Effect Size	95% CI	Effect Size	95% CI
<i>Barnacle Recruitment</i>						
Central vs. Southern	5.3	3.3-8.4	10.4	6.4-16.7	ns	ns
CF vs. CP	ns	ns	ns	ns	2.3	1.1-4.5
CF vs. CB	5.7	3.1-10.4	12.5	6.9-22.9	1.8	1.0-3.3
CP vs. CB	4.9	2.8-8.5	8.6	4.8-15.2	ns	ns
<i>Mussel Recruitment</i>						
Central vs. Southern	5.4	2.3-12.3	14.3	6.2-32.8	15.8	6.9-36.2
CF vs. CP	ns	ns	ns	ns	ns	ns
CF vs. CB	3.7	1.2-10.9	17.8	6.0-52.7	12.7	4.3-37.5
CP vs. CB	7.8	3.2-19.4	11.5	4.5-29.7	19.6	7.6-50.7
<i>Mussel Growth</i>						
Mid Zone						
Central vs. Southern	4.5	2.5-7.8	4.6	2.6-8.1	4.3	2.4-7.5
CF vs. CP	ns	ns	0.4	0.2-0.8	ns	ns
CF vs. CB	3.3	1.7-6.4	3.0	1.6-5.9	3.4	1.8-6.6
CP vs. CB	6.0	3.2-11.1	6.9	3.7-13.1	5.4	2.8-10.1
Low Zone						
Central vs. Southern			ns	ns	1.6	1.1-2.4
CF vs. CP			ns	ns	ns	ns
CF vs. CB			ns	ns	ns	ns
CP vs. CB			ns	ns	2.0	1.2-3.3

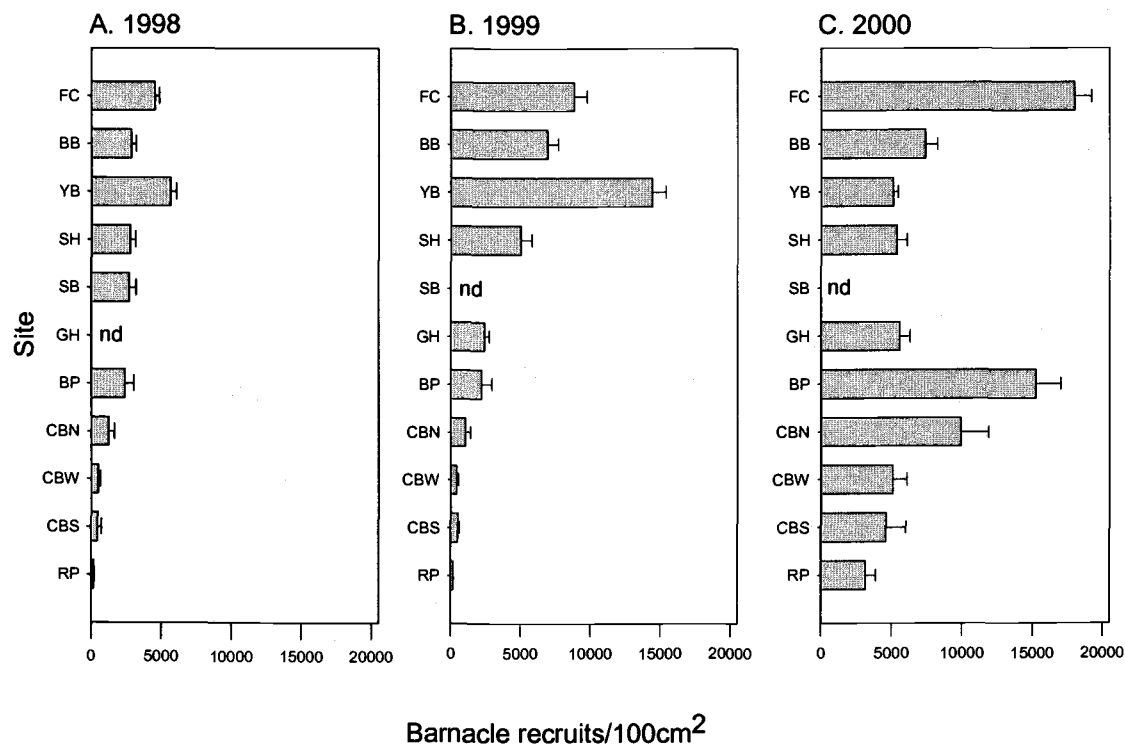


Figure 2.3. Average (+1 SE) recruitment of barnacles (*Balanus* and *Chthamalus*) to the mid intertidal zone at sites along the Oregon coast. Recruitment was measured between May and October of (A) 1998, (B) 1999, and (C) 2000. Recruitment was measured in three regions: Cape Foulweather (FC and BB), Cape Perpetua (YB, SH, SB, GH) and Cape Blanco (BP, CBN, CBW, CBS, RP). Sites are arranged in latitudinal order with the northernmost sites at the top.

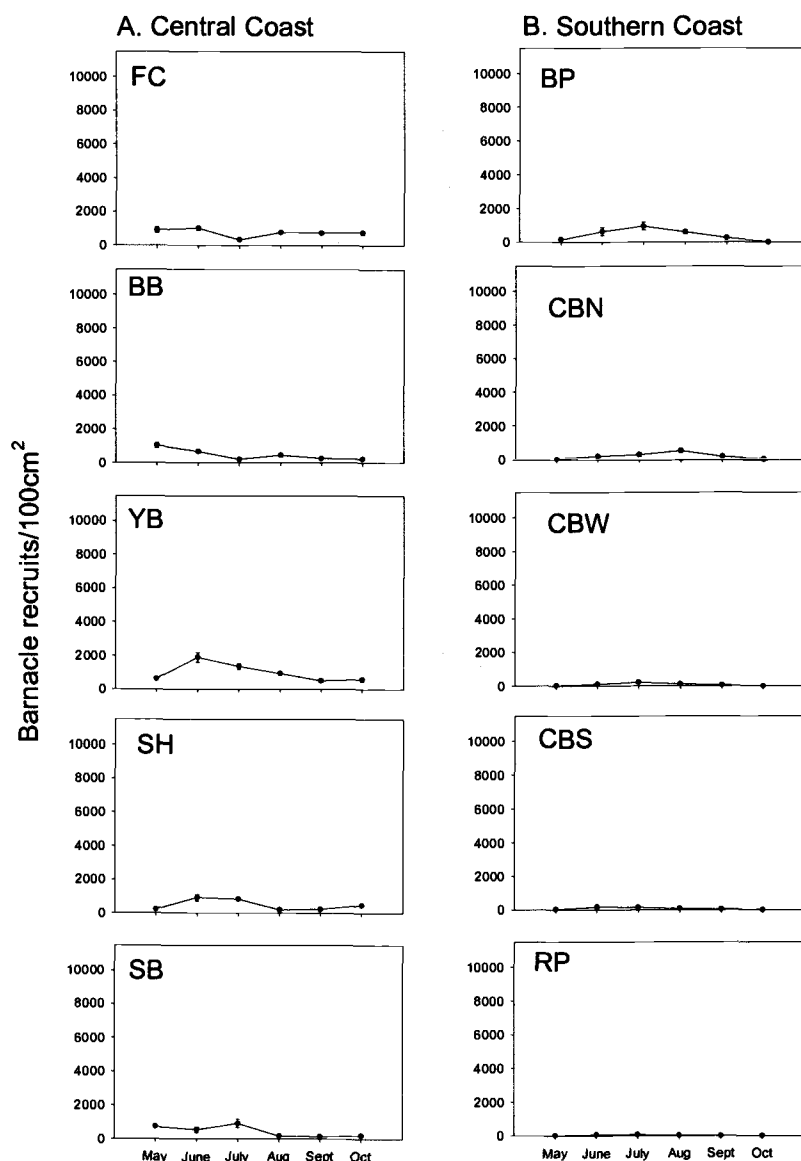


Figure 2.4. Average (+1 SE) monthly recruitment of barnacles (*Balanus* and *Chthamalus*) from May through October 1998 at sites on the (A) central coast and (B) southern coast. Recruitment was measured in two regions on the central coast: Cape Foulweather (FC, BB), Cape Perpetua (YB, SH, SB). Sites are arranged in latitudinal order for the central and southern coasts with the northernmost sites at the top.

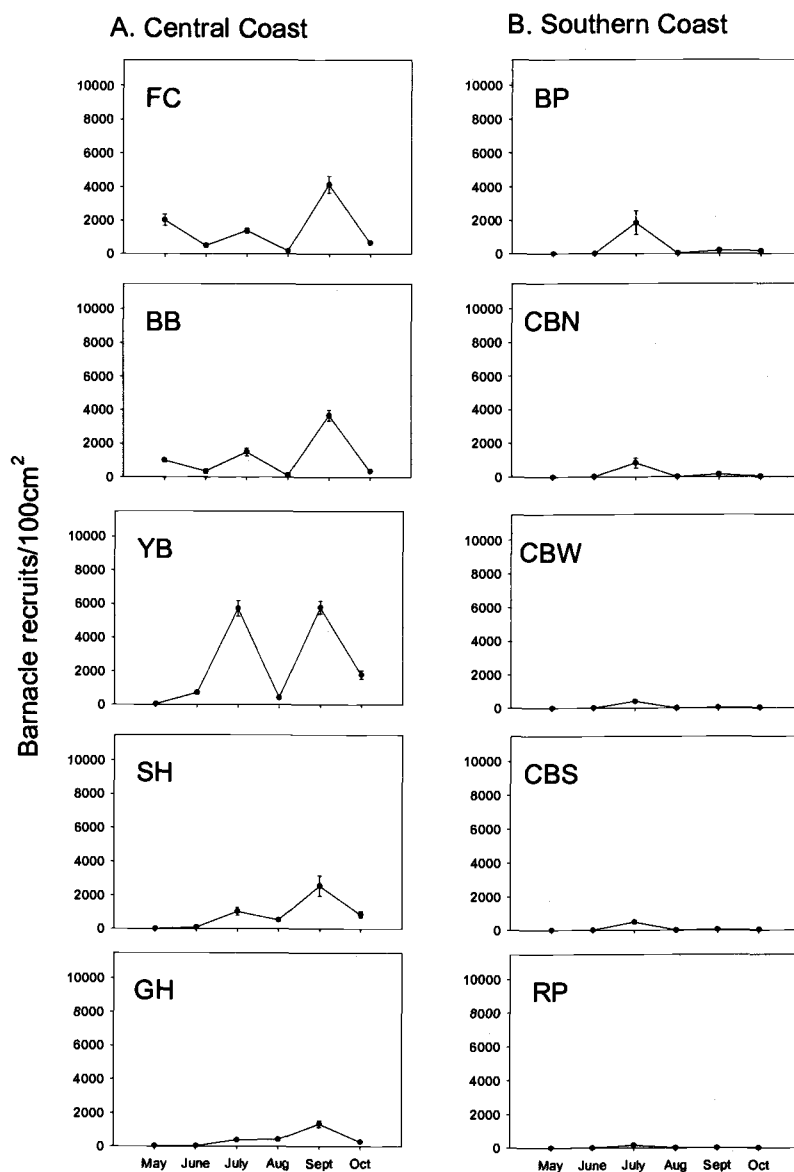


Figure 2.5. Average (+1 SE) monthly recruitment of barnacles (*Balanus* and *Chthamalus*) from May through October 1999 at sites on the (A) central coast and (B) southern coast. Recruitment was measured in two regions on the central coast: Cape Foulweather (FC, BB), Cape Perpetua (YB, SH, GH). Sites are arranged in latitudinal order for the central and southern coasts with the northernmost sites at the top.

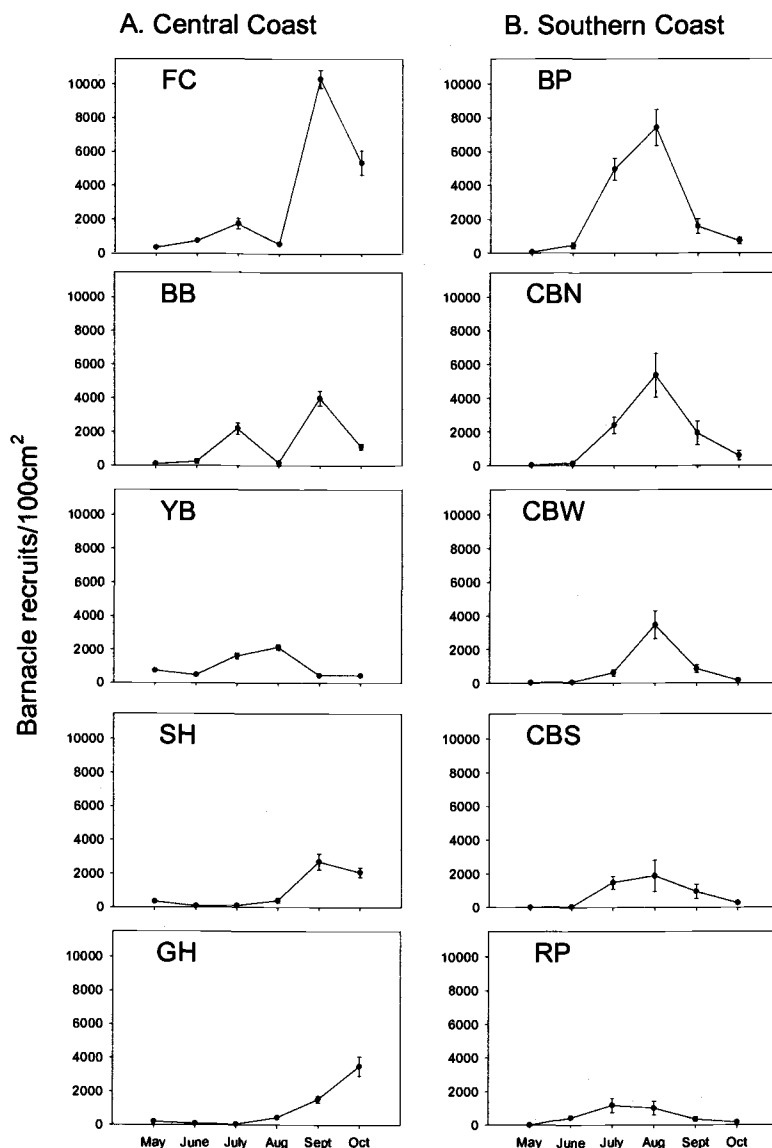


Figure 2.6. Average (+1 SE) monthly recruitment of barnacles (*Balanus* and *Chthamalus*) from May through October 2000 at sites on the (A) central coast and (B) southern coast. Recruitment was measured in two regions on the central coast: Cape Foulweather (FC, BB), Cape Perpetua (YB, SH, GH). Sites are arranged in latitudinal order for the central and southern coasts with the northernmost sites at the top.

Mussel recruitment

Mussel recruitment varied among regions, years, and sites within regions, and regional differences were similar among years (Table 2.1). The central coast had consistently higher recruitment than the southern coast in all years ($P < 0.001$ for each comparison) (Table 2.2, Figure 2.7). There were no regional differences between sites in the Cape Foulweather region and sites in the Cape Perpetua region during any year (1998: $P = 0.19$; 1999: $P = 0.44$; 2000: $P = 0.44$). In each year, sites in the Cape Blanco region experienced lower recruitment of mussels than both the Cape Foulweather (1998: $P = 0.022$, 1999: $P < 0.0001$, 2000: $P = 0.0002$) and Cape Perpetua (1998: $P = 0.0004$, 1999: $P < 0.0001$, 2000: $P < 0.0001$) region (Table 2.2, Figure 2.7).

Mussel recruitment was relatively low at all sites in 1998 and 1999, but high on the central coast and low on the southern coast in 2000 (Figures 2.8, 2.9, 2.10). In 1998, there was a small peak in recruitment in September at nearly all sites (Figure 2.8). There was a moderate peak in recruitment in June and July 1999 on the central coast, but minimal recruitment on the southern coast throughout the summer (Figure 2.9). In 2000, sites on the central coast experienced a pulse of recruitment that lasted from July to October, although there was considerable variation in the magnitude of recruitment among sites (Figure 2.10). As in previous years, mussel recruitment was consistently low at all sites on the southern coast.

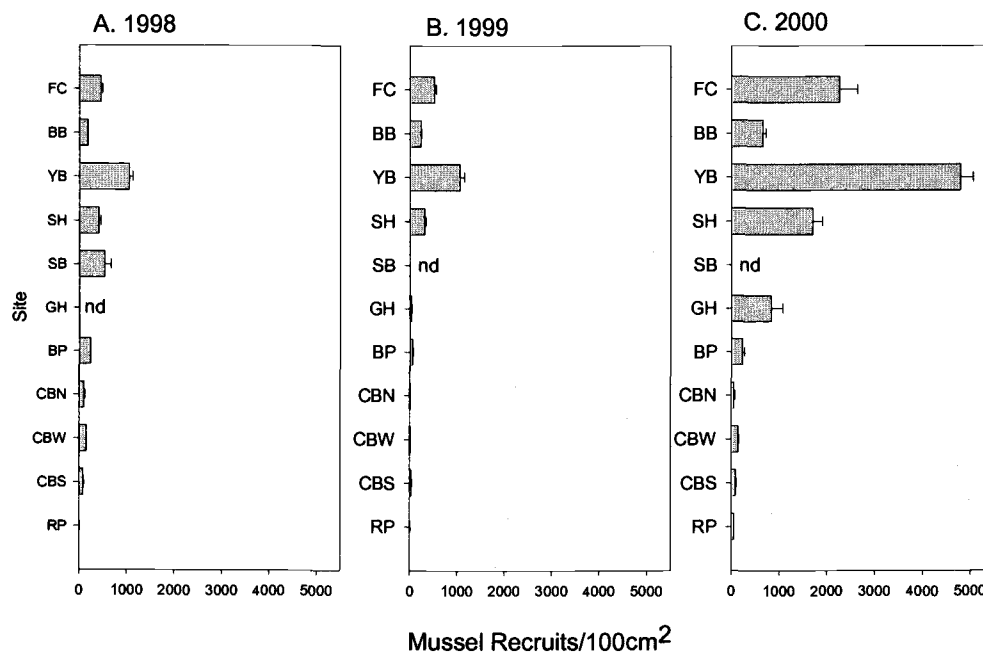


Figure 2.7. Average (+1 SE) recruitment of mussels (*Mytilus spp.*) to the mid intertidal zone at sites along the Oregon coast. Recruitment was measured between May and October of (A) 1998, (B) 1999, and (C) 2000. Recruitment was measured in three regions: Cape Foulweather (FC and BB), Cape Perpetua (YB, SH, SB, GH), and Cape Blanco (BP, CBN, CBW, CBS, RP). Sites are arranged in latitudinal order with the northernmost sites at the top.

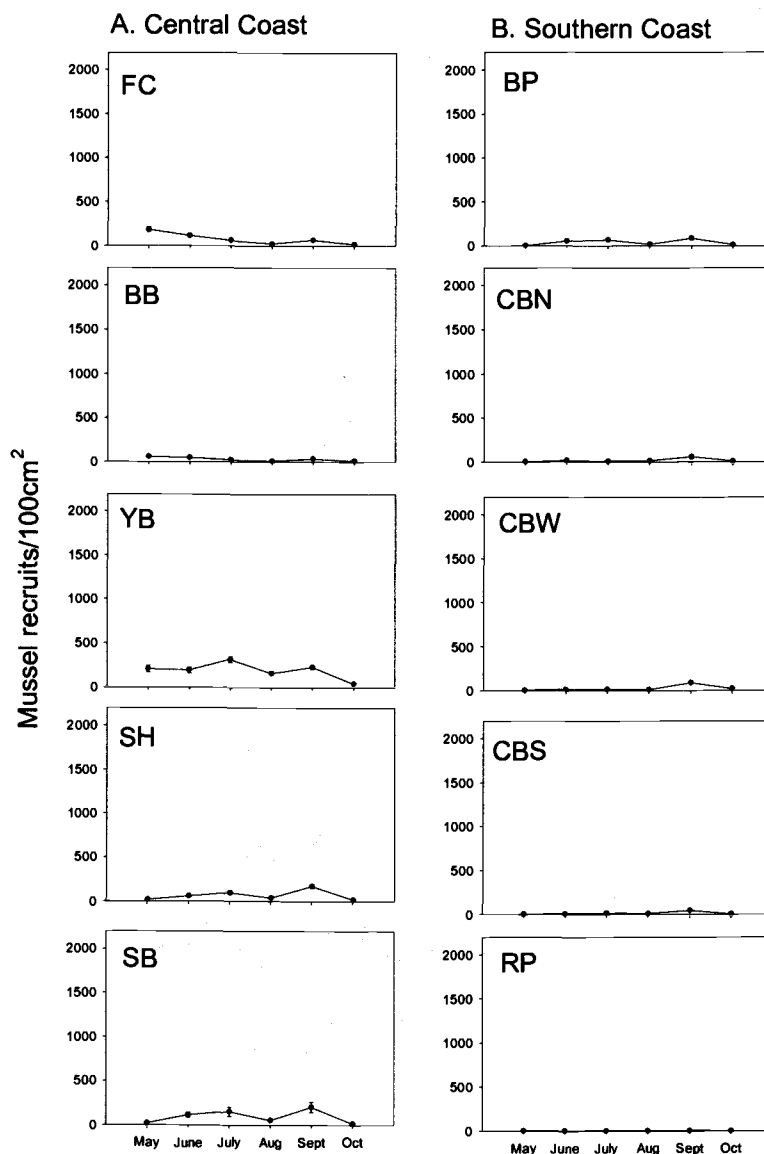


Figure 2.8. Average (+1 SE) monthly recruitment of mussels (*Mytilus spp.*) from May through October 1998 at sites on the (A) central coast and (B) southern coast. Recruitment was measured in two regions on the central coast: Cape Foulweather (FC, BB), Cape Perpetua (YB, SH, SB). Sites are arranged in latitudinal order for the central and southern coasts with the northernmost sites at the top.

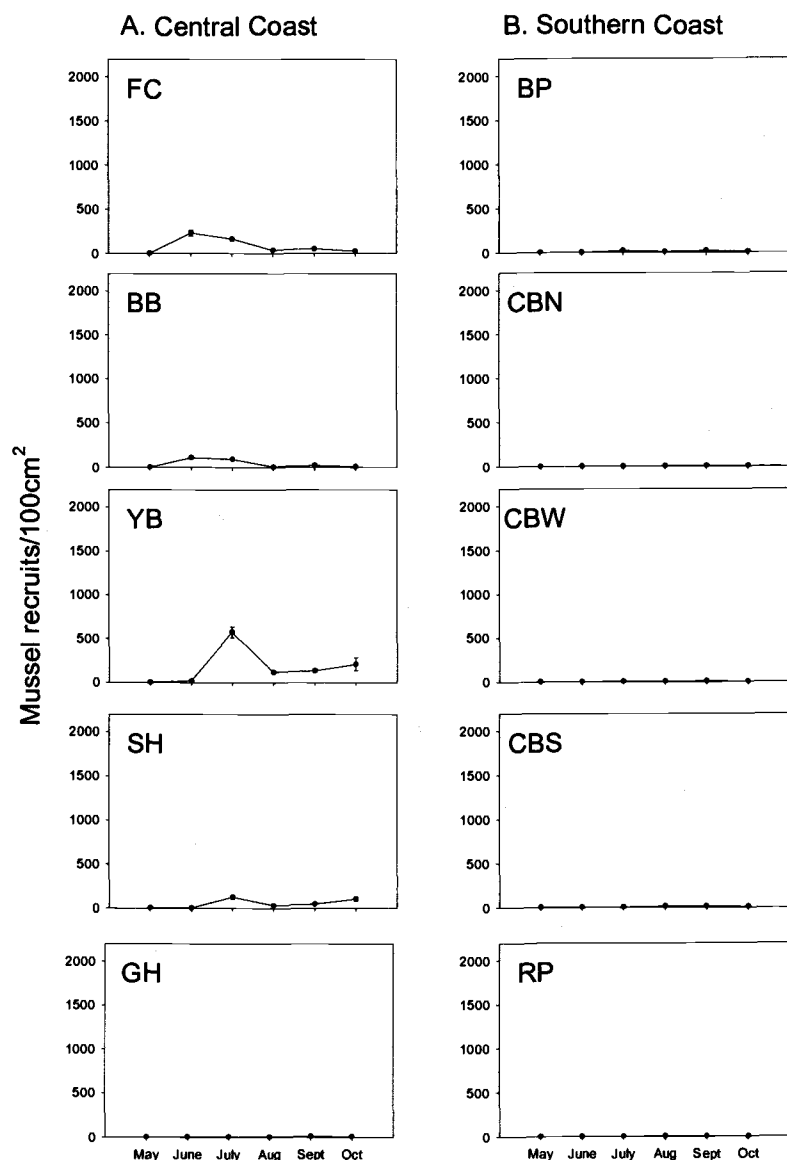


Figure 2.9. Average (+1 SE) monthly recruitment of mussels (*Mytilus spp.*) from May through October 1999 at sites on the (A) central coast and (B) southern coast. Recruitment was measured in two regions on the central coast: Cape Foulweather (FC, BB), Cape Perpetua (YB, SH, GH). Sites are arranged in latitudinal order for the central and southern coasts with the northernmost sites at the top.

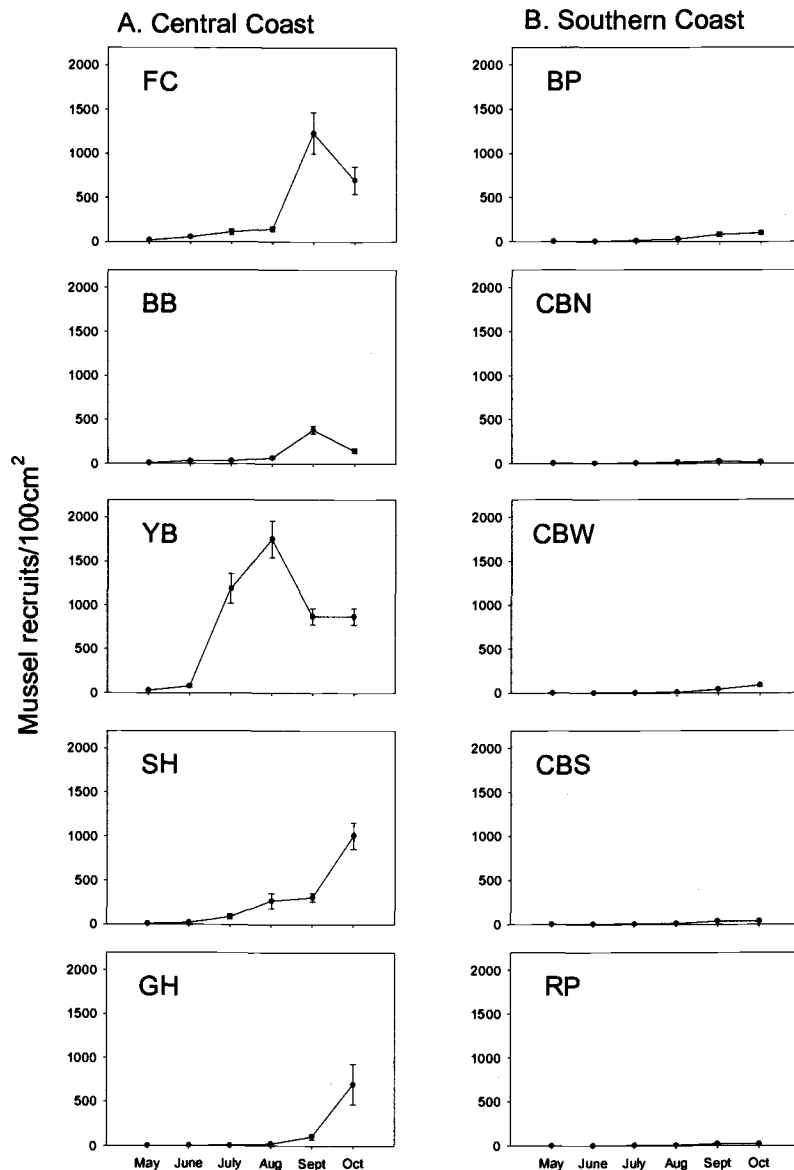


Figure 2.10. Average (+1 SE) monthly recruitment of mussels (*Mytilus spp.*) from May through October 2000 at sites on the (A) central coast and (B) southern coast. Recruitment was measured in two regions on the central coast: Cape Foulweather (FC, BB), Cape Perpetua (YB, SH, GH). Sites are arranged in latitudinal order for the central and southern coasts with the northernmost sites at the top.

Mussel growth

Mussel growth rates in the mid zone differed among regions and years, but did not vary among sites within regions and regional differences in growth rates were similar among years (Table 2.1). Mussel growth rates in the mid zone were consistently higher at sites on the central coast than the southern coast in all years (Table 2.2, Figure 2.11). In 1998 and 1999, mussel growth was higher at sites in the Cape Perpetua region than at sites in the Cape Foulweather region (1998: $P=0.041$, 1999: $P=0.013$), however in 2000 there little evidence for differences in growth rates between these regions ($P=0.094$) (Table 2.2, Figure 2.11). In each year, the Cape Blanco region had lower growth rates than either the Cape Foulweather (1998: $P=0.0010$, 1999: $P=0.0058$, 2000: $P=0.0013$) or Cape Perpetua (1998: $P=0.0002$, 1999: $P=0.0006$, 2000: $P=0.0004$) regions (Table 2.2, Figure 2.11). Patterns of growth rates for mussels in the low zone differed from those in the mid zone. There were no differences in growth rates among regions, years or sites within regions (Table 2.1). Linear contrasts between regions revealed no regional differences in 1999 ($P>0.5$ for each comparison) (Table 2.2). In 2000, growth rates were higher on the central coast than on the southern coast ($P=0.037$), but the magnitude of the difference was much greater for mussels in the mid zone (Table 2.2). There were no differences in growth rates between Cape Foulweather and

either Cape Perpetua ($P=0.064$) or Cape Blanco ($P=0.16$). Growth rates were two times higher at Cape Perpetua than Cape Blanco ($P=0.025$) (Table 2.2, Figure 2.12).

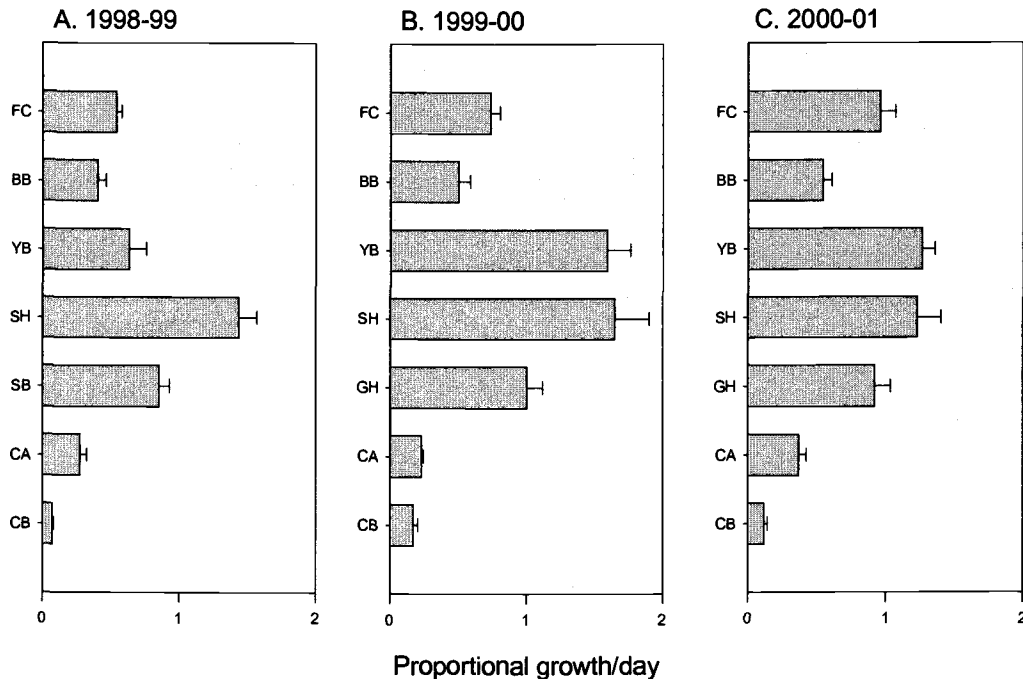


Figure 2.11. Proportional mussel (*Mytilus californianus*) growth ($\mu\text{m} + 1 \text{ SE}$) in the mid intertidal zone along the Oregon coast in (A) 1998-1999, (B) 1999-2000, and (C) 2000-2001. Growth was measured in three regions: Cape Foulweather (FC, BB), Cape Perpetua (YB, SH, SB, GH), and Cape Blanco (CA, CB). Sites are arranged in latitudinal order with the northernmost sites at the top.

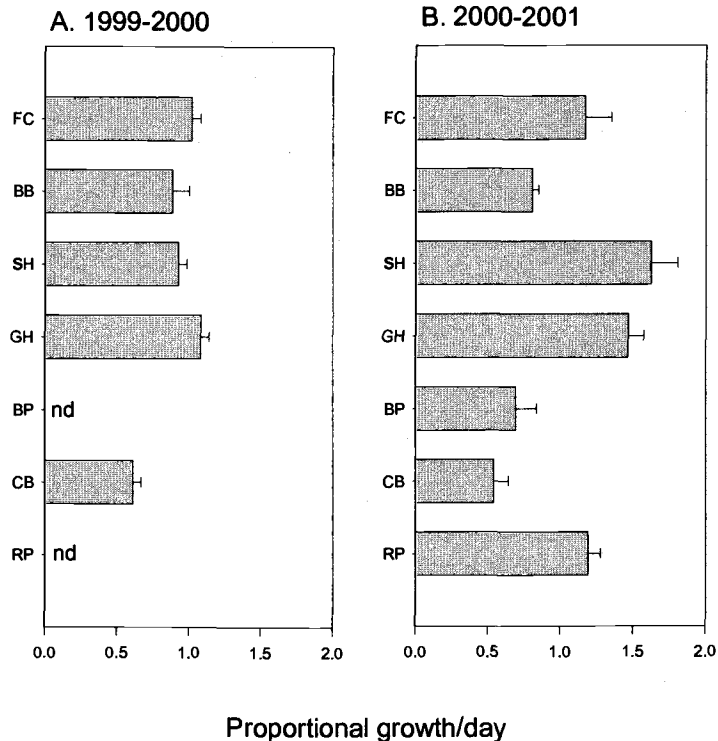


Figure 2.12. Proportional mussel (*M. californianus*) growth ($\mu\text{m} + 1 \text{ SE}$) in the low intertidal zone along the Oregon coast in (A) 1999-2000 and (B) 2000-2001. Growth was measured in three regions: Cape Foulweather (FC, BB), Cape Perpetua (SH, GH), and Cape Blanco (BP, CB, RP). Sites are arranged in latitudinal order with the northernmost sites at the top.

Chlorophyll concentrations

Chlorophyll-a (Chl-a) concentrations were consistently low at all sites in 1998 and 1999, with the exception of a peak at YB in 1998 (Figure 2.13). In each year, the highest Chl-a concentrations were seen in the Cape Perpetua and Cape Blanco region, while levels were always low in the Cape Foulweather region. In

2000, Chl-a concentrations were much higher at all sites except FC and BB, which had levels similar to previous years.

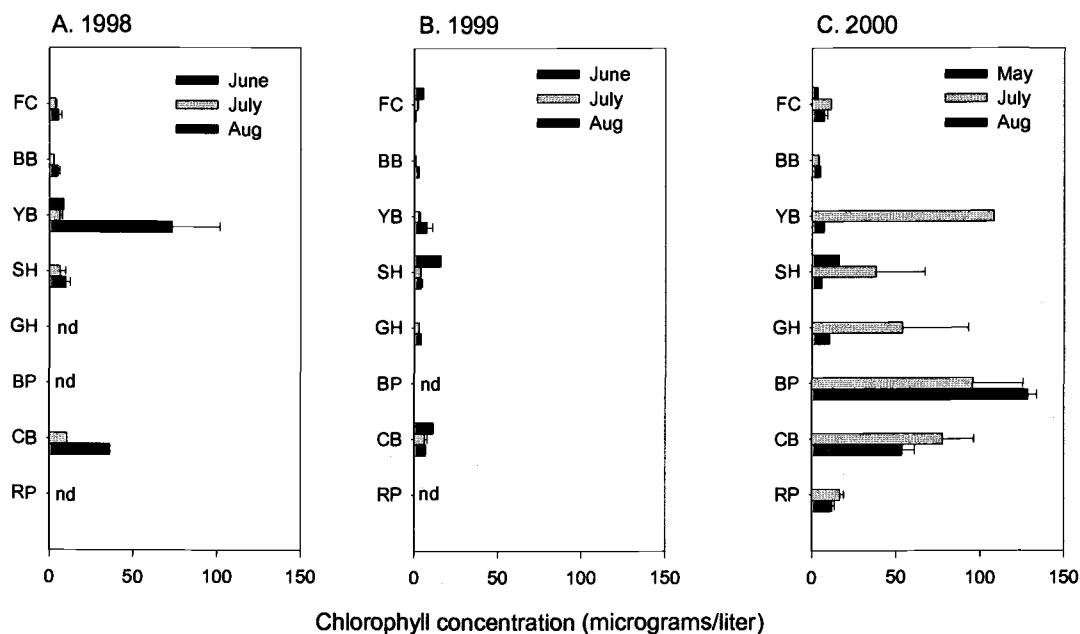


Figure 2.13. Chlorophyll-a concentrations (+1 SE) from water samples taken at sites along the Oregon coast. Samples were collected during summer months in (A) 1998, (B) 1999, and (C) 2000. Sites are arranged in latitudinal order with the northernmost sites at the top.

Temperature

Visual inspection of time series plots of daily water temperature in the three regions (Cape Foulweather, Cape Perpetua and Cape Blanco) revealed numerous upwelling and relaxation events in each year (Figure 2.14). In each year, water

temperature ranged from approximately 8°C to 14°C , with the exception of 1998 at end of the El Niño, when temperatures reached 16°C at Cape Foulweather. Water temperatures above 10.5°C , which are indicative of relaxation of upwelling, occurred throughout the summer in each year, although there were differences in the relative frequency of these relaxation days among years within each region (Chi-square $P < 0.0001$ for each region). The highest proportion of relaxation days was observed in 1998 (Cape Foulweather = 0.79, Cape Perpetua = 0.71, and Cape Blanco = 0.60), the lowest in 1999 (Cape Foulweather = 0.37, Cape Perpetua = 0.37, and Cape Blanco = 0.33), and 2000 was intermediate (Cape Foulweather = 0.46, Cape Perpetua = 0.51, and Cape Blanco = 0.51).

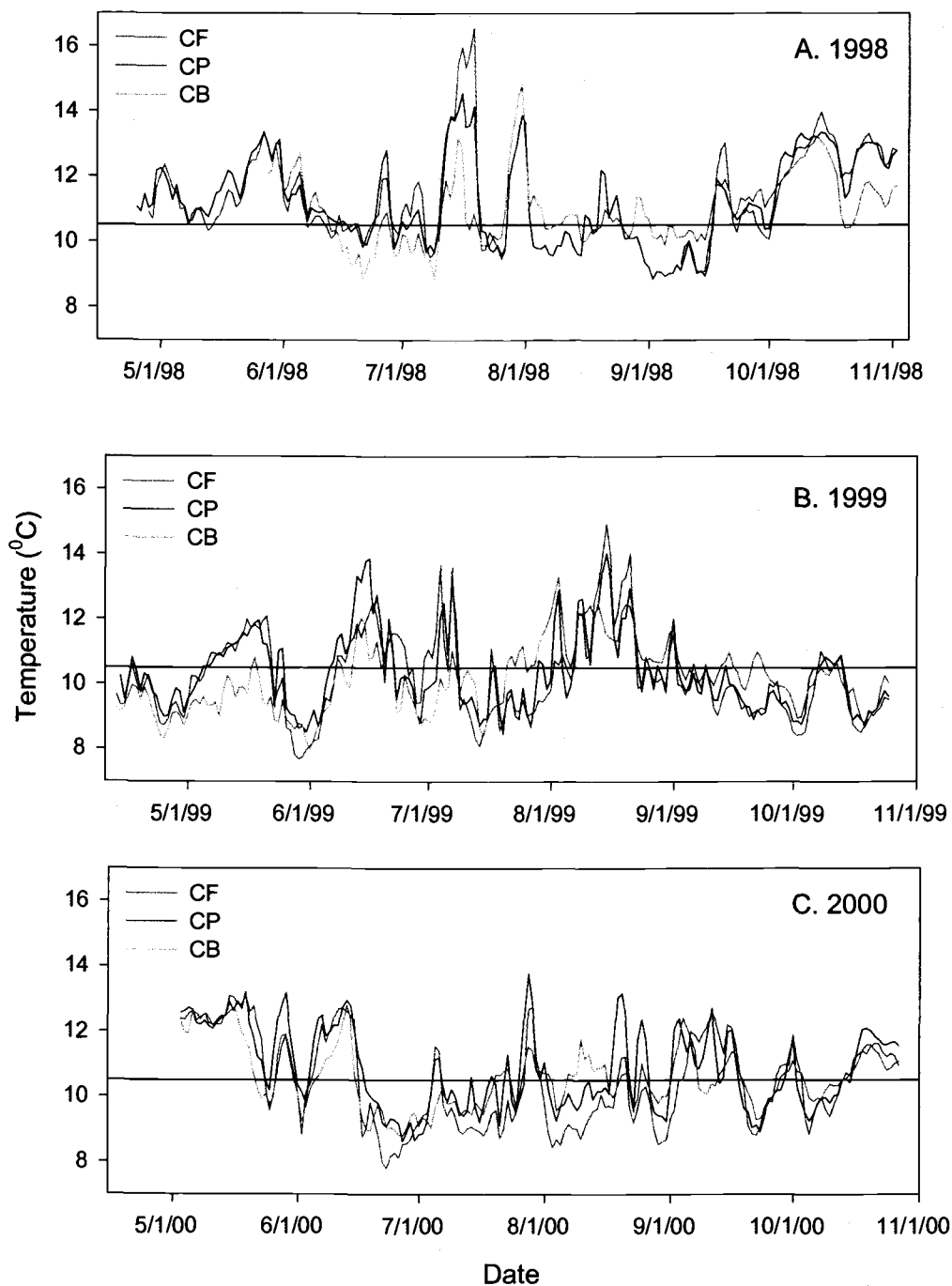


Figure 2.14. Average daily (+1 SE) spring and summer water temperatures from sites in three regions, Cape Foulweather (CF), Cape Perpetua (CP), and Cape Blanco (CB) in (A) 1998, (B) 1999, and (C) 2000.

DISCUSSION

Previous theoretical and empirical research points to larval transport associated with coastal upwelling as a critical factor influencing recruitment rates of sessile invertebrates, and consequently structuring onshore communities (Gaines and Roughgarden 1985, Roughgarden et al. 1988, Roughgarden et al. 1991, Wing et al. 1995a, Wing et al. 1995b, Menge et al. 1997a, Connolly and Roughgarden 1998, Connolly et al. 2001). The larvae of sessile invertebrates such as barnacles and mussels can be transported offshore during upwelling events and later returned to shore during relaxation/downwelling events (Roughgarden et al. 1988, 1991). Along areas of the coast where the continental shelf is wide and the bottom topography complex, eddies and gyres can form that may act to concentrate larvae such that when relaxation events occur, large pulses of recruitment are observed (Menge et al. 1997a). Processes that influence larval transport may also influence phytoplankton concentrations. Upwelled water is nutrient-rich and thus can fuel the growth of phytoplankton, which may subsequently accumulate in upwelling fronts (Menge et al. 1997a, 1997b). As with invertebrate larvae, phytoplankton can be delivered to shore during upwelling relaxation, and can fuel the growth of filter-feeding invertebrates (Dahlhoff and Menge 1996, Sanford and Menge 2001).

Based on oceanographic patterns along the Oregon coast, we expected to see higher recruitment rates of mussels and barnacles on the central coast, where

upwelling is relatively intermittent, than on the southern coast, where upwelling is more persistent. Within the central coast region, we hypothesized that recruitment rates would tend to be higher at sites in the Cape Perpetua region, where the continental shelf is wide and the bottom topography complex such that larvae become concentrated in eddies and gyres, than sites in the Cape Foulweather region, where the continental shelf is narrow.

Recruitment

Previous research on barnacle recruitment dynamics has demonstrated that recruitment events co-occur with downwelling (Farrell et al. 1991, Grantham unpubl. data). Our results suggest that relaxation events are not the only factor driving recruitment dynamics. Regional patterns of barnacle recruitment were consistent with our hypotheses in 1998 and 1999, but not in 2000. Recruitment levels were five and ten times higher on the central coast relative to the southern coast in 1998 and 1999, respectively (Table 2.2). In 2000 recruitment was much higher on the southern coast than in previous years (Figure 2.3C), such that there were no differences between the central and southern coast. Within the central coast, rates of recruitment did not differ between the Cape Foulweather and Cape Perpetua regions in 1998 and 1999, but were two times higher at sites in the Cape Foulweather region in 2000. These differences in 2000 suggest a shift in the

processes that drive barnacle recruitment. An increase in the frequency or duration of relaxation events would provide an explanation for the high recruitment on the southern coast consistent with our hypotheses. However, examination of water temperatures revealed no such change in relaxation events (Figure 2.14). While the frequency of periods of time where the temperature rose above 10.5°C differed among years, within each region it was highest in 1998, lowest in 1999 and intermediate in 2000. This suggests that a shift in the proportion of relaxation days was not responsible for the increase in recruitment in 2000.

What process was responsible for high barnacle recruitment on the southern coast in 2000 relative to 1998 and 1999? One possibility is that larval supply was higher in 2000 than in previous years. Our sampling of Chl-a suggests that phytoplankton concentrations were higher in 2000 than in previous years. It is possible that higher phytoplankton concentrations resulted in either increased reproductive output or higher larval survival, which translated into higher recruitment (Phillips in press, Phillips and Gaines in press). However, no concomitant increases in recruitment were observed on the central coast where Chl-a concentrations were also elevated.

Alternatively, changes in ocean circulation around Cape Blanco that were not evident in onshore water temperature measurements may have been responsible. Recent oceanographic research has demonstrated that north of Cape Blanco an upwelling jet is inshore of the continental shelf break (Barth et al. 1998, 2000). When the jet nears the Cape it turns, moving up to 100 km offshore, which

results in cross-shelf transport of material from the coast to the deep ocean (Barth et al. 1998, 2000). The consequences of this deflection may be seen in patterns of recruitment and phytoplankton concentration around the Cape. In each year, barnacle and mussel recruitment and Chl-a concentration decreased steadily around the Cape: levels were typically highest at BP, intermediate at sites on the Cape, and low farther south at RP (Figure 2.3). We postulate that this pattern is due to the transport of larvae and phytoplankton, which can be entrained in the offshore jet. Barth et al. (1998) observed both seasonal and interannual variation in the strength of upwelling, which affected the behavior of the upwelling jet. It is possible that in 2000 the upwelling jet failed to separate from the continental shelf, retaining barnacle larvae close to shore, which increased recruitment to intertidal communities.

Comparisons of recruitment rates between the central and southern coast were consistent with our hypotheses that mussel recruitment would be high on the central coast relative to the southern coast. Mussel recruitment was over five, fourteen and fifteen times higher on the central coast than on the southern coast in 1998, 1999 and 2000, respectively (Table 2.2). Consistent differences in mussel recruitment between the central and southern coast suggest that the magnitude of recruitment may indeed be partially determined by regional differences in upwelling. Surprisingly, we did not see regional differences within the central coast regions in any year (Table 2.2). This pattern suggests that any effect of differences

in oceanography between these regions did not translate into large differences in the recruitment of mussels.

For both mussels and barnacles, recruitment was frequently low in August, relative to July and September. This pattern can be seen most clearly in barnacle recruitment in 1999. What process may be responsible for the low recruitment in August? One possibility is that barnacle reproduction is low in mid summer, however we have no data on reproduction output to test this. Alternatively, intense upwelling at this time of the year may result in low transport of larvae to shore.

Mussel growth

Consistent with our predictions, mussel growth rates were higher at sites on the central coast than at sites on the southern coast in all years in the mid intertidal zone, and during 2000, but not 1999, in the low zone (Table 2.2). Interestingly, comparisons between the two central coast regions did not yield consistent results. In 1998 and 2000 there were no differences in growth rates in the mid zone between Cape Foulweather and Cape Perpetua, while in 1999 growth rates were higher at sites in the Cape Perpetua region. However, in the low zone, these regions were different in 2000, but not 1999. The disparity between the low and mid zone suggests that phytoplankton concentrations do not consistently predict mussel growth rates. Furthermore, while phytoplankton concentrations were

typically higher near Cape Perpetua than Cape Foulweather, mussel growth did not differ between these regions in the mid zone in 2000, when differences in phytoplankton concentrations were greatest. Finally, phytoplankton concentrations were typically similar between the Cape Blanco and Cape Perpetua regions, yet mussels at Cape Perpetua had consistently higher growth. While some of these differences may be explained by low resolution due to small sample sizes, we suspect that factors besides phytoplankton concentration partly determine growth. In particular, the composition of phytoplankton communities and the availability of alternate food such as detritus, zooplankton, or other plankton such as bacteria may influence mussel growth.

Other factors that may underlie differences in growth rates between sites and zones include variation in temperature during emersion and water flow. Examination of heat shock proteins has demonstrated that mid zone mussels may experience more thermal stress than mussels lower in the intertidal zone (Roberts et al. 1997). Such thermal stress could cause between zone differences in growth, which may extend to regional differences if temperatures during emersion differ among regions (e.g. due differences in fog or cloud cover). Between site differences in flow may also account for differences in growth rates (Sanford et al. 1994, Leonard et al. 1998). While we attempted to place replicate clumps in areas of similar wave exposure, where flow rates would likely be similar, it is possible that microhabitat differences in flow within and between sites affected growth rates. This study was designed to look at large-scale differences in growth rates and

local-scale factors were not explicitly measured. Ideally, any future studies would incorporate measurement of flow at each site.

Effects of regional differences in oceanography on sessile invertebrates

We observed consistent differences in the recruitment of mussels and barnacles and the growth of mussels between the central and southern Oregon coast. These results indicate that, consistent with our hypotheses, these two regions differ fundamentally in the processes that drive invertebrate recruitment and mussel growth. However, we did not observe similar differences when comparing these parameters at sites in the Cape Foulweather and Cape Perpetua regions on the central coast. These results seem in contrast to previous work at Cape Foulweather and Cape Perpetua (Menge 1992, Menge et al. 1997a, Menge 2000b), where recruitment at SH was consistently higher than BB. How can these conflicting results be reconciled?

In this study, recruitment and growth rates did remain consistently lower at BB than SH. However, these site differences did not scale-up to regional differences. Instead, between-site variability within regions was high relative to any hypothesized regional differences within the central coast. It is possible that coastal morphology plays an important role in influencing recruitment between sites within regions. For example, within the Cape Foulweather region FC had

consistently higher recruitment rates than BB. FC is the first rocky reef after extensive sandy beach habitat to the north, and thus may be the first suitable habitat that larvae encounter, leading to high recruitment. FC may also cast a recruitment shadow on BB, which is 1km south of FC, by depleting larval supply before water masses reach BB. Our results suggest that such between-site sources of variability have a greater influence on recruitment than regional differences in ocean circulation within the central coast.

CHAPTER THREE: EFFECTS OF SPATIAL AND TEMPORAL VARIABILITY IN COASTAL UPWELLING ON INTERTIDAL ALGAE

ABSTRACT

Coastal upwelling is an oceanographic process that delivers cold, nutrient-rich water to onshore communities. During El Niño events, the frequency and intensity of upwelling is sharply reduced. Furthermore, due to the depression of the thermocline, when upwelling does occur, upwelled water is warm and nutrient-depleted. While the effects of El Niño on subtidal kelp communities have been well studied, the impact on intertidal kelps is not as well understood. We investigated the effect of the 1997-98 El Niño on intertidal kelps along the Oregon coast at sites within two upwelling regions. On the central Oregon coast the upwelling season is shorter, and upwelling is more intermittent than at Cape Blanco, a site on the southern Oregon coast where the upwelling season begins earlier in the spring and is more persistent. Using both observational and experimental studies we examined the responses of intertidal kelps to large-scale changes in oceanographic conditions observed during and subsequent to the 1997-98 El Niño. Our results show that immediately following the El Niño kelps were more abundant at Cape Blanco than at sites on the central Oregon coast. However, in the 2 years following

the El Niño, kelps on the central Oregon coast recovered such that the differences between regions ended. We conclude that large-scale variation in nutrient supply associated with coastal upwelling was responsible for the observed variation in algal cover and that in areas with persistent upwelling, such as Cape Blanco, the negative impacts of El Niño on kelp communities is less pronounced.

INTRODUCTION

Coastal oceans have historically been viewed as homogenous over large spatial scales (e.g., 10s-100s km) such that they do not differentially affect onshore communities. Recent research has shown that oceanographic conditions can indeed vary over relatively short distances (10s of km), resulting in strikingly different intertidal communities (Menge 1992, Menge et al. 1994, 1997a, 1997b). An important source of variability in oceanographic conditions stems from differences in the transport of surface water associated with coastal upwelling. Coastal upwelling occurs on west coasts when equatorward winds, combined with the Coriolis effect, move surface water offshore. This surface water is replaced by nutrient-rich water from depth (Parrish et al. 1981, Brink 1983, Huyer 1983) While the effects of upwelling on patterns of recruitment of intertidal invertebrates has been the focus of many empirical and theoretical studies (Roughgarden et al. 1988, Farrell et al. 1991, Wing and Botsford 1995, Wing et al. 1995b, Connolly and

Roughgarden 1998, Connolly et al.), less attention has been paid to the effects of upwelling on intertidal algal communities.

The growth of marine plants is often limited by the availability of nutrients, particularly nitrogen (Howarth 1988, Lobban and Harrison 1994). Water that is upwelled from below the thermocline has high levels of fixed nitrogen in the form of nitrates (Mann and Lazier 1996). In many coastal ecosystems, upwelled nutrients fuel the growth of both phytoplankton (Eppley et al. 1979, Small and Menzies 1981, Abbott and Zion 1985, Menge et al. 1997b) and macrophytes (Tegner and Dayton 1987, Fujita et al. 1989, Dayton et al. 1999). While macroalgae can store excess nitrogen for use when it is unavailable in the seawater, decreases in the frequency of upwelling are likely to cause periodic nutrient limitation (Fujita et al. 1989, Wheeler and Bjornsater 1992).

El Niño, a periodic global-scale atmospheric/oceanographic phenomenon, can dramatically alter patterns of coastal upwelling. During El Niño events, the thermocline along the U.S. West Coast is depressed, resulting in a deeper mixed layer. When surface water is transported offshore it is replaced with warm, nutrient-depleted water from the mixed layer, rather than with cool, nutrient-rich water from below the thermocline (Mann and Lazier 1996). The consequent reduction in upwelled nutrients can have profound effects on coastal ecosystems (Barber and Chavez 1983).

The effect of El Niño events on subtidal kelp forests has been well studied (Dayton and Tegner 1984, Gerard 1984, Dayton 1985, Zimmerman and Robertson

1985, Tegner and Dayton 1987, Tegner and Dayton 1991, Lada et al. 1999, Hernandez-Carmona et al. 2001). Dayton and Tegner (1984) documented dramatic declines in the abundance of the giant kelp, *Macrocystis pyrifera* in Southern California during the 1982-83 El Niño. They attributed high mortality rates to severe nutrient limitation during the summer and early fall that weakened plants, which were then damaged during severe winter storms. Zimmerman and Robertson (1985) observed similar patterns of mortality in *M. pyrifera* at Santa Catalina Island during the 1982-83 El Niño, which they attributed to reduced input of nutrients from internal waves due to a deepening of the thermocline. Similar studies during the 1997-98 El Niño also found that *M. pyrifera* suffered high mortality and reduced recruitment near the southern limit of its range in Baja California (Hernandez-Carmona et al. 2001).

The impact of El Niño events on intertidal algae is not as well understood as its effects on subtidal kelps. Paine (1986) examined a long-term data set of maximum lengths of *Postelsia palmaeformis* on Tatoosh Island, Washington, from 1973 to 1984. He did not find any evidence for differences in maximum length due to the 1982-83 El Niño and concluded that effects were not as strong at higher latitudes as at lower latitudes. Gunnill (1985) reported that the 1982-83 El Niño had different effects on seven species of intertidal algae. Adults and juveniles of two kelps, *Egregia menziesii* and *Eisenia arborea*, suffered both reduced recruitment and high mortality rates in response to warm water and nutrient depletion in 1982-

83. In contrast, he found that recruitment rates were high for the furoid alga, *Pelvetia fastigiata*, and the green alga, *Codium fragile*.

During the 1997-98 El Niño, we observed that intertidal kelps (*Hedophyllum sessile*, *Postelsia palmaeformis*, *Egregia menziesii*) were negatively affected along the central Oregon coast. In summer 1997 they were small, slow growing and generally appeared unhealthy: rather than the normal deep brown color seen in these species, plants were a gray-brown color that we had never observed before. However, we noticed that at Cape Blanco (hereafter CB), a site in southern Oregon, intertidal kelps were large, abundant and appeared healthy. CB is a point of transition between upwelling regions (Parrish et al. 1981, Barth et al. 2000). North of CB, upwelling occurs intermittently, primarily from May – September. In contrast, south of CB, upwelling is more persistent and begins earlier in the spring (Mann and Lazier 1996). This shift in upwelling regimes is thought to be a result of both increasing Ekman transport at lower latitudes and because CB is the first of a series of major headlands that extend into northern and central California. Headlands are associated with an increase in the intensity of upwelling favorable winds and with the deflection of the California Current offshore (Parrish et al. 1981, Brink 1983, Smith 1983, Rosenfeld et al. 1997).

Our goal in this study was to document regional variation in the abundance and growth rates of intertidal kelps along the Oregon coast. We hypothesized that large-scale variation in nutrient supply associated with coastal upwelling was responsible for variation in intertidal kelp communities. We examined how kelp

communities in central and southern Oregon fared differentially following the 1997-98 El Niño. We then investigated how persistent differences in upwelling regimes in each region affected intertidal kelps in non-El Niño years. Our evidence indicates that the 1997-98 El Niño indeed negatively impacted kelps and that afterward kelps recovered more quickly in southern Oregon. However, we observed few regional differences in growth and abundance after kelp communities appeared fully recovered.

METHODS

Study sites and organisms

Study sites

Our study sites spanned approximately 300 km of the Oregon coast from Fogarty Creek (hereafter FC) on the central coast to CB on the southern coast (Figure 3.1). Each site has rocky intertidal benches in wave-exposed and wave-protected areas. Each of the sites is characterized by a high zone dominated by barnacles and fucoid algae and a mid zone dominated by mussels. Low zone characteristics varied among sites, ranging from domination by macroalgae at sites such as Boiler Bay (hereafter BB) and CB, to domination by invertebrates at

Strawberry Hill (hereafter SH) and Stonefield Beach (hereafter SB). We located the replicates for each study in areas that were similar in degree of wave exposure.

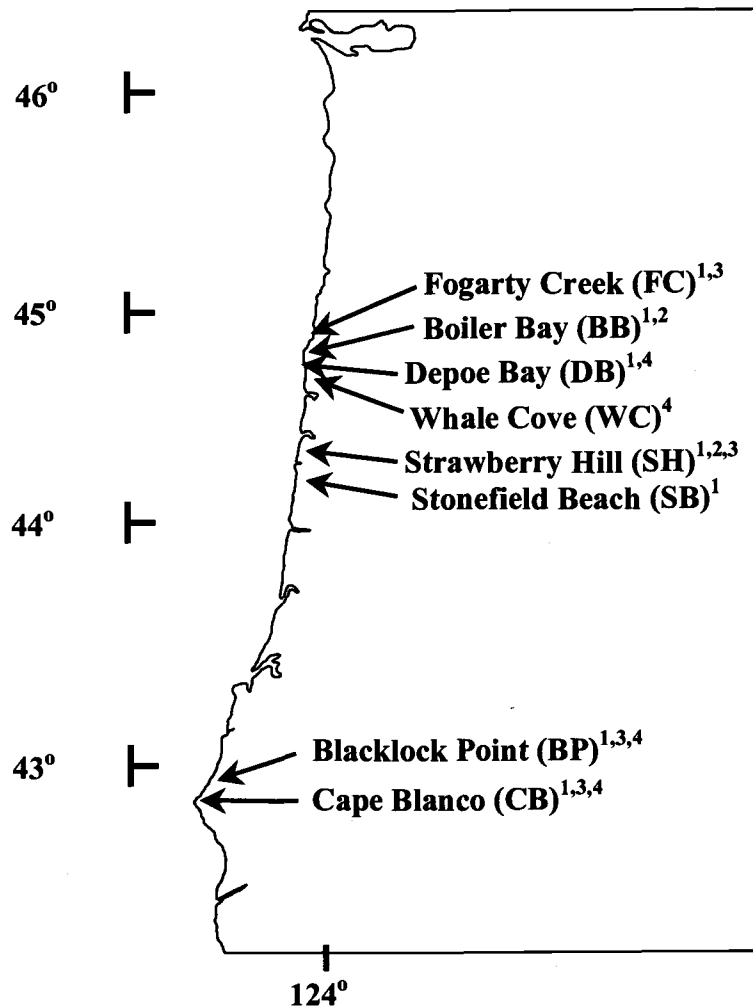


Figure 3.1. Map of study sites along the Oregon coast. BB, FC, DB, WC, SH and SB are on the central Oregon coast and BP and CB are in the Cape Blanco region on the southern Oregon coast. The numbers following the site codes indicate the type of study done at that site. 1 = small algal grid surveys, 2 = large permanently marked grids, 3 = *Egregia* transplants and *in situ* growth and 4 = *Postelsia* transplants.

Study organisms

Postelsia palmaeformis, *Egregia menziesii*, and *Hedophyllum sessile* are intertidal kelps with heteromorphic life-histories comprised of a microscopic gametophyte stage followed by a macroscopic sporophyte stage. *Postelsia* is an annual species that can form large aggregations in the high to mid intertidal zone in areas of high wave exposure (Bold and Wynne 1985). Along the Oregon coast, sporophytes grow throughout the spring and summer and become reproductive in the late spring and early summer (Blanchette 1996). Mature plants are commonly removed from the substrate during fall and winter storms, which can free bare space on which new individuals recruit (Dayton 1973, Paine 1979, 1988, Blanchette 1996). *Postelsia*'s geographic range extends from Vancouver Island, British Columbia to San Luis Obispo County, California (Abbott and Hollenberg 1976). *Egregia* and *Hedophyllum* are perennials that occur in the mid to low intertidal zone in both wave-exposed and wave-protected environments. *Egregia* can be fertile throughout the year, but is most commonly reproductive in the spring through summer. It occurs from Alaska to Baja California (Abbott and Hollenberg 1976). *Hedophyllum* is distributed from Attu Island, Alaska to Point Sur, California (Abbott and Hollenberg 1976)

We carried out four studies aimed at determining the responses of these macroalgal species to the large-scale changes observed during and subsequent to

the 1997-98 El Niño (see Figure 3.1). Small algal grid surveys were done to examine changes in algal abundance and size along the central and southern Oregon coast. Large permanently marked grids were monitored to evaluate spatially explicit changes in large plots. *In situ* growth rates of marked plants were quantified to examine how growth and size varied. Finally, we performed reciprocal transplant experiments to test both the postulated oceanographic effects and any source site effects.

Small algal grid surveys

We quantified the length, density, and percent cover of two species of intertidal algae, *Postelsia palmaeformis* and *Egregia menziesii*. We sampled *Postelsia* in June and August 1998, and August 1999 and 2000 at four sites. We sampled *Egregia* in June and August 1998 at five sites and in August 1999 at four sites. At each site we established five permanent transects in areas where the target species appeared to be most abundant. Each transect was 5 x 1 m and was sampled using 0.25m² quadrats to take measurements in each contiguous plot of the grid of 2 x 10 = 20 quadrats.

Large permanently-marked grids

In July 1997 we established permanent survey grids on wave-exposed intertidal benches at BB and SH. Each grid was 40m long and spanned 8m (BB) to 10m (SH) vertically, encompassing the low, mid, and high intertidal zones. Within the grids, we used 1m² quadrats to visually estimate the percent cover of dominant space occupiers. By permanently marking the exact location of each grid, we assessed changes in percent cover during six subsequent sampling dates in May and August of 1998 and 1999 (data were not collected from SH in May 1999). Using these data, we examined changes in percent cover of an abundant algal species in these plots, the kelp *Hedophyllum sessile*. These data are unreplicated (i.e. one grid per site), therefore we could not conduct any statistical analyses.

In situ growth

We quantified the maximum length of 20 individual *Egrecia in situ* at four sites, two on the southern coast, and two on the central coast, in 1999 and 2000. Individuals were identified using coded plastic tags, which were attached to the substrate adjacent to each plant with a stainless steel screw. We marked plants in May of each year and measured maximum length approximately every two weeks thereafter until August. In 2000 we also examined the growth rate of individuals by

punching a hole in the longest blade 5 cm above the meristematic region every two weeks. Growth was then measured as the distance between the base of the plant and the previous hole.

Algal transplants

Genetic differentiation and physiological condition of plants among sites is one possible explanation for observed differences in size and growth. To control for this potential effect, in addition to making *in situ* measures of growth, we also measured the growth of transplanted *Egregia* and *Postelsia*.

Egregia

We transplanted 25 individual *Egregia* to each of 4 sites, two on the southern coast, and two on the central coast. We removed plants from a common source site by chiseling the rocky substrate beneath their holdfast. We then transplanted them by chiseling holes in the substrate and affixing individuals using Z-spar, a marine epoxy putty (Z-sparTM Splash Zone Compound, Seattle Marine, Seattle, Washington, USA). *Egregia* were transplanted in May and sampled every two weeks thereafter until August. In 1999 and 2000 we measured maximum

length. In 2000 we also measured growth by punching holes in the blades above the meristematic region, as with the *in situ* *Egregia*.

Postelsia

Postelsia were transplanted to four sites in 1999. *Postelsia* commonly grow on the shells of mussels in wave-exposed areas. We collected juvenile plants (ranging from approximately 3-5cm in length) that were growing on mussels and transplanted them by chipping holes in the substrate and attaching the mussels with Z-spar. Chipping holes in which to place the mussels insured that the holdfasts were level with the substrate. 80 plants were collected from each of four sites, two on the southern coast and two on the central coast, and then 20 of these were transplanted to each site in a fully reciprocal design. We measured the length of each plant approximately every two weeks from late May through August.

Temperature and Nutrients

We measured water temperature hourly at each site using temperature data-loggers that were attached to the substrate in the low intertidal zone. We used tide predictions to differentiate between high and low tide measurements. In our

analyses, we use only high tide temperature measurements. In Oregon, coastal upwelling occurs during spring and summer, which is also the primary growing period for intertidal kelps. Therefore we have restricted our temperature analyses to these seasons. We defined spring as April 1 through June 30 and summer as July 1 through September 30. Temperature data were collected for one site, FC, in spring 1997 and three sites in summer 1997, FC, SH and CB. In 1998 we collected temperature data for BB and SH in the spring, and SH, BP, and CB in the summer. In both 1999 and 2000 we collected temperature data from FC, BB, SH, BP and CB for both spring and summer.

Nutrient samples were collected from the shore periodically during the spring and summer from 1993-1999. Water samples were collected approximately 30 cm beneath the ocean surface 3 m off the seaward edge of intertidal rocky reefs. Samples were filtered immediately through a glass fiber filter to remove any phytoplankton, which could continue to incorporate dissolved nutrients. Filtered water samples were then frozen until analyzed with an autoanalyzer for nitrate, nitrate+nitrite, phosphate and silicate.

Water temperature is closely tied to nitrate concentration in marine systems (Jackson 1977, Dayton et al. 1999). Cold, recently upwelled water has a relatively high nitrate concentration, which can be utilized by phytoplankton and macrophytes for growth (Eppley et al. 1979, Small and Menzies 1981, Fujita et al. 1989, Björnsäter and Wheeler 1990). We used simple linear regression to estimate

the relationship between water temperature and nitrate concentrations. Using this relationship, we then predicted nitrate concentrations using temperature data.

Data Analysis

We used one-way ANOVA to test for differences among sites and linear contrasts to test *a priori* hypotheses about differences between regions for the small grid surveys and for the algal *in situ* and transplant experiments. To analyze the small grid surveys, we used the grid averages as the sampling unit so that $n=5$ for each site for data collected in June and August 1998 and August 1999 and 2000. For *Egrecia in situ* and transplant experiments, we used individual plants as experimental units to test for differences between regions in maximum length in 1999 and 2000, and growth rates in 2000. Analyses were conducted separately for each sampling date, approximately every 2 weeks from May through August. For each analysis, we visually examined probability plots of residuals and plots of residuals vs. estimated values to evaluate assumptions of normality and homogeneity of variance, respectively. When necessary, data were log transformed ($\ln \{y + 1\}$).

A split-plot design was used in the *Postelsia* transplant experiment. However, due to high mortality we had insufficient degrees of freedom to conduct the analysis. Instead, we first compared the proportional growth of plants from

different sources (local vs. non-local sites) within a site to determine if there was an effect of source site on growth patterns. We found no significant differences ($P > 0.05$ for all comparisons) in growth rates of plants from different sources.

Therefore, we lumped plants from different sources and analyzed the data using one-way ANOVA to determine if there were differences in regional growth patterns as we did with *Egrewia* maximum length and growth. While this technique does not test for source site effects, it is conservative for examining regional effects because each site had individuals from every source.

We examined regional differences in water temperature frequency histograms using Chi-square tests. We first divided daily water temperature data into 1°C bins for spring and summer. We then pooled daily water temperature data across sites within each region. To test for differences between regions, we then calculated a Chi-square statistic, where a significant P-value indicates that the regional temperature distributions were not equal (Zar 1974).

We also analyzed predicted daily nitrate concentrations using Chi-square tests. We began by using simple linear regression results to predict daily nitrate concentrations based on water temperature. We then sorted nitrate concentrations into three micromolar bins, and pooled across regions.

RESULTS

Small algal grid surveys

Postelsia

In 1998, we observed large differences in the size, density and cover of *Postelsia* between CB and central coast sites (Fogarty Creek, FC; Depoe Bay, DB; Yachats Beach, YB; Fig. 3.2). These differences diminished or disappeared in 1999 and 2000. The average length of *Postelsia* was almost two times greater at CB than at the sites on the central coast in both June and August 1998 ($P < 0.0001$ for both contrasts, Table 3.1, Figure 3.2A). While plants were consistently larger at CB than on the central coast in August 1999 and August 2000, these differences were not as great ($P = 0.003$ for both contrasts, Table 3.1, Figure 3.2A). *Postelsia* density was over two times greater at CB in 1998 ($P = 0.015$ for June 1998, $P = 0.014$ for August 1998, Table 1, Figure 3.2B) but not significantly different from the central coast sites in 1999 or 2000 ($P > 0.50$ for both contrasts, Figure 3.2B). Percent cover of *Postelsia* was three times higher at CB than on the central coast by August 1998 ($P = 0.0001$, Table 1, Figure 3.2C), but did not differ between regions in 1999 or 2000 ($P > 0.30$ for both contrasts, Figure 3.2C).

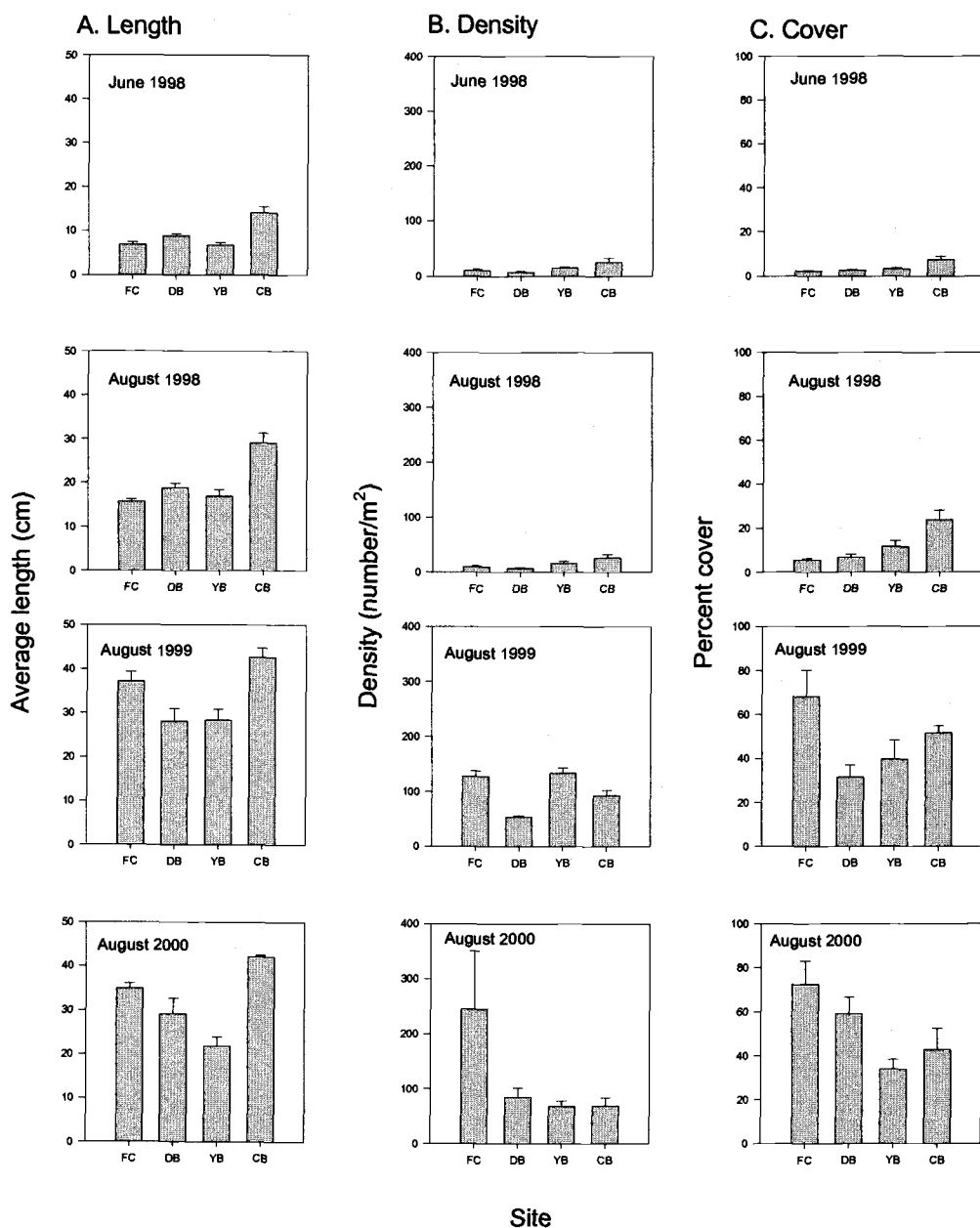


Figure 3.2. (A) Length, (B) density and (C) percent cover of *Postelsia* at 4 sites along the Oregon coast in June and August 1998, August 1999, August 2000. Sites are arranged in latitudinal order with the northernmost site, FC, at the left and the southernmost site, CB, at the right of each panel. In each case, values are averages of $n=5$ transects per site. Length is the average ($+1$ SE) distance from the holdfast

Table 3.1. Results of linear contrasts comparing differences in the length, density and percent cover of *Postelsia* and *Egregia* between sites on the central vs. southern coast. The effect size is the number of times greater the value is at sites on the southern relative to the central coast. For example, *Postelsia* were 1.90 times larger on the southern coast in June of 1998.

	Length		Density		Cover	
	Effect Size	95% CI	Effect Size	95% CI	Effect Size	95% CI
<i>Postelsia</i>						
June 1998	1.90	1.57 – 2.29	2.1	1.19 – 3.7	2.50	1.58 – 3.95
August 1998	1.70	1.44 – 2.01	2.35	1.23 – 4.5	3.15	1.95 – 5.09
August 1999	1.40	1.15 – 1.7	ns	ns	ns	ns
August 2000	ns	ns	ns	ns	ns	ns
<i>Egregia</i>						
June 1998	3.90	2.92 – 5.2	0.27	0.17 – 0.41	ns	ns
August 1998	3.95	2.95 – 5.29	0.32	0.18 – 0.57	19.53	5.14 – 33.92
August 1999	1.93	1.47 – 2.53	0.45	0.29 – 0.7	23.20	8.01 – 38.39

Egregia

In 1998, *Egregia* was almost four times longer at sites on the southern coast than at sites on the central coast ($P < 0.0001$ for June and August contrasts, Table 3.1, Figure 3.3A). While this pattern persisted in 1999 ($P = 0.0001$, Table 3.1, Figure 3.3A), the differences in length between regions was not as striking. In contrast to the differences we saw in *Postelsia* density, density of *Egregia* was only 0.27 times as high at sites in the CB region relative to density on the central coast in June 1998 ($P < 0.0001$, Table 3.1, Figure 3.3B). We saw similar patterns in August 1998 and August 1999 where density was 0.32 and 0.45 times as high, respectively, at sites

in the CB region ($P=0.0009$ for August 1999 and $P=0.0019$ for August 1999, Table 3.1, Figure 3.3B). Percent cover of *Egretta* did not differ between regions in June 1998 ($P=0.28$), but by August was almost 20% higher in the CB region than on the central coast ($P=0.013$, Table 3.1, Figure 3.3C). This difference persisted in 1999 when percent cover was over 20% higher at sites in the CB region than on the central coast ($P=0.006$, Table 3.1, Figure 3.3C).

Large permanently-marked grids

In July 1997 *Hedophyllum* covered 7.5 percent of the grid at BB and 10 percent at SH. In May 1998, at the end of the El Niño, percent cover had dropped to 0.4% at BB and 0.6% at SH (Figure 3.4). By August 1998, cover was 3.3% and 2.5% at BB and SH, respectively. Cover of *Hedophyllum* did not recover to pre-El Niño levels until August 1999 (Figure 3.4). This return to pre- El Niño levels persisted in 2000 (Figure 3.4).

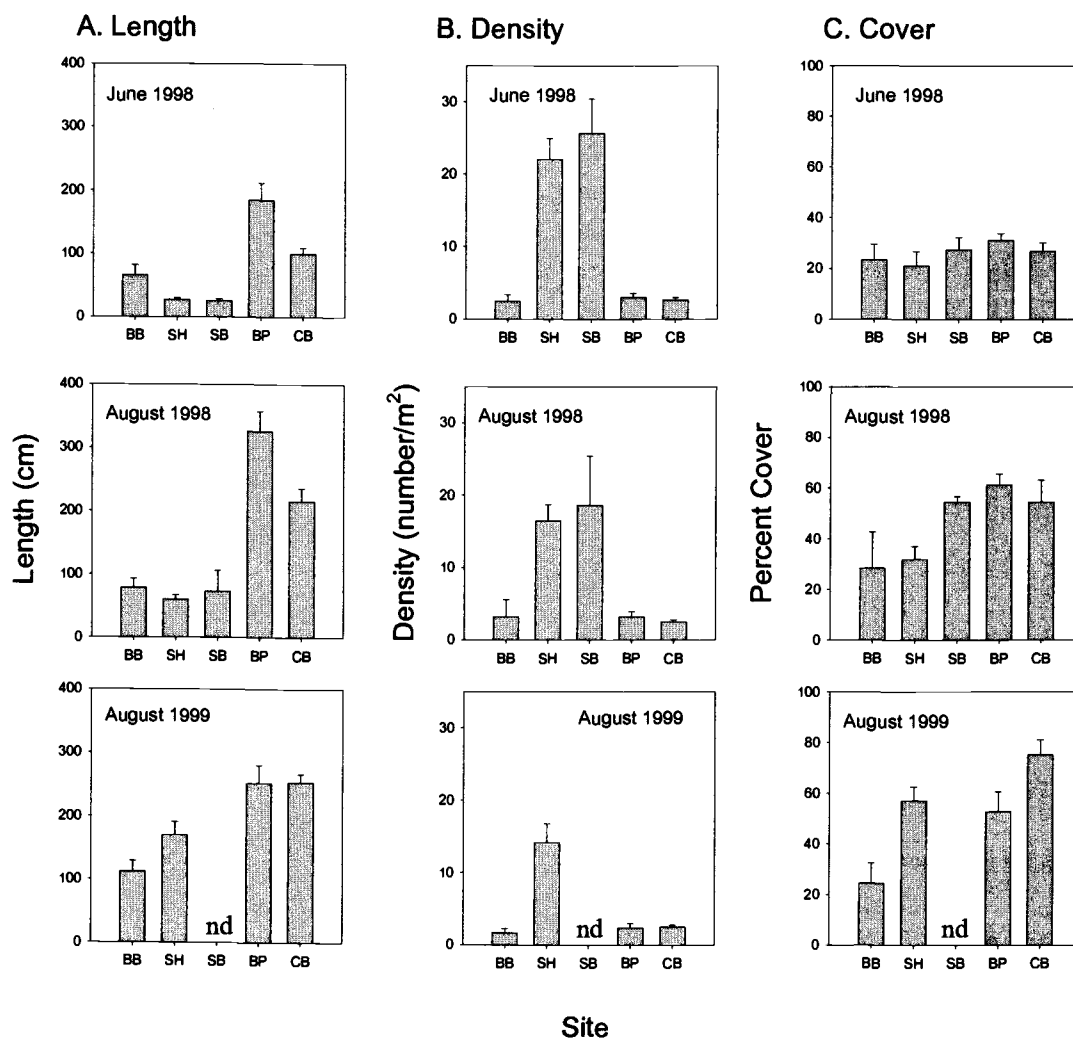


Figure 3.3. (A) Length, (B) density and (C) percent cover of *Egregia*. We sampled at five sites along the Oregon coast in June and August 1998 and four sites in August 1999. Sites are arranged in latitudinal order with the northernmost site, BB, at the left and the southernmost site, CB, at the right of each panel. In each case, values are averages of $n=5$ transects per site. Length is the average ($+ 1$ SE) distance from the holdfast to the end of the stipe, density is the average ($+ 1$ SE) number of plants/m² and percent cover is the average ($+ 1$ SE) proportion of area covered by *Egregia*.

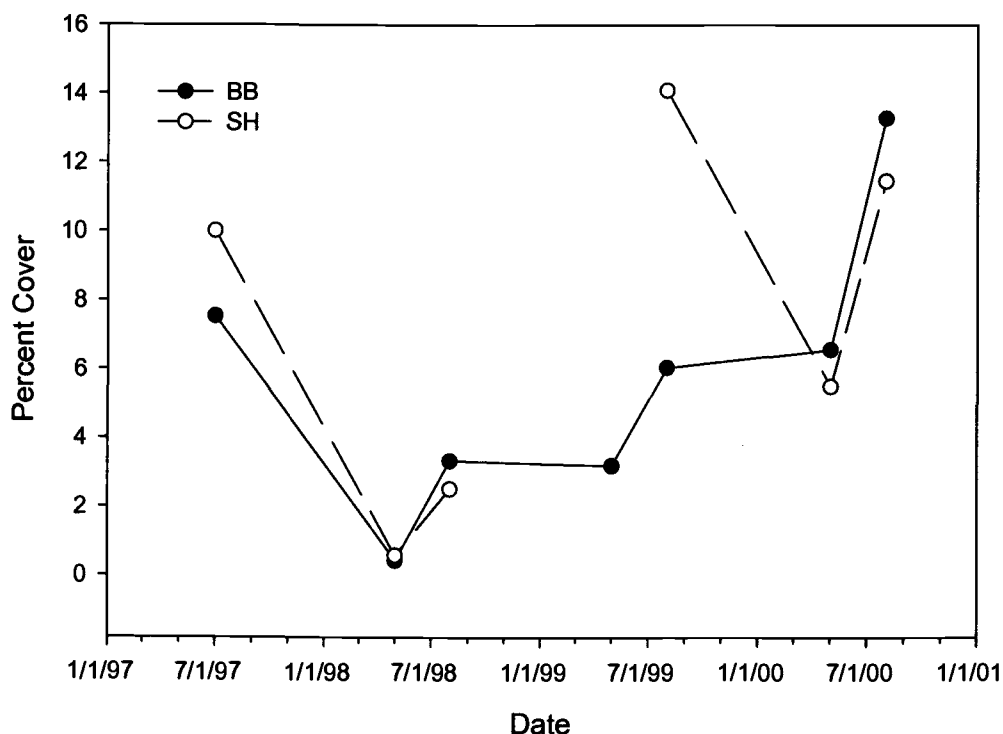


Figure 3.4. Percent cover of *Hedophyllum* in large permanently-marked grids. We sampled at BB (grid area=312m²) and SH (grid area=360m²) from July 1997 to August 2000. Data were not collected at SH in May 1999.

In situ growth

In 1999 and 2000, maximum length of marked *in situ* *Egria* was generally greater at southern coast sites than at central coast sites, although these differences were significant for only three sampling dates in 1999 and one in 2000 (Figure 3.5A,B). Daily growth rates of *Egria* plants were higher on the southern coast than the central coast in early June 2000 (Figure 3.5C). However, in July

there was a switch from higher growth on the southern coast to higher growth on the central coast. This difference persisted until mid August (Figure 3.5C).

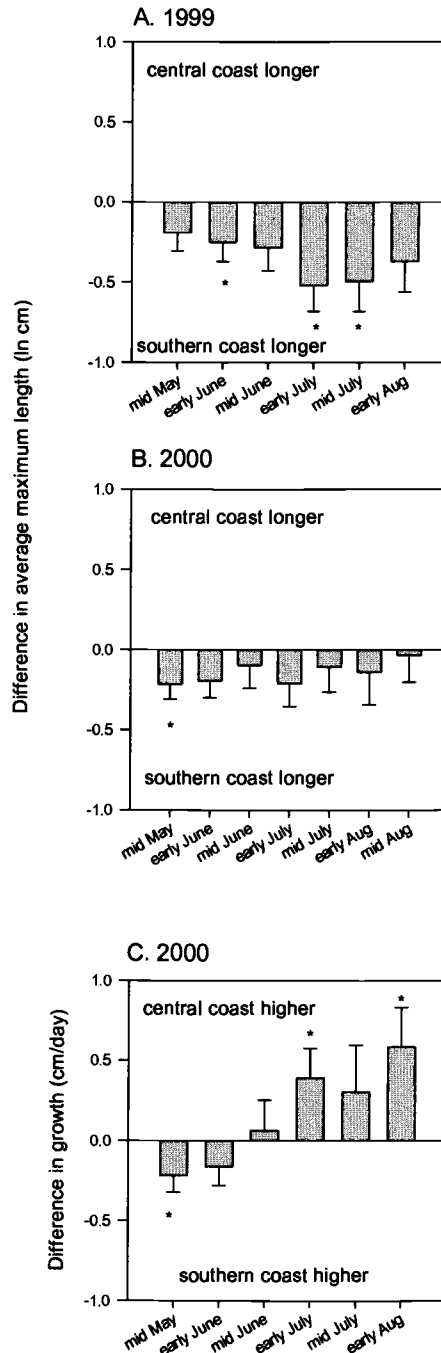


Figure 3.5. Difference in maximum length (+ 1 SE) in (A) 1999 and (B) 2000 and (C) differences in growth (cm/day) in 2000 of in situ *Egregia* at sites on the central coast (FC and SH) relative to sites on the southern coast (BP and CB). Positive values indicate higher values on the central coast while negative values indicate higher values on the southern coast. The symbol ‘*’ indicates a significant difference ($P < 0.05$) between the central and southern regions.

Algal transplants

Egregia

Maximum lengths of transplanted *Egregia* were consistently greater at sites in the Cape Blanco region than at sites on the central coast throughout the summer in 1999 (Figure 3.6A). In contrast, there were no differences between regions in maximum length of transplanted plants at any time in 2000 ($P > 0.35$ for all contrasts, Figure 3.6B). There were also generally no regional differences in growth rates in 2000, with the exception of measurements in mid July (Figure 3.6C).

Our goal in transplanting *Egregia* from a common source site was to control for differences in condition or genetic make-up that may affect growth rates. However, the mortality rates for transplanted individuals were much higher than that of plants that were measured *in situ* (on average transplant mortality was 72% while *in situ* mortality was 30%). The apparent negative impact of the transplanting procedure on *Egregia* and the scarcity of individuals at the end of the experiment (2-8 per site) lead us to interpret these results with caution.

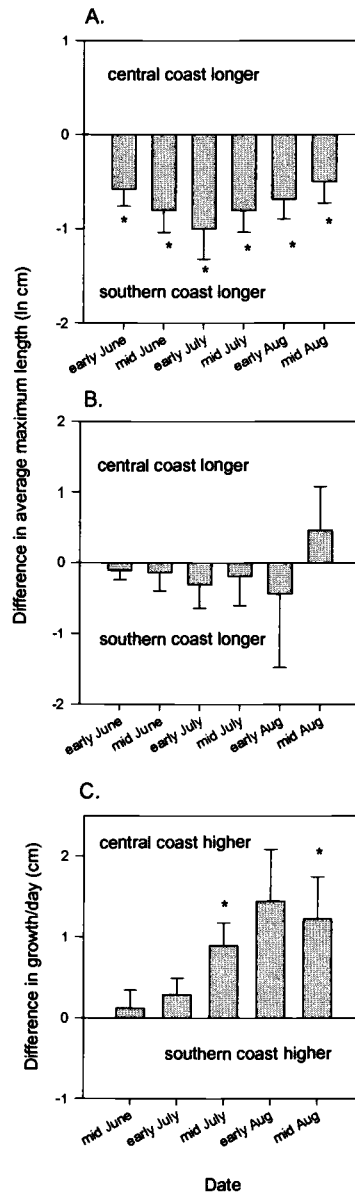


Figure 3.6. Difference in maximum length (+ 1 SE) in (A) 1999 and (B) 2000 and (C) differences in growth (cm/day) in 2000 of transplanted *Egregia* at sites on the central coast (FC and SH) relative to sites on the southern coast (BP and CB). Positive values indicate higher values on the central coast while negative values indicate higher values on the southern coast. The symbol ‘*’ indicates a significant difference ($P < 0.05$) between the central and southern regions.

Postelsia

Based on our observations following the 1997-98 El Niño, we hypothesized that *Postelsia* would grow faster on the southern coast than at sites on the central coast. However, during summer 1999, transplanted *Postelsia* grew faster at sites on the central Oregon coast in two out of six time periods. There were no differences in growth rates during the other sampling periods (Figure 3.7).

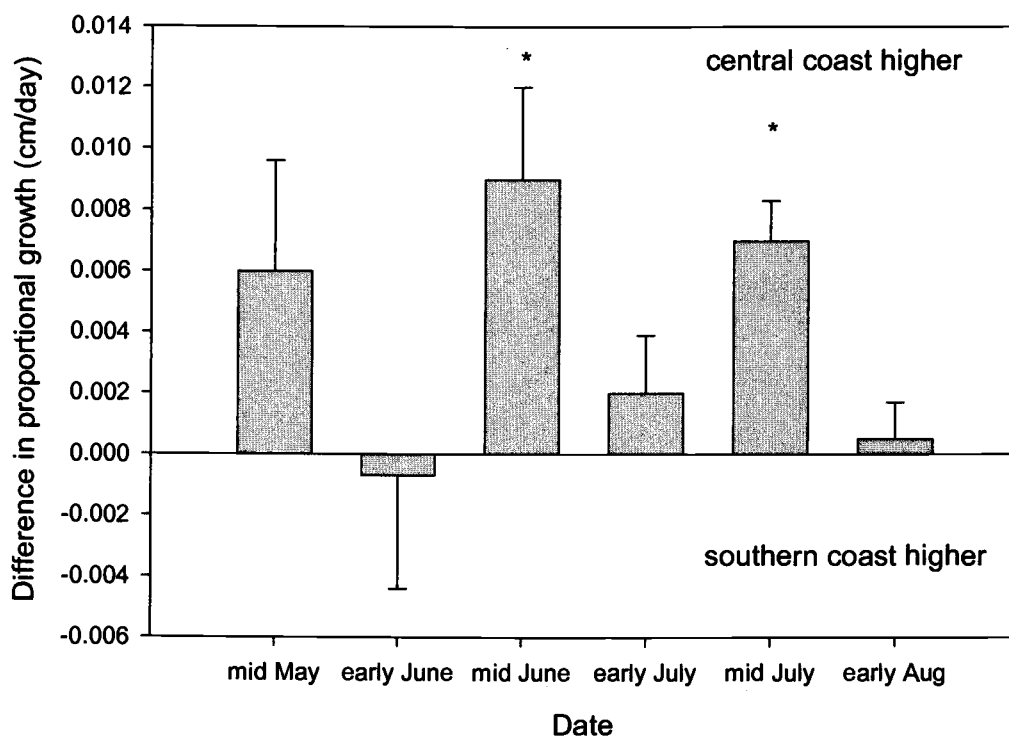


Figure 3.7. Difference in growth (cm/day) of individually marked *Postelsia* at sites on the central coast (DB and WC) relative to sites on the southern coast (BP and CB) from June to August 1999. Positive values indicate higher growth rates on the central coast while negative values indicate higher growth rates on the southern coast. The symbol '*' indicates a significant difference ($P < 0.05$) between the central and southern regions.

Temperature and nutrients

Spring (March-June) water temperature distributions varied among years (Chi-square; $P < 0.0001$ for both the central and southern regions) and between regions in each year (Chi-square; $P < 0.005$ for all regional comparisons) (Figure 3.8). In 1999 and 2000, average water temperatures were generally lower on the southern coast, although in 2000 this difference was not as great. Data from the central coast in 1997 shows the effects of the El Niño with temperatures commonly exceeding 12°C (Figure 3.8A). Such high water temperatures were uncommon during the spring of the following years. Spring water temperatures in 1998 were similar to temperatures in 2000, and only slightly warmer than temperatures in 1999, suggesting that the effects of the El Niño on water temperature had diminished.

Summer water temperature distributions varied among years (Chi-square; $P < 0.0001$ for both the southern and central coast) and were higher during 1997, at the height of the El Niño relative to the following three years (Figure 3.9). The frequency histograms also differed regionally (Chi-square; $P < 0.0001$ for all regional comparisons) with temperatures on the southern coast tending to be less variable than temperatures on the central coast. Average summer temperatures were more similar among regions in the summer than in the spring. However, mean temperatures were greater on the southern coast than the central coast in 1998, 1999, and 2000, but not in 1997.

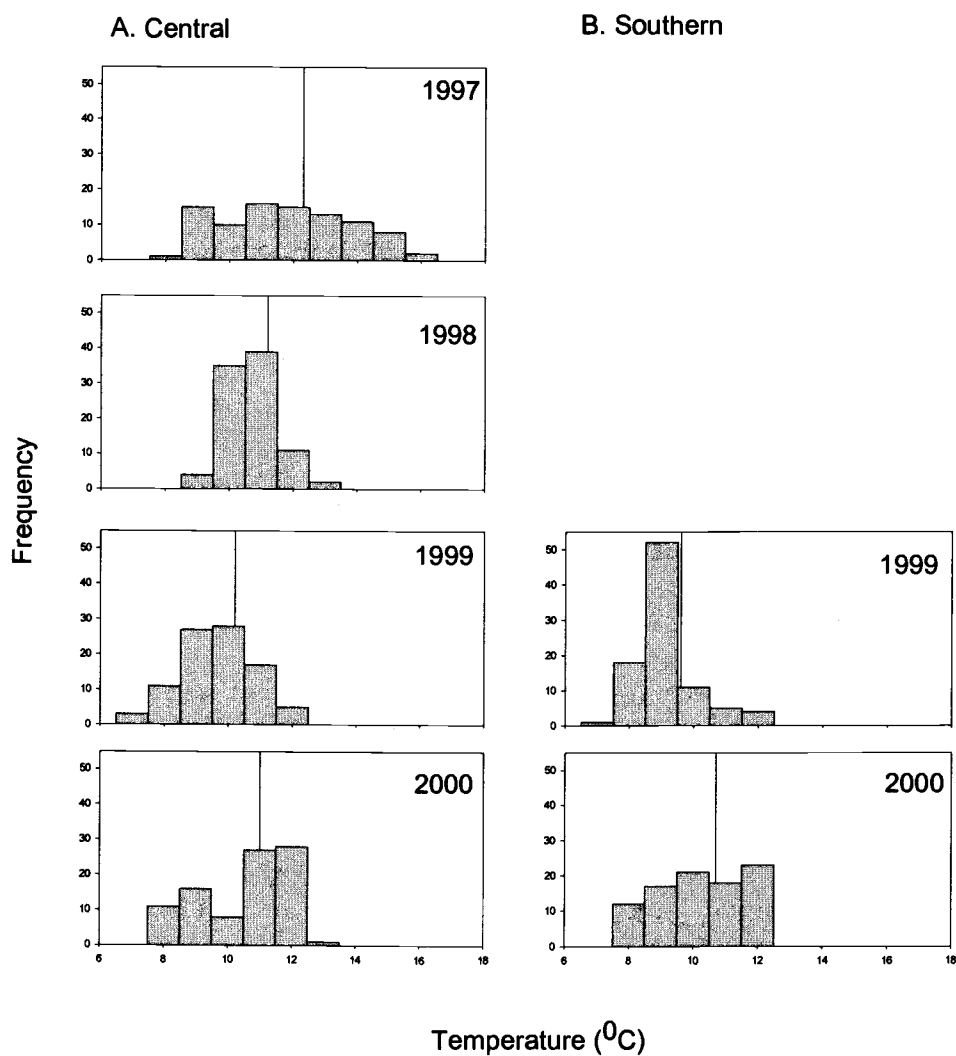


Figure 3.8. Spring (April-June) water temperature frequencies (number of days) along the (A) central and (B) southern Oregon coast from 1997-2000. The vertical line indicates the average water temperature during that time period.

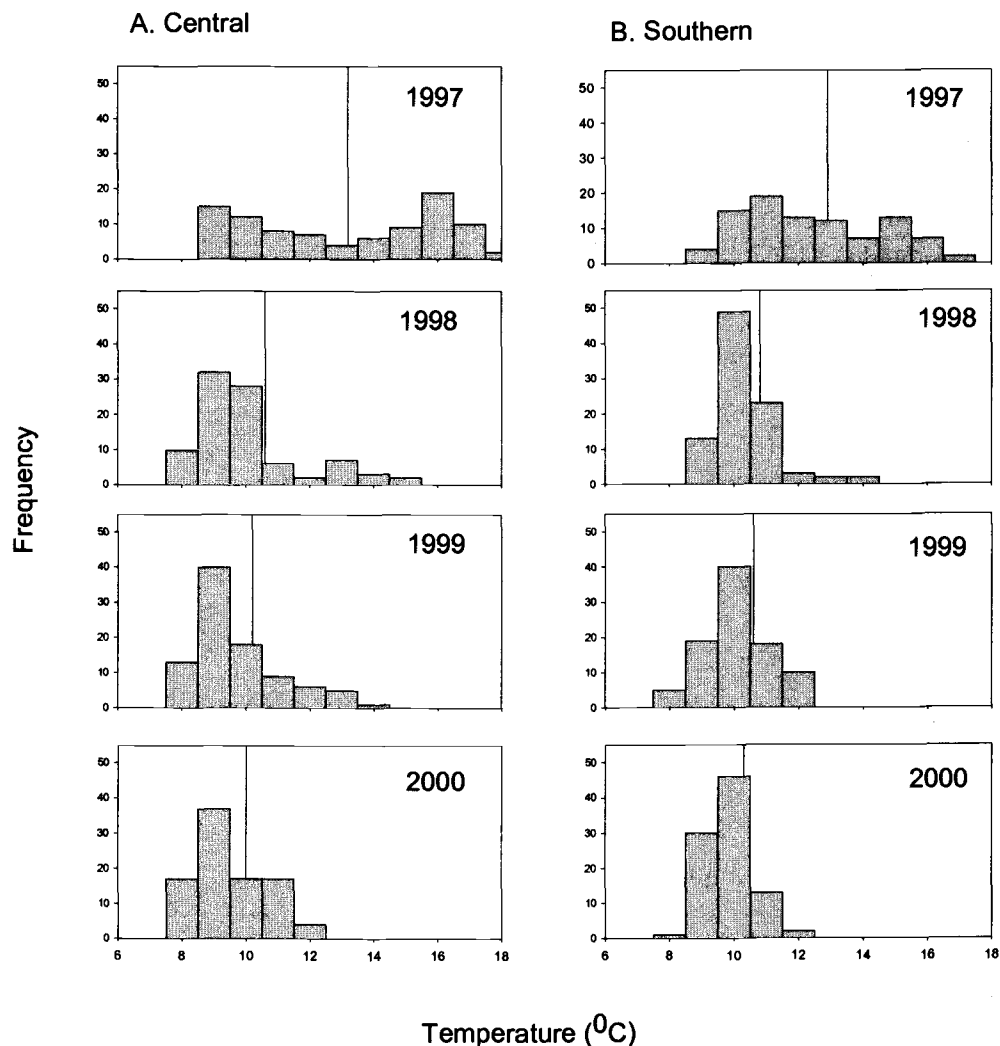


Figure 3.9. Summer (July-September) water temperature frequencies (number of days) on the (A) central and (B) southern Oregon coast from 1997-2000. The vertical line indicates the average water temperature during that time period.

Water temperature explained 60.6% of the variability in nitrate concentration ($P < 0.0001$; nitrate concentration = $-32.36 + 487.39 \cdot [1/\{\text{water temperature in } ^{\circ}\text{C}\}]$). Using this relationship, we used water temperature to approximate nitrate concentrations based on daily temperature measurements. The

distribution of estimated nitrate concentrations based on water temperature differed among regions (Chi-square; $P < 0.005$) and years (Chi-square; $P < 0.0001$). Estimated nitrate concentrations were lowest in both the spring and summer of 1997 (Figures 3.10, 3.11), when warm El Niño conditions were at their peak. In spring 1999 and 2000, years for which we have data for the southern coast, average estimated nitrate concentrations were higher on the southern coast than on the central coast (Figure 3.10). In contrast, average estimated nitrate concentrations during summer 1998-2000 were higher on the central coast (Figure 3.11). In summer 1997, average estimated nitrate concentrations were higher on the southern coast.

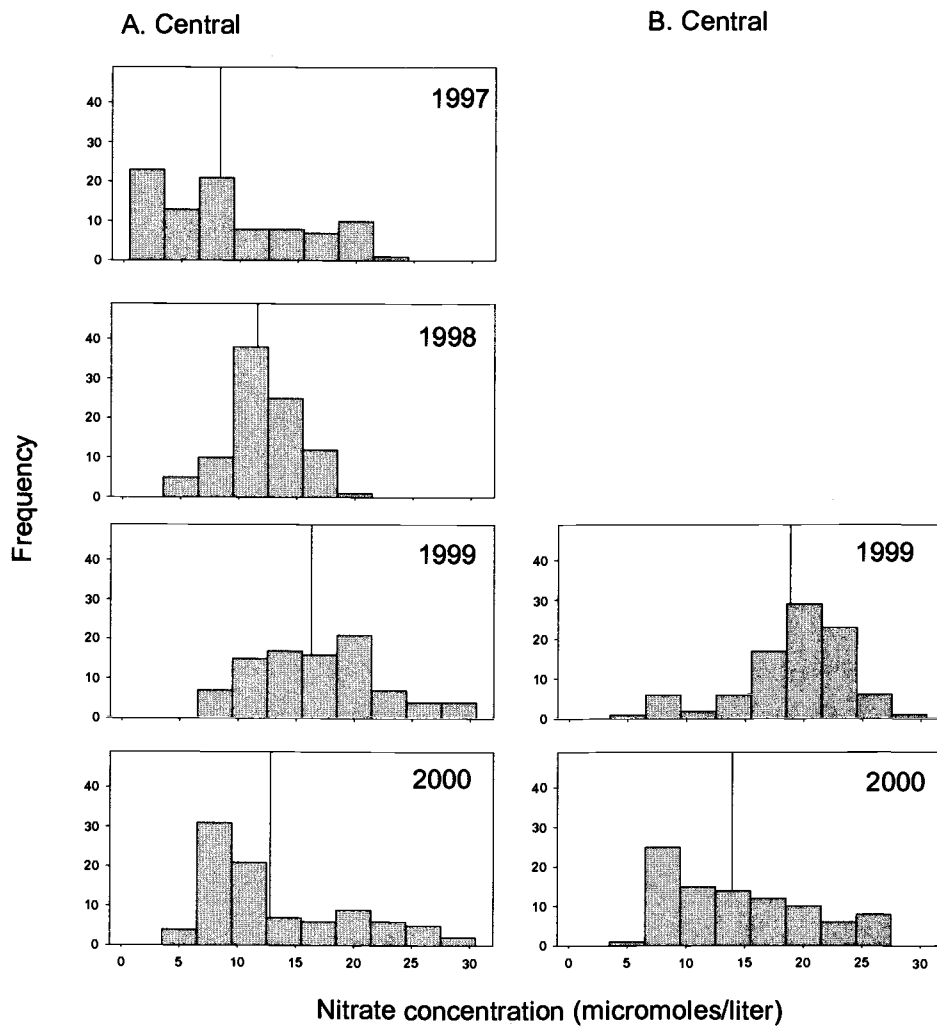


Figure 3.10. Estimated nitrate concentration frequencies along the (A) central and (B) southern Oregon coast during spring (April – June) from 1997-2000. The vertical line indicates the average estimated nitrate concentration during that time period.

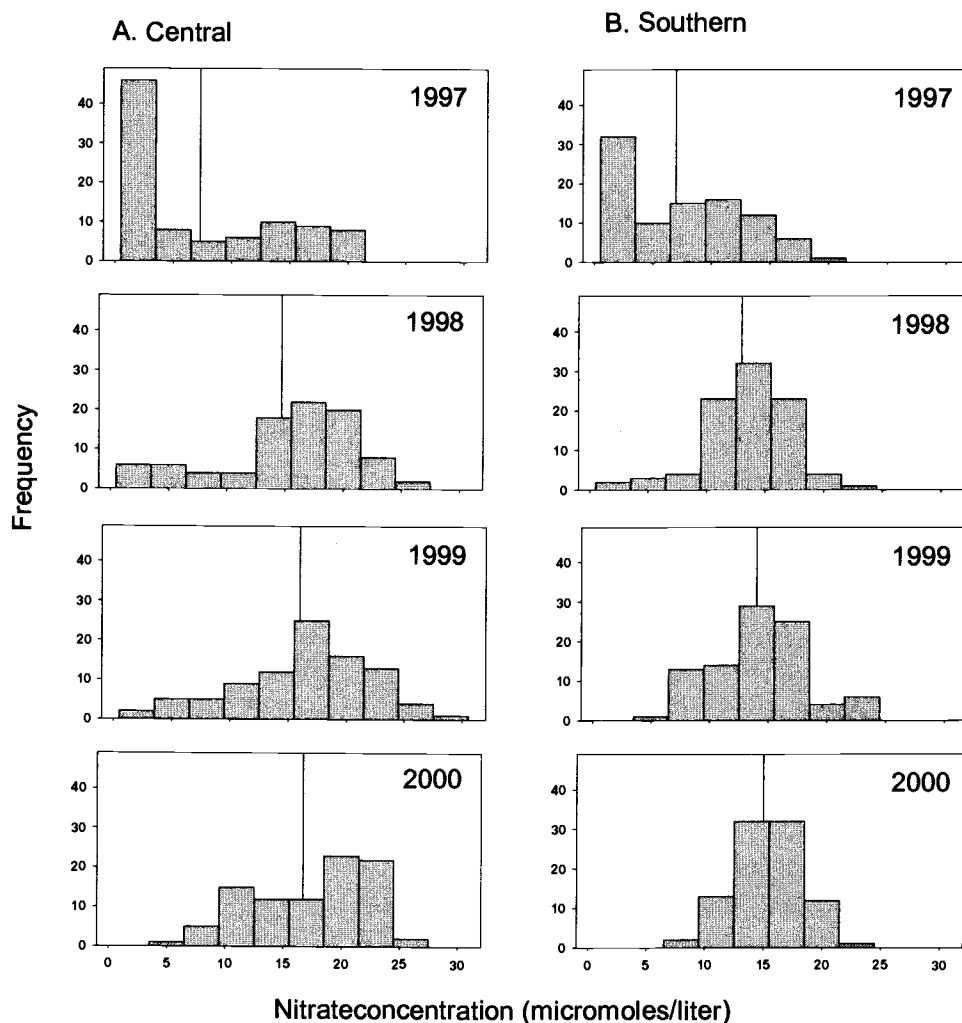


Figure 3.11. Estimated nitrate concentration frequencies along the (A) central and (B) southern Oregon coast during summer (July - September) from 1997-2000. The vertical line indicates the average estimated nitrate concentration during that time period.

DISCUSSION

Warm, nutrient-depleted water during the 1997-98 El Niño likely contributed to a dramatic reduction in abundance and cover of intertidal kelps along the Oregon coast. This effect can be seen clearly in the striking decline in cover of *Hedophyllum* at sites on the central Oregon coast. However, our evidence indicates that local oceanographic processes can modify the effect of El Niño on intertidal kelps. The El Niño ended in May 1998 (McPhaden 1999) and we began monitoring *Postelsia* and *Egregia* in June. We found that both *Postelsia* and *Egregia* were larger at sites around Cape Blanco than at sites on the central Oregon coast suggesting that sites on the southern coast were less affected by the El Niño.

These differences did not persist during the two years following the El Niño. While the average length of *Postelsia* was almost two times as great on the southern coast than on the central coast in 1998, this difference diminished in 1999 and disappeared by 2000. Similarly, differences in the average length of *Egregia* diminished in 1999. *Hedophyllum* cover also increased after the El Niño, returning to pre-El Niño levels by late summer 1999 on the central Oregon coast.

Measurement of maximum length and growth of *Egregia* suggest that the southern Oregon coast had superior conditions for growth in 1999, but not in 2000. Maximum length of both *in situ* and transplanted individuals tended to be longer on the southern coast in 1999. In 2000, the southern region had longer *in situ* plants during the first monitoring period but did not differ from the central coast during

any other time period. There were no regional differences in maximum length at any time for transplanted individuals. *Egregia* marked *in situ* grew faster on the southern coast in mid May but in mid July and mid August they grew faster on the central coast. Likewise, transplanted individuals grew similarly between regions in the early summer but faster on the central coast in July and August. Based on these observations, we postulate that if superior conditions for growth occurred in the Cape Blanco region during these years, then they were present only in the spring and diminished or reversed in the summer. This hypothesis is further supported by between-region differences in temperature and estimated nitrate concentration, which were largest in the spring (Figures 3.8, 3.10A).

Growth of transplanted *Postelsia* was greater on central coast in mid June and mid July 1999 but there were no differences during other sampling periods. These results were surprising given the differences in maximum length that we observed in the algal transects in August of that year. We suspect that by transplanting in May we may have missed critical differences in growth during early spring. Thus, differences in the size of *Postelsia* in transects in August may have arisen from differences that existed prior to May. This is consistent with results from the *Egregia* experiments in 2000 also suggest that regional differences in maximum length may be due to differences in growth in the spring, not the summer.

During the 1997-98 El Niño, sea surface temperature (SST) was much warmer along the Oregon coast than in following years (Figures 3.8A, 3.9A). Such

warm water is indicative of reduced upwelling of cold water that is typical during El Niño years, both along the Oregon coast and at coastal upwelling regions elsewhere (Barber and Chavez 1983). Since this warm water is typically nutrient-depleted, the El Niño likely resulted in depressed growth of intertidal kelps.

Anomalously high water temperature could have further weakened already stressed plants making them more susceptible to winter storms as has been seen for the giant kelp, *Macrocystis pyrifera* (Dayton and Tegner 1984). In 1999 and 2000 SST was relatively cold, indicating more intense upwelling of deep, nutrient-rich water. At the same time, we observed an apparent recovery of kelps that had been hard hit by the El Niño conditions: *Egregia* and *Postelsia* were large and grew quickly, and *Hedophyllum* returned to pre-El Niño percent cover.

Temperature data from 1998 to 2000 suggest that the distribution of water temperatures differed between the central and southern coast sites in the spring and summer. Thus, more nutrients are likely available for algal growth on the southern coast in the spring. We hypothesize that higher nutrient concentrations in spring result in higher growth early in the season and greater maximum size in late summer in the Cape Blanco region, as we observed in the algal transect results. Differences in spring water temperatures may reflect fundamental differences in the processes that drive upwelling on the southern versus central coast. The central coast is relatively straight and dominated by wind driven offshore transport, which depends on the vagaries of wind direction and is most intense in summer. In contrast, Cape Blanco is a prominent headland and thus not only concentrates

upwelling-favorable winds, but also deflects the California Current offshore, resulting in more persistent upwelling (Brink 1983, Rosenfeld et al. 1997). In typical years, these differences may be masked by intense upwelling along the central coast that results in relatively high algal growth in mid to late summer as we observed for *Egregia* and *Postelsia*. However, in El Niño years, when conditions are less favorable for coastal upwelling, intertidal kelps appear to fare much better near Cape Blanco.

These results add to a growing body of literature that indicates that El Niño events can have detrimental effects on intertidal and subtidal (Dayton and Tegner 1984, Gunnill 1985, Zimmerman and Robertson 1985, Lada et al. 1999, Hernandez-Carmona et al. 2001) algae along the US West Coast. El Niño events affect marine algae in three ways: through nutrient depletion, high water temperatures and greater wave forces during winter storms. Our study indicates that local oceanographic features may significantly modify the intensity of El Niño effects. In particular, persistent upwelling at Cape Blanco may buffer intertidal kelps from El Niño-related nutrient depletion. Given trends for more frequent and more severe El Niño events, areas like Cape Blanco may provide increasingly important refugia for kelp communities.

CHAPTER FOUR: TOP-DOWN AND BOTTOM-UP EFFECTS IN ROCKY INTERTIDAL COMMUNITIES: LIMPET-ALGAL INTERACTIONS AND REGIONAL VARIATION IN OCEANOGRAPHIC PROCESSES

ABSTRACT

In recent years ecologists have increasingly recognized the importance of both top-down and bottom-up factors in structuring communities. Previous studies suggested that in Oregon rocky intertidal communities, between site differences in bottom-up forces (e.g. phytoplankton concentration, recruitment of sessile invertebrates) were associated with differences in top-down interactions (e.g. predation, grazing). However, the generality and spatial scales of these differences remained unclear. We explored how top-down and bottom-up interactions in intertidal communities vary in response to differences in oceanographic processes on local (within site) to mesoscale (among sites within region) to regional scales (among regions). We focused on the effects of limpets on algal and barnacle cover and the manner in which this varied between zones (scales of m), among sites (scales of km) and among regions (scales of 10s to 100s of km) with different patterns of seasonal upwelling. We conducted two types of grazing experiments to measure the effect and rate of herbivory at sites spanning approximately 300 km of the Oregon coast. These experiments included sites in southern Oregon, at Cape Blanco, where upwelling is relatively persistent and sites in central Oregon where

upwelling is relatively intermittent. Within central Oregon, our sites were further subdivided into two regions where the effects of upwelling are modified by the width of the continental shelf. At Cape Perpetua the continental shelf is wide, macrophyte abundance is relatively low and invertebrate recruitment is relatively high. In contrast, at Cape Foulweather the continental shelf is narrow, macrophyte abundance is relatively high and invertebrate recruitment is relatively low. In addition, upwelling tends to be relatively more intense at Cape Foulweather than at Cape Perpetua. Our results show that there were consistent differences among regions in the effects and rate of herbivory. Generally, limpets had the strongest effect on algal recolonization and the highest grazing rates at sites in the Cape Perpetua region, where bottom-up effects on benthic algae tend to be relatively weaker than at either Cape Blanco or Cape Foulweather. Hence, limpet effects were weaker and grazing rates were lower at sites of relatively more persistent upwelling. Herbivores had no effect on barnacle cover at any site. Per capita effects of limpets neither varied consistently among regions nor were they related to the per population grazing rate or effect of herbivory, suggesting that individual effects of limpets were relatively constant across the different environmental gradients of tide level and oceanographic conditions. We conclude that, in the limpet-algal component of this ecosystem, top-down effects vary inversely to bottom-up (nutrient input, algal growth) processes. Comparison to prior results with the predator-sessile prey components of this system suggests that herbivore-

plant and predator-prey components respond differently to the different bottom-up influences that underlie these interactions.

INTRODUCTION

Since Hairston et al. (1960) proposed a top-down model of community regulation, ecologists have debated whether predation or primary productivity is most important in determining community structure and dynamics (Oksanen et al. 1981, Fretwell 1987, Polis 1999, Polis et al. 2000, Schmitz et al. 2000, White 2001). Proponents of the top-down view maintain that predators hold herbivore populations in check, and thus release plants from herbivory. In contrast, champions of the bottom-up view contend that nutrients and primary productivity determine the nature of interactions between trophic levels. Increases in primary productivity support higher abundances of herbivores that in turn support greater numbers of predators. While there are still proponents of these seemingly opposing views, ecologists are increasingly adopting an integrated perspective that recognizes that top-down and bottom-up processes are dynamically linked (Hunter and Price 1992, Menge 1992, Menge et al. 1997a, Fraser 1998, Leonard et al. 1998, Menge et al. 1999b, Nielsen 2001). This modified view proposes that community structure is a consequence of both processes. Therefore, determining the relative

impacts of and linkages between, top-down and bottom-up processes is crucial to understanding variation in community structure.

Studies in marine intertidal systems have been particularly fruitful in exploring the relative contributions of top-down and bottom-up processes. For example, in South Africa, researchers demonstrated that increases in nutrient supply from bird guano modified community structure through enhancement of algal production, which led to increased growth of limpets and greater abundance of algal-dwelling invertebrates (Bosman et al. 1986, Bosman and Hockey 1986). Invertebrates associated with the algal turf in areas with inputs of guano in turn provided food for small shorebirds. In unenriched areas, algal mats and their associated communities of invertebrates and shorebird predators were absent. In another example, differences in flow velocity influenced the delivery of nutrients, food and larvae to intertidal habitats in New England, thereby affecting the strength of top-down and bottom-up forces. In high flow environments, bottom-up effects were stronger due to both higher delivery rates of planktonic larvae and food and to inhibition of foraging by predatory crabs. In low flow environments, top-down effects were stronger as foraging rates of crabs increased (Leonard et al. 1998, Leonard et al. 1999).

Recent work on the Oregon coast has shown that both top-down (i.e. predation and grazing) and bottom-up (i.e. phytoplankton concentrations and prey recruitment) factors affect intertidal community structure (Menge 1992, Menge et al. 1994, Menge et al. 1997a). However, the magnitude of these effects differs

substantially between two sites. Boiler Bay (hereafter BB), and Strawberry Hill (hereafter SH), 80 km apart on the Oregon coast, have strikingly different patterns of community structure in the low intertidal zone. BB has a high cover of algae and low cover of sessile invertebrates while SH has a low cover of algae and high cover of sessile invertebrates (Menge 1992). Observation and experimental studies have demonstrated that at SH, where phytoplankton productivity and recruitment rates are consistently higher, predation and grazing rates are also higher (Menge et al. 1997a, Menge 2000b). Menge and colleagues have postulated that greater top-down and bottom-up forces at SH are caused by differences in nearshore (0 ~ 10 km from shore) oceanographic patterns.

Regional differences in top-down and bottom-up forces may stem from variability in the intensity of seasonal upwelling. On the US West Coast seasonal upwelling occurs during the spring and summer when strong equatorward winds, combined with the Coriolis effect, drive surface water offshore. Displaced surface water is replaced by cold, nutrient-rich water from depth (Parrish et al. 1981, Brink 1983, Huyer 1983). Nutrient-laden upwelled water can fuel the growth of phytoplankton and macrophytes leading to not only bottom up, but also, through trophic linkages, to top-down effects on intertidal community structure and dynamics. Upwelling-induced phytoplankton blooms can provide food for filter-feeding invertebrates such as barnacles and mussels leading to higher growth rates (Menge 1992, Menge et al. 1994, Dahlhoff and Menge 1996, Sanford and Menge 2001) and possibly also to higher larval and recruit survival. This type of bottom-

up effect may indirectly influence algal communities if fast-growing sessile invertebrates preempt space or inhibit grazers (Dungan 1986, Farrell 1991). Elevated macrophyte growth, another bottom-up effect presumably responding to nutrient inputs, may cause an increase in grazer density (Bustamante et al. 1995a, 1995b) thus indirectly leading to an impact on communities from the top-down.

Previous studies of predation and grazing at BB and SH led to a seeming paradox. While both predation and grazing were strongest at SH, their association with their respective bottom-up resources contrasted. Mussels and barnacles, the primary prey of sea stars and whelks, were generally more abundant at SH, where predation was strong. However, benthic algae, the primary food resources of limpets, were generally less, not more, abundant at SH. Inverse relationships between resource and consumer abundance has classically been a sign that top-down, and not bottom-up forces were responsible for the low resource abundance, and in this case, field measurements of algal growth did not differ between BB and SH (Menge, unpublished data). Thus, the trophic chains topped by limpet and by invertebrate predators seem to exhibit qualitatively different dynamics, suggesting that nutrient-macrophyte based chains and nutrient-phytoplankton based chains might show different responses to oceanographic conditions. Understanding limpet-algal interactions may thus depend on understanding factors influencing limpet abundance rather than on factors affecting benthic algal abundance. In this case, however, other evidence (see Chapter 3) suggested that in fact, bottom-up effects on macrophytes did vary among regions and sites. Further investigation of

the limpet-algal interaction, particularly at spatial scales that incorporate variation in inputs of nutrients to benthic algae, seems warranted.

The intensity of seasonal upwelling varies along the West Coast of North America in response to both latitude and local geographic features. The Coriolis effect weakens at high latitudes reducing offshore transport of surface water (Mann and Lazier 1996). Upwelling is locally strengthened near major headlands where upwelling favorable winds intensify and the California Current is deflected offshore (Parrish et al. 1981, Brink 1983, Smith 1983, Rosenfeld et al. 1997). Oceanographic evidence suggests that upwelling intensity does not decrease gradually with increased latitude as predicted by the weakening of the Coriolis effect. Rather the coast is comprised of distinct upwelling regions bounded by oceanographic discontinuities (Parrish et al. 1981). One such discontinuity is Cape Blanco (hereafter CB) on the southern Oregon coast. North of CB, upwelling is relatively intermittent while at CB and southward, upwelling is more persistent (Parrish et al. 1981) (Figure 4.1, 4.2).

Local differences in bathymetry and continental shelf width also may have important ecological consequences within an upwelling region. Upwelling fronts, areas where cold, upwelled water and warm surface water meet, often occur at the edge of the continental shelf. At BB, the continental shelf is narrow so the upwelling front does not extend far offshore. At SH, the shelf is wider and the upwelling front is typically farther from shore. Between the front and shore on this

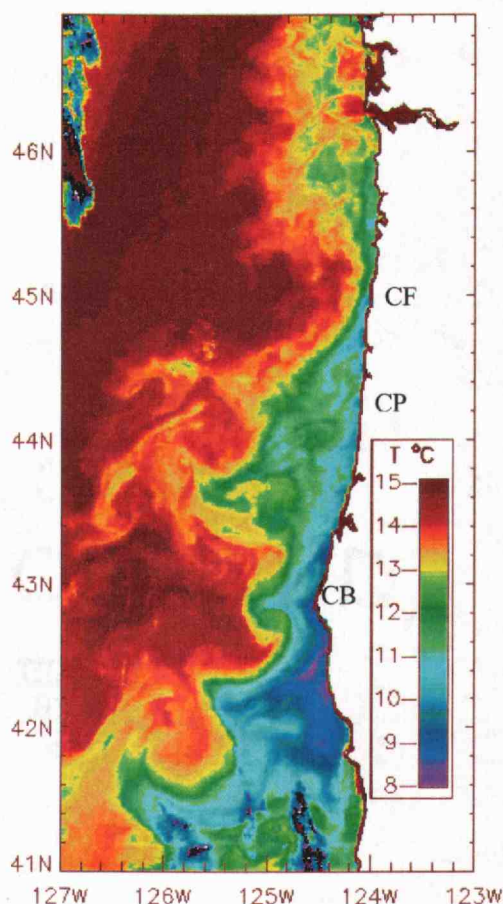


Figure 4.1. AVHRR image showing sea surface temperature (SST) along the Oregon coast on August 13, 1995. Cold upwelled water is near the coast and warm surface is water offshore. CF = Cape Foulweather, CP = Cape Perpetua, CB = Cape Blanco

wider shelf region, eddies form that can concentrate phytoplankton and larvae. As shown by surface current measurements from high-frequency radar (Kosro et al. 1997), currents off BB tend to be stronger and more persistently southward than at SH, where currents are both weaker and more variable in direction. Water masses off SH appear to move shoreward during upwelling relaxation, enhancing local

rates of recruitment and particulate food delivery. Differences in community structure and dynamics between BB and SH, have been attributed in part to this mesoscale variation in nearshore currents (Menge et al. 1997a, 1997b).

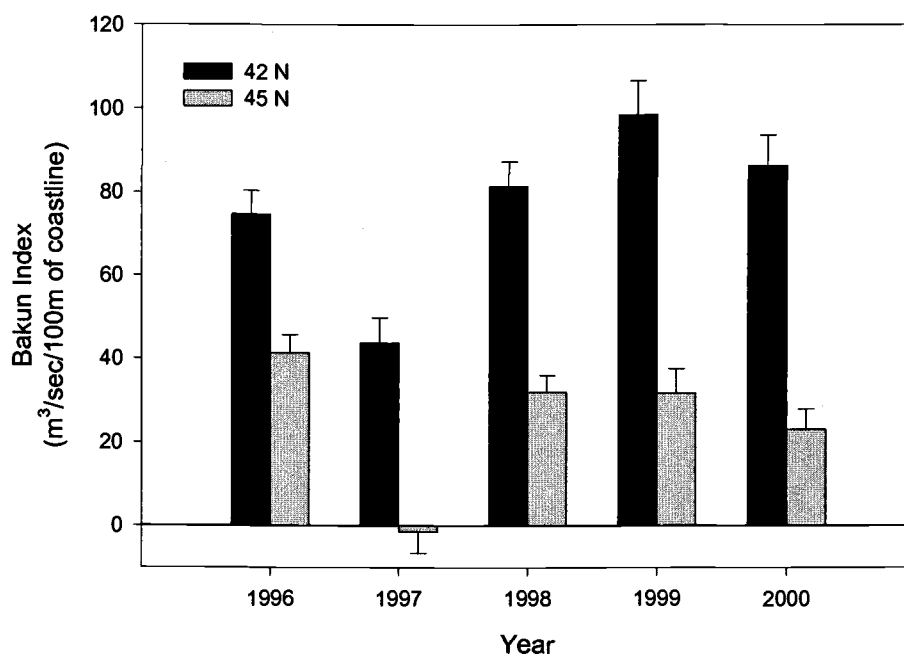


Figure 4.2. Upwelling intensity as measured by the Bakun Index, which estimates the amount of water transported offshore. Positive values indicate upwelling favorable conditions while negative values indicate downwelling. The latitude 42 N is 93 km south of Cape Blanco and 45 N is 19 km north of Cape Foulweather and 83 km north of Cape Perpetua.

Our goal in the present study was to explore how intertidal communities respond to differences both within and between upwelling regions. We examined sites in two upwelling regions, near CB, where upwelling is relatively persistent, and on the central Oregon coast, where upwelling is relatively intermittent. As

described above, within the central Oregon region, water transport patterns also vary due to differences in the width and bathymetry of the continental shelf. These differences in oceanographic conditions can be seen in AVHRR images of sea surface temperature (SST) (Figure 4.1). In the Cape Foulweather region (which includes BB), the width of the continental shelf is narrow, which is reflected in the narrow band of cool water close to shore. To the south, at the Cape Perpetua region (which includes SH), the shelf is wider as is the band of cool water – with currents beginning to form eddies. At Cape Blanco, the band of cold water extending offshore south of the headland indicates that intense upwelling is occurring. These patterns can be observed repeatedly in images taken both within and between years.

We examined how the interaction between algae and grazers responds to local to mesoscale to macroscale variation in oceanographic conditions. Specifically, we compared the effects of grazers on early successional algae at sites nested within each of the three regions described above: Cape Foulweather, Cape Perpetua and Cape Blanco. Our analyses focused on limpets rather than other grazers because previous studies have documented the strong impact of limpets, *Lottia sp.*, on intertidal algal assemblages (Castenholz 1961, Dayton 1971, Cubit 1984, Farrell 1991). While sea urchins (*Strongylocentrotus purpuratus*) may also have strong effects on intertidal algae (Paine and Vadas 1969), they are patchily distributed at our study sites and do not occur in the areas we investigated. Further, urchins are restricted to the low intertidal zone while limpets occur at all shore levels. Limpets may therefore be more influential to overall variation in intertidal

community structure. Our study focused on five key questions: (1) How does the presence of grazers affect recolonization of bare space? (2) How does grazing rate vary among zones, sites and regions? (3) How do the per capita effects of grazers vary among zones, sites and regions? (4) How do algal-barnacle interactions influence the limpet-algal relationship? And (5) How do these rates and effects vary in relation to bottom-up, oceanographic processes?

METHODS

Study sites

We conducted grazing experiments at five sites in 1999 and seven sites in 2000. Sites ranged from Fogarty Creek (FC) on the central Oregon coast to Rocky Point (RP) on the southern coast (Figure 4.3). Each site consists of rocky benches and outcrops that vary in wave-exposure. All sites are characterized by a fucoid algal- and barnacle-dominated high zone with a band of mussels dominating the mid zone. However, striking among-site differences are seen in the low zone assemblages. BB, FC, and the sites on the southern coast, Blacklock Point (BP), CB and RP, have macrophyte-dominated low zones (Menge 1995, Menge et al. 1997b, Freidenburg and Menge personal observation). In contrast, SH and Gull Haven (GH) have low zones dominated by sessile and mobile invertebrates, bare

space and “turfy” algae (Menge 1995, Menge et al. 1997b). We established experiments at these sites in areas that were similar in degree of wave-exposure, slope and aspect.

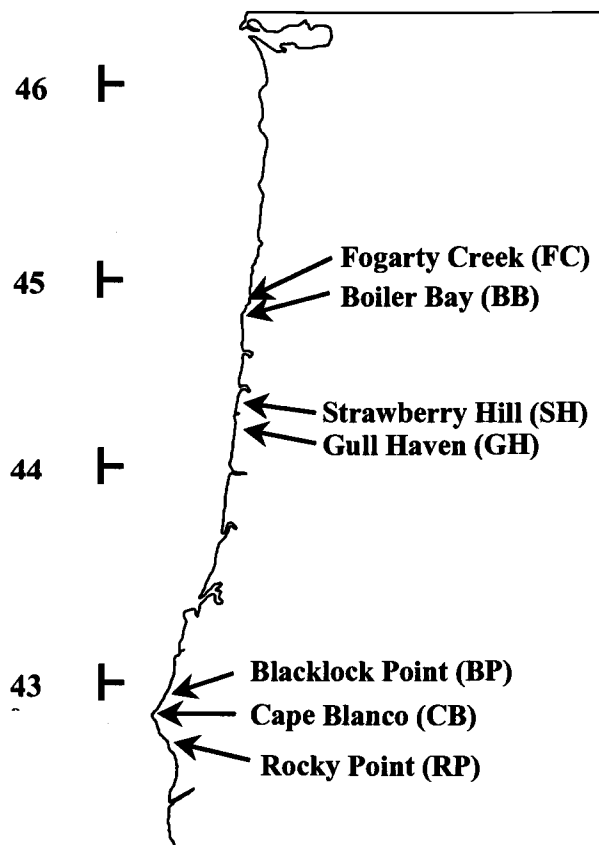


Figure 4.3. Map of study sites along the Oregon coast. FC and BB are in the Cape Foulweather region, SH and GH are in the Cape Perpetua region and BP, CB and RP are in the Cape Blanco region.

We conducted two types of experiments to examine the effect of herbivores on the early stages of colonization by benthic algae, primarily algal sporelings and diatoms, in rocky intertidal communities and to study how the effect and rate of herbivory varied in space and time. In the *herbivore effect* experiments we quantified how the presence of herbivores affected the recolonization of bare space. In the *herbivore rate* experiments we measured how quickly herbivores consumed algae.

Herbivore effect experiments

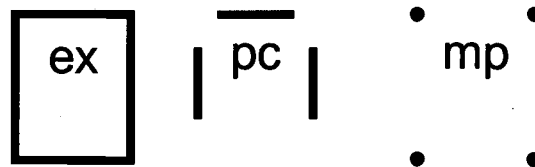
In both 1999 and 2000 we conducted herbivore effect experiments in the low and in the mid intertidal zones. Experiments began in June of each year and ended in August. In 1999 we used five sites: BB, FC, SH, GH and CB (Figure 4.3). In 2000 we repeated the experiments at each of the 1999 sites and added two sites on the southern coast, BP and RP (Figure 4.3).

At each site we established three treatments in a randomized block design: total herbivore exclosure, partial herbivore exclosure and marked plot (Figure 4.4A). In 1999 plots were approximately 20 x 30 cm, while in 2000 they were approximately 15 x 20cm. We used smaller plots in 2000 to allow us to photograph the plots with greater resolution. To start the experiment we scraped each plot clear of benthic organisms manually and then applied oven cleaner (NaOH) to ensure

that all the algae, including crusts, were removed. We then coated the border of each total enclosure plot with a band of Z-spar, a marine epoxy putty (Z-sparTM Splash Zone Compound, Seattle Marine, Seattle, Washington, USA) (Figure 4.4A). This provided an even substrate on which to apply copper anti-fouling paint. Copper paint is a barrier for limpets (Cubit 1984, Paine 1984, Menge et al. 1999a, but see Benedetti-Cecchi and Cinelli 1997 for a critique of this method), but not for littorine snails. To control for the possible effect of copper paint on algal recolonization, we established partial enclosures in which we used Z-spar and copper paint to construct a partial barrier that gave herbivores free access to the plots (Figure 4.4A) but also had paint present. Unpainted Z-spar was used to mark the 4 corners of the marked plots (Figure 4.4A). Thus, coded by effect, the three treatments were: total exclusion (-limpet + paint), partial enclosure (+ limpet + paint) and marked plot (+ limpet -paint). In total, in 1999 there were 6 replicates x 3 treatments x 5 sites, or 90 plots and in 2000 there were 5 replicates x 3 treatments x 7 sites x 2 zones, or 210 plots.

Once experimental plots were established, we visually estimated the percent cover of dominant space occupiers (e.g., sessile organisms including algae, barnacles, mussels) during spring low tides, approximately every 2 weeks. When possible we identified algae to species, but in many cases we were only able to identify functional groups (i.e. filaments, crusts, diatoms etc.). We counted the number of limpets in all plots and removed any found within the enclosures.

A. Herbivore effect experiment



B. Herbivore rate experiment

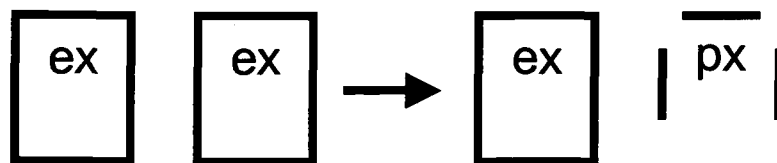


Figure 4.4. Diagram of experimental design. A. herbivore effect experiment (ex = full exclosure, pc = paint control, mp = marked plot) and B. herbivore rate experiment (ex = full exclosure, px = partial exclosure – after some of the initial barrier was removed).

Herbivore rate experiments

We quantified the rate of herbivory in the mid zone in 1999 and 2000 and in the low zone in 2000. In 1999 we established experiments at three sites: BB, SH and CB (Figure 3). In 2000 we repeated the experiments at those sites and added four more: FC, GH, BP, and RP (Figure 4.3).

In the mid zone in 1999 we established 8 pairs of total exclosures measuring approximately 10 cm x 10 cm using Z-spar and copper paint as in the herbivore effect experiments. In total there were 8 replicates x 2 treatments x 4 sites, or 64

plots. After one month the percent cover of algae had increased to approximately 100% in all plots. We then randomly selected one plot from each pair where we breached the Z-spar/copper paint barrier, allowing limpets access (Figure 4.4B). Thereafter, we quantified both the percent cover of dominant space occupiers and the density of herbivores each monitoring period.

In 2000 we conducted the rate experiments in tandem with the effect experiments in each zone. As in 1999, pairs of total exclosures were established, but in 2000 the plots were larger than the 1999 herbivore rate plots, measuring 15 cm x 20 cm. In total there were 5 replicates x 2 treatments x 7 sites x 2 zones, or 140 plots. The total exclosure plot in the effect experiment was also the total exclosure plot for the rate experiment. After algal cover was approximately 100% (after ~1 month), we randomly selected one of the two total exclosure plots and breached the barrier. We then monitored the percent cover of space occupiers and density of herbivores.

Statistical analysis

Herbivore effect experiments

To determine if there were any experimental artifacts caused by copper paint, we compared the final percent cover of algae in partial exclosure and marked

plots separately for each site using paired t-tests. As in previous experiments in the intertidal (e.g., Menge 2000), there were no significant differences ($p > 0.05$) between the two treatments in any case. Therefore, we used the average of the partial enclosure and the marked plot as our “+ herbivore” response in all of our subsequent analyses.

We were interested in three response variables: algal cover, barnacle cover and limpet density. In our analyses of algal cover, we analyzed the difference in total percent cover between the - limpet (exclosure) and + limpet treatments as our response. Our response for barnacles was the average cover across treatments because cover did not vary among treatments in any of the experiments ($p > 0.20$). Copper paint was effective at excluding limpets at all sites, so we analyzed the density of limpets only in the + limpet treatments.

Percent cover of algae and barnacles, and the density of limpets were analyzed using repeated-measures ANOVA (Crowder and Hand 1990, SAS Institute 2000). We first examined each site individually to determine whether there was an effect of excluding limpets, and then explored whether there was variation in the effect of limpets among sites. Repeated measures analyses can use two approaches, univariate or multivariate. The univariate approach is more powerful, but can only be applied when assumptions of sphericity are met (von Ende 1993, SAS Institute 2000). In cases where our data violated this assumption, we determined significance of effects using the more conservative multivariate results. We visually examined probability plots of residuals and plots of residuals vs.

estimated values from univariate analyses to evaluate assumptions of normality and equal variance, respectively. When necessary, data were log transformed ($\ln [y + 1]$).

We also compared algal cover at the end of each experiment using linear combinations to test four *a priori* hypotheses about differences among regions. Specifically, we examined differences between: (1) sites near Cape Blanco on the southern Oregon coast (BP, CB, RP) and sites on the central Oregon coast (FC, BB, SH, GH), (2) the Cape Foulweather region (BB and FC) and the Cape Perpetua region (SH and GH), (3) the Cape Foulweather region and the Cape Blanco region, and (4) the Cape Perpetua region and the Cape Blanco region. We investigated whether each of these models met assumptions of normality and equal variance by examining probability plots and p-values from Levene's test for unequal variance. When necessary, data were natural log transformed ($\ln [y + 1]$).

We examined how tidal height, barnacle cover and limpet density affected the cover of algae at the end of the effect experiment, and whether these relationships varied among sites using multiple linear regression. We fit an initial model with algal cover as the response and tidal height, barnacle cover, limpet density and site as the explanatory variables. Because all explanatory variables were significant, we did not use backward elimination to fit a reduced model.

Herbivore rate experiments

The herbivore rate experiments had two treatments, full exclosure (- limpet) and partial exclosure (+ limpet). The two response variables of interest in these experiments were the daily rate of change in percent cover of dominant organisms between the start and the end of the experiment and the per capita effect of limpets. To calculate the daily rate of change, we first examined the difference in percent cover between the two treatments at the start and end of the experiment. Because algae continue to grow throughout the experiment, examining the difference between treatments adjusts for differences in productivity among the sites. We subtracted the difference in percent cover at the final monitoring period from the difference at the first monitoring period to obtain an estimate of total change in abundance due to herbivores. To estimate the daily rate of change, we divided the percent difference by the number of days of the experiment. We then estimated the per capita effect of limpets, by dividing the daily rate of change in percent cover by the average density of limpets in the + limpet plots. We used one-way ANOVAs to test for differences in the daily rate of change and in the per capita effects of limpets between sites.

We examined how level on the shore, barnacle cover and limpet density affected the cover of algae at the end of the rate experiment, and whether these relationships varied among sites using multiple linear regression. We fit an initial model with algal cover as the response and zone (mid or low), barnacle cover,

limpet density and site as the explanatory variables. Because all explanatory variables were significant, we did not use backward elimination to fit a reduced model.

RESULTS

Effect of herbivores

Algal cover

Low zone 1999 – Grazing effects on abundance of algae (percent cover) differed among sites and among sampling dates, but differences varied similarly through time (i.e., there was no time by site interaction; Table 4.1). These results were consistent in both univariate and multivariate analyses (Table 4.1). The effects of limpets were generally greatest at SH and GH (Figures 4.5A, 4.6A). However, by the end of the experiment there were no differences among sites (one-way ANOVA: $P=0.12$). To test for regional differences in herbivore effects, we conducted linear contrasts of *a priori* hypotheses on the final sampling date. We found differences between the Cape Perpetua and Cape Foulweather regions ($P=0.016$), suggestive evidence for differences between the Cape Perpetua and Cape Blanco regions ($P=0.064$), but no differences between the Cape Foulweather

and Cape Blanco regions ($P=0.84$). There were no differences between the central and southern coasts (linear contrast $P=0.36$). We conclude that in the low zone in 1999, grazers had the strongest effect on abundance of recolonizing algae (algal sporelings and diatoms) at sites in the Cape Perpetua region.

Table 4.1. Results of repeated-measures ANOVA testing the effect of site on differences in algal cover between the + herbivore and – herbivore treatments. Data for the mid zone effect experiment in 2000 are log-transformed ($\ln[y+1]$).

Univariate analysis					Multivariate Analysis			
Source	df	MS	<i>F</i>	<i>P</i>	Wilks' λ	df	<i>F</i>	<i>P</i>
Low effect 1999								
Between subjects								
Site	4	12767.9161	5.56	0.003				
Error	22	2295.3873						
Within subjects								
Time	3	2845.1806	6.29	0.0008	0.5841	3, 20	4.75	0.012
Time X Site	12	764.8042	1.69	0.089	0.4787	12, 53	1.42	0.185
Error	66	452.5249						
Low effect 2000								
Between subjects								
Site	6	25969.4811	11.26	<<0.0001				
Error	27	2305.9128						
Within subjects								
Time	4	20363.9624	22.37	<<0.0001	0.1940	4, 24	24.93	<<0.0001
Time X Site	24	3574.7882	3.93	<<0.0001	0.0991	24, 84	3.33	<<0.0001
Error	108	910.4591						
Mid effect 2000								
Between subjects								
Site	6	1.3933	8.14	<<0.0001				
Error	28	0.1713						
Within subjects								
Time	3	2.7848	52.26	<<0.0001	0.2139	3, 26	31.86	<<0.0001
Time X Site	18	0.1206	2.26	0.008	0.2344	18, 74	2.76	0.001
Error	84	0.0533						

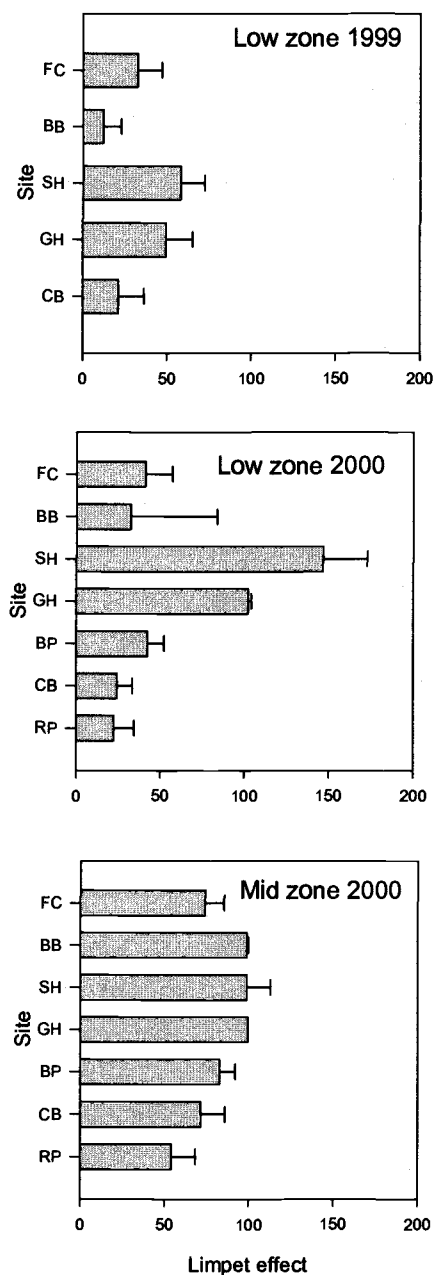


Figure 4.5. The effect of limpets on the recolonization of bare space by algal sporelings and diatoms in (A) the low zone in 1999, (B) the low zone in 2000 and (C) the mid zone in 2000. Sites are arranged in latitudinal order with the FC, the northernmost, at the top and RP, the southernmost, at the bottom. The limpet effect is the difference in algal cover between the -limpet plots and the +limpet plots at the end of the experiment, which lasted 60 days in 1999 and 75 days in 2000.

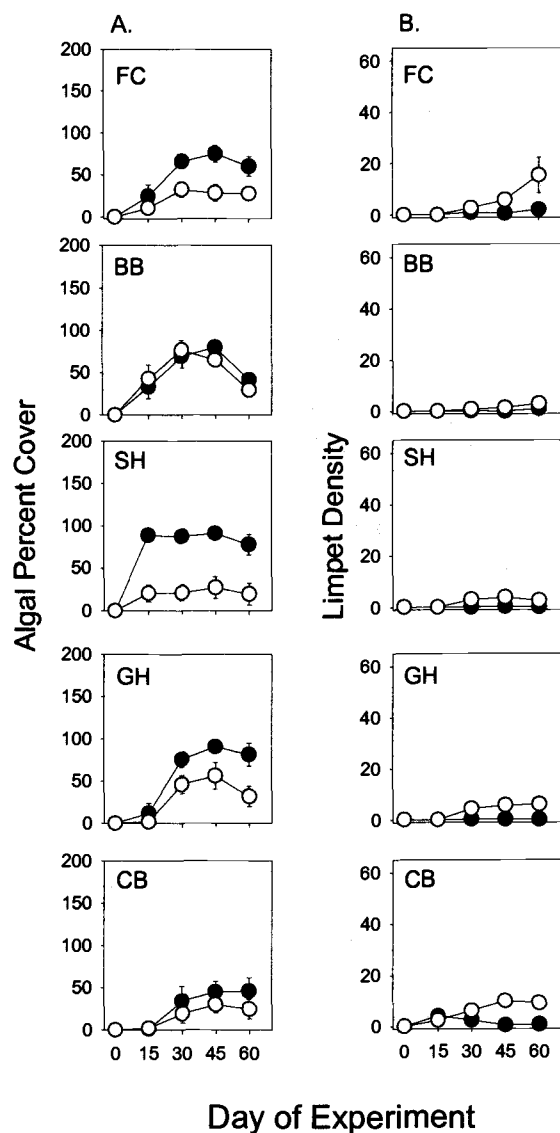


Figure 4.6. Results of the low zone herbivore effect experiment in 1999.

Column (A) is the effect of limpets on the recolonization of bare space by algae, and column (B) is the density of limpets (herbivores) over 60 days at five sites on the Oregon coast. Filled dots indicate -limpet treatment, open dots indicate + limpet treatments. Sites are arranged in latitudinal order with the northernmost site, FC, at the top and the southernmost site, CB, at the bottom. BB and FC are in the Cape Foulweather region, SH and GH are in the Cape Perpetua region, CB is in the Cape Blanco region.

Low zone 2000 – Grazing effects on abundance of algal colonists differed among sites in the low zone in 2000, and the effect varied through time (time by site interaction, Table 4.1). As in 1999, the effect was strongest at SH and GH (Figures 4.5B, 4.7A). At the end of the experiment the impact of grazers varied among sites (one-way ANOVA: $P < 0.0001$). We conducted linear contrasts of *a priori* hypotheses about regional differences in herbivore effects. Regional differences in 2000 were consistent with those in 1999. In 2000, grazing was stronger in the Cape Perpetua region than the Cape Foulweather region ($P < 0.0001$) and stronger in the Cape Perpetua region than the Cape Blanco region ($P < 0.0001$). Grazing did not differ between the Cape Foulweather and the Cape Blanco regions ($P = 0.40$). In contrast to 1999, herbivore effects were weaker on the southern than on the central coast ($P = 0.0065$), a difference due, again, mostly to the strong effects at Cape Perpetua.

Mid zone 2000 – As in the low zone in 2000, algal cover varied among sites through time (time by site interaction, Table 1). However, there were no among-site differences in the effect of limpets by the end of the experiment (Figures 4.5C, 4.8A). Regional comparisons in the mid zone were somewhat different from the low zone (Figure 4.8A). Cape Perpetua did not differ from Cape Foulweather ($P = 0.34$) nor did Cape Foulweather differ from Cape Blanco ($P = 0.099$). The Cape Perpetua region, however, had stronger grazer effects than the Cape Blanco region ($P = 0.0098$). Grazer effects differed between the southern and central coasts ($P = 0.012$).

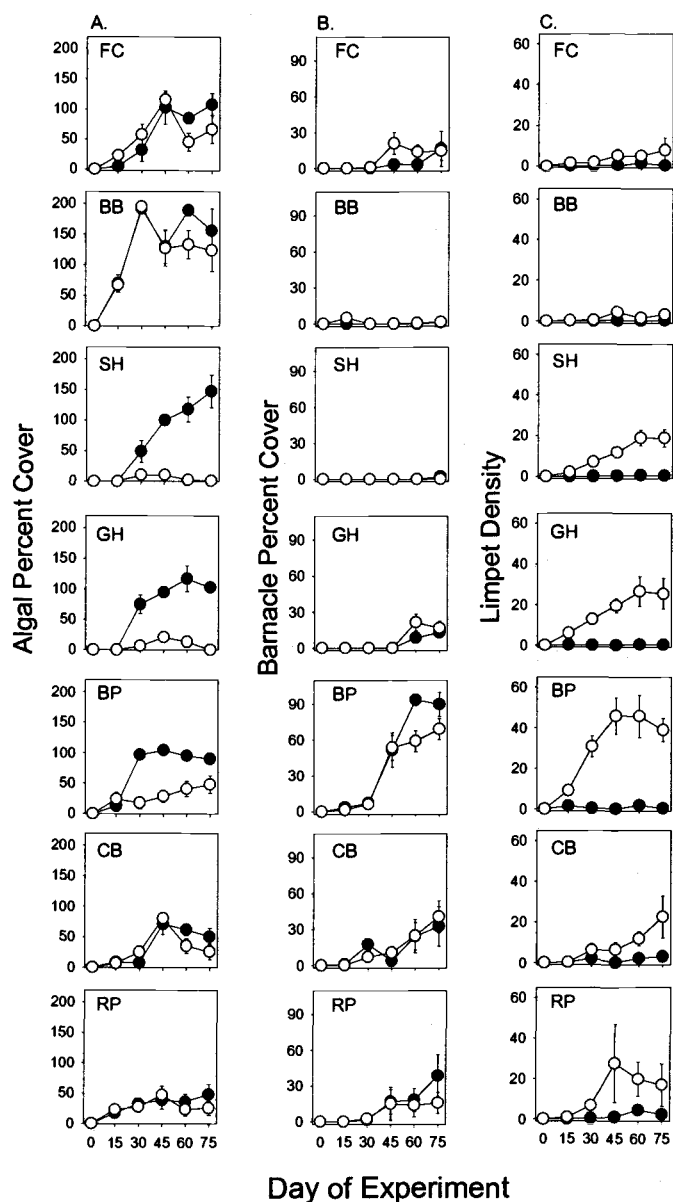


Figure 4.7. Results of the low zone herbivore effect experiment in 2000.

Column (A) is the effect of limpets on the recolonization of bare space by algae, column (B) is the effect of limpets on the recolonization of bare space by barnacles and column (C) is the density of limpets (herbivores) over 75 days at seven sites on the Oregon coast. Filled dots indicate -limpet treatment, open dots indicate + limpet treatments. Sites are arranged in latitudinal order with the northernmost site, FC, at the top and the southernmost site, RP, at the bottom. BB and FC are in the Cape Foulweather region, SH and GH are in the Cape Perpetua region, BP, CB and RP are in the Cape Blanco region

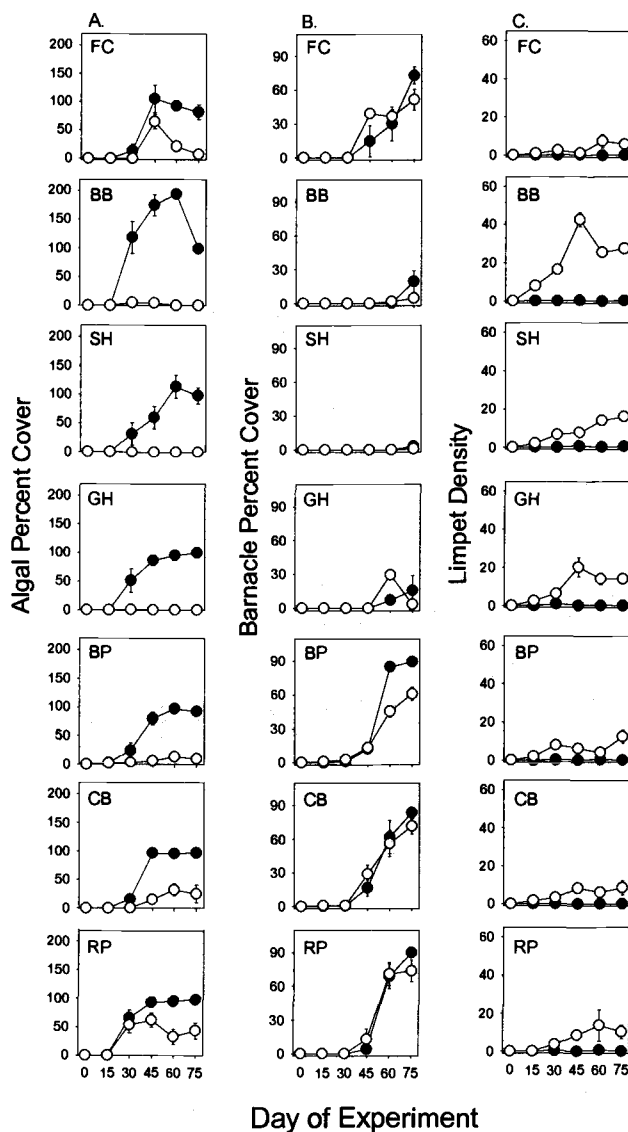


Figure 4.8. Results of the mid zone herbivore effect experiment in 2000.

Column (A) is the effect of limpets on the recolonization of bare space by algae, column (B) is the effect of limpets on the recolonization of bare space by barnacles and column (C) is the density of limpets (herbivores) over 75 days at seven sites on the Oregon coast. Filled dots indicate -limpet treatment, open dots indicate + limpet treatments. Sites are arranged in latitudinal order with the northernmost site, FC, at the top and the southernmost site, RP, at the bottom. BB and FC are in the Cape Foulweather region, SH and GH are in the Cape Perpetua region, BP, CB and RP are in the Cape Blanco region.

In summary, we found that the effect of grazers differed between the central and southern coasts in both zones in 2000, but not in the low zone in 1999. Algal cover was 40% lower in the presence vs. the absence of grazers in the low zone on the central coast, while in the mid zone algal cover was 22% lower (Table 4.2). In the low zone in both years the effect of limpets varied between the Cape Foulweather and Cape Perpetua regions, with the most striking difference occurring in 2000 (Table 4.2). In 2000 in both zones, herbivores had a stronger impact on algal cover at Cape Perpetua than at Cape Blanco (Table 4.2). Algal cover did not vary between Cape Foulweather and Cape Blanco regions in either year or zone (Table 4.2).

Barnacle Cover

Barnacle cover was measured in the low and mid zone experiments in 2000. Data from sampling periods 1-3 in both the mid and low zone did not meet assumptions of normality. Since normality could not be achieved through data transformations, we dropped these data from the analyses. Because there were only 2 sampling periods in the reduced analyses, we were unable to do multivariate repeated-measures analyses. Thus, we report the univariate results only.

Table 4.2. Results of linear contrasts on regional differences from the effect and rate experiments in the mid and low intertidal zones in 1999 and 2000. For each response we examined four contrasts: central vs. southern coast and each pairwise comparison between Cape Foulweather (CF), Cape Perpetua (CP) and Cape Blanco (CB). Non-significant comparisons are indicated with "ns". For each comparison we present the effect size, measured as difference in mean responses between regions, and the associated 95% confidence interval from the linear contrasts. Positive values indicate that the first region was greater than the second, while negative values indicate that the second region was greater. Our measure of algal cover was the difference between the -limpet and +limpet plots. In both the effect and rate experiments, barnacle cover was measured as the average percent cover in the -limpet and +limpet plots. The algal rate of change was the daily rate of loss of algae (percent cover) in the -limpet plots relative to the +limpet plots. Per capita effects were measured as the algal rate of change divided by the average number of limpets in the +limpet plots.

	Low 1999		Mid 1999		Low 2000		Mid 2000	
	Effect Size	95% CI	Effect Size	95% CI	Effect Size	95% CI	Effect Size	95% CI
<i>Effect Experiments</i>								
Algal cover								
Central vs. Southern	ns	ns			40	12-68	25	6, 49
CF vs. CP	-36	-7, -65			-109	-72, -146	ns	ns
CF vs. CB	ns	ns			ns	ns	ns	ns
CP vs. CB	ns	ns			95	62, 128	32	8, 62
Barnacle cover								
Central vs. Southern					-40	-26, -54	-57	-50, -64
CF vs. CP					ns	ns	31	21, 41
CF vs. CB					-39	-23, -55	-41	-32, -50
CP vs. CB					-40	-24, -56	-72	-63, -81
<i>Rate Experiments</i>								
Algal rate of change								
Central vs. Southern			-1.1	-0.5, -2.1	2.2	0.6, 3.8	1.5	0.9, 2.1
CF vs. CP			-3.0	-1.9, -4.1	-2.5	-0.7, -4.3	ns	ns
CF vs. CB			-2.8	-1.9, -3.7	ns	ns	1.7	1, 2.4
CP vs. CB			ns	ns	3.5	1.9, 5.1	1.4	0.7, 2.1
Barnacle cover								
Central vs. Southern					-42	-27, -57	-69	-61, -77
CF vs. CP					ns	ns	27	17, 37
CF vs. CB					-44	-26, -62	-55	-46, -64
CP vs. CB					-40	-22, -58	-83	-74, -92
Per capita effect								
Central vs. Southern			-0.2	-0.02, -0.38	ns	ns	ns	ns
CF vs. CP			-0.2	-0, -0.04	ns	ns	ns	ns
CF vs. CB			-0.3	-0.1, -0.5	ns	ns	ns	ns
CP vs. CB			ns	ns	ns	ns	ns	ns

Low zone 2000 – Barnacle cover varied among sites consistently through time (no site by time interaction, Table 4.3). By the end of the experiment, barnacle cover differed among sites (One-way ANOVA: $P < 0.0001$), and was highest at BP and CB on the southern coast (Figure 4.7B). There were no differences in barnacle cover between the Cape Foulweather and Cape Perpetua regions ($P = 0.96$) while the Cape Blanco region differed from both the Cape Foulweather and Cape Perpetua regions ($P < 0.0001$ for both contrasts). Barnacle cover differed between the central and southern coasts ($P < 0.0001$).

Table 4.3. Results of repeated-measures ANOVA testing the effect of site on barnacle cover. Non-normality could not be corrected for time periods 1-3 so they were dropped from the analysis.

Univariate analysis				
Source	df	MS	<i>F</i>	<i>P</i>
<i>Low effect 2000</i>				
Between subjects				
Site	6	7080.1067	15.12	$<<0.0001$
Error	28	468.1247		
Within subjects				
Time	1	447.7468	4.26	0.048
Time X Site	6	64.0559	0.61	0.72
Error	28	105.1446		
<i>Mid effect 2000</i>				
Between subjects				
Site	6	10645.3093	38.02	$<<0.0001$
Error	28	279.9931		
Within subjects				
Time	1	1943.3126	17.34	0.0003
Time X Site	6	355.1765	3.17	0.017
Error	28	112.0432		

Mid zone 2000 – In the mid zone, barnacle abundance differed among sites through time (time by site interaction, Table 4.3). As in the low zone, barnacle cover was highest at the three sites on the southern coast, BP, CB, and RP. One site on the central coast, FC, also had high cover of barnacles (Figure 4.8B). As in the low zone, barnacle cover differed among sites by the end of the experiment (one-way ANOVA: $P < 0.0001$). Barnacle abundance differed between the central and southern coasts ($P < 0.0001$) and among the three regions ($P < 0.0001$ for each pairwise comparison).

To summarize, barnacle cover was consistently higher in the Cape Blanco region than the regions on the central coast in both the mid and the low zones (Figures 4.7B, 4.8B Table 4.2). While barnacle cover in the low zone did not vary between the Cape Foulweather and Cape Perpetua regions, cover in the mid zone was 31% higher in the Cape Foulweather region (Table 4.2). This difference was due in large part to the relatively high cover at FC (Figure 4.7B).

Limpet density

Copper paint barriers effectively excluded limpets (Figures 4.6B, 4.7C, 4.8C). In both years and zones, limpet abundance increased with time (Figures 4.6B, 4.7C, 4.8C). This temporal pattern was likely due to limpet recruitment throughout the summer. In the low zone in 1999, limpet abundance varied among

sites and through time (time by site interaction, Table 4.4). In both the mid and low zones in 2000, limpet density varied among sites through time (time by site interactions, Table 4.4). In the low zone, limpet abundance was highest at SH, GH and BP (Figure 4.7C), while in the mid zone abundance was highest at BB (Figure 4.8C).

Table 4.4. Results of repeated-measures ANOVA testing the effect of site on limpet density. All data are log-transformed ($\ln[y+1]$).

Source	Univariate analysis				Multivariate Analysis			
	df	MS	<i>F</i>	<i>P</i>	Wilks ' λ	df	<i>F</i>	<i>P</i>
Low effect 1999								
Between subjects								
Site	4	0.2831	2.73	0.056				
Error	21	0.1036						
Within subjects								
Time	2	0.1732	17.17	<<0.0001	0.4637	2, 20	11.57	0.0005
Time X Site	8	0.0498	4.94	0.0003	0.2972	8, 40	4.17	0.001
Error	42	0.0101						
Low effect 2000								
Between subjects								
Site	6	0.6603	7.55	<<0.0001				
Error	27	0.0875						
Within subjects								
Time	4	0.4205	25.34	<<0.0001	0.1895	4, 24	25.66	<<0.0001
Time X Site	24	0.0301	1.81	0.03	0.1235	24, 84	2.91	0.0002
Error	108	0.0166						
Mid effect 2000								
Between subjects								
Site	6	1.3124	14.07	<<0.0001				
Error	28	0.0933						
Within subjects								
Time	4	1.1784	59.74	<<0.0001	0.0775	4, 25	74.35	<<0.0001
Time X Site	24	0.0897	4.55	<<0.0001	0.0641	24, 88	4.42	<<0.0001
Error	11	0.0197						
	2							

Rate of herbivory

Algal Cover

Mid zone 1999 – The daily rate of change in algal cover in 1999 varied among sites with the greatest changes observed at SH, BP and CB (one-way ANOVA, $P < 0.0001$; Figure 4.9A). The rate of change was lower at the Cape Foulweather region than at the Cape Perpetua and Cape Blanco regions ($P < 0.0001$ for both comparisons), but did not differ between the Cape Perpetua and Cape Blanco regions ($P = 0.71$). The daily rate of change of algal cover was less in the central than in the southern coasts ($P = 0.0013$).

Low zone 2000 – In 2000, the daily rate of change in algal cover in the low zone varied among sites ($P = 0.0054$), with the greatest changes occurring at SH and GH (Figure 4.10A). While the results of regional comparisons were not consistent with results from the 1999 mid zone rate experiment, they were consistent with the 2000 low effect experiment. The grazing rate at the Cape Foulweather region was less than at the Cape Perpetua region ($P = 0.0081$), but was similar to the Cape Blanco region ($P = 0.22$). The grazing rate at the Cape Perpetua region was greater than at the Cape Blanco region ($P = 0.0001$). As in 1999, the daily rate of change was greater in the central than in the southern coast ($P = 0.0020$).

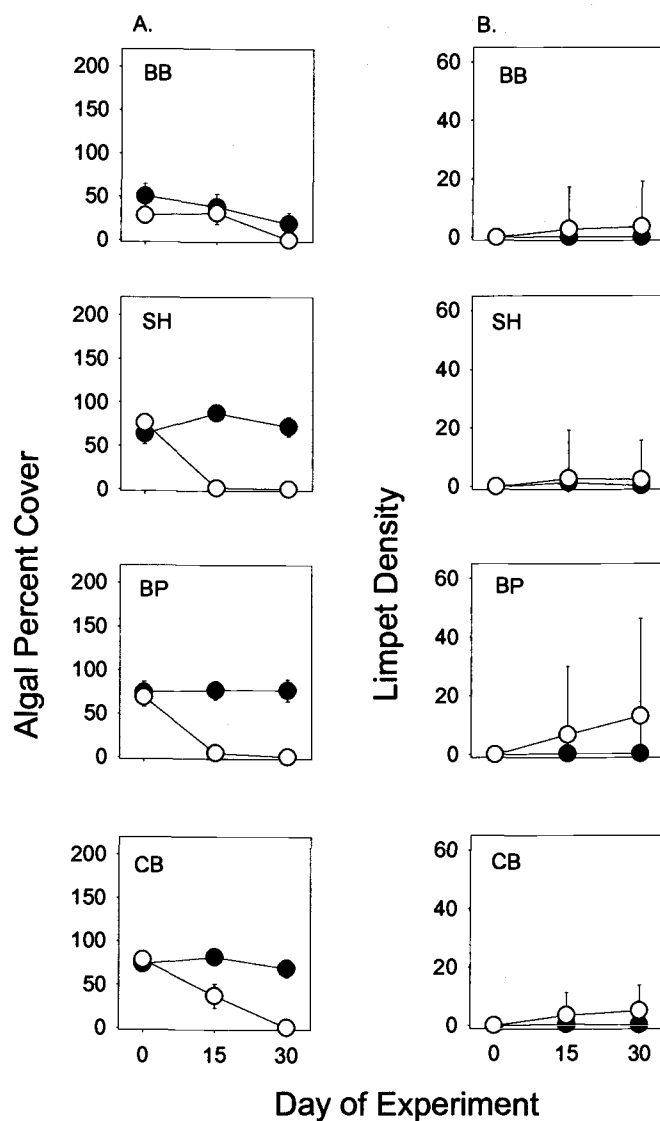


Figure 4.9. Results of the mid zone grazing rate experiment in 1999. Column (A) is the rate of algal consumption by limpets, and column (B) is the density of limpets (herbivores) over 30 days at four sites on the Oregon coast. Filled dots indicate -limpet treatments, open dots indicate + limpet treatments. Sites are arranged in latitudinal order with the northernmost site, BB, at the top and the southernmost site, CB, at the bottom. BB is in the Cape Foulweather region, SH is in the Cape Perpetua region, BP and CB are in the Cape Blanco region.

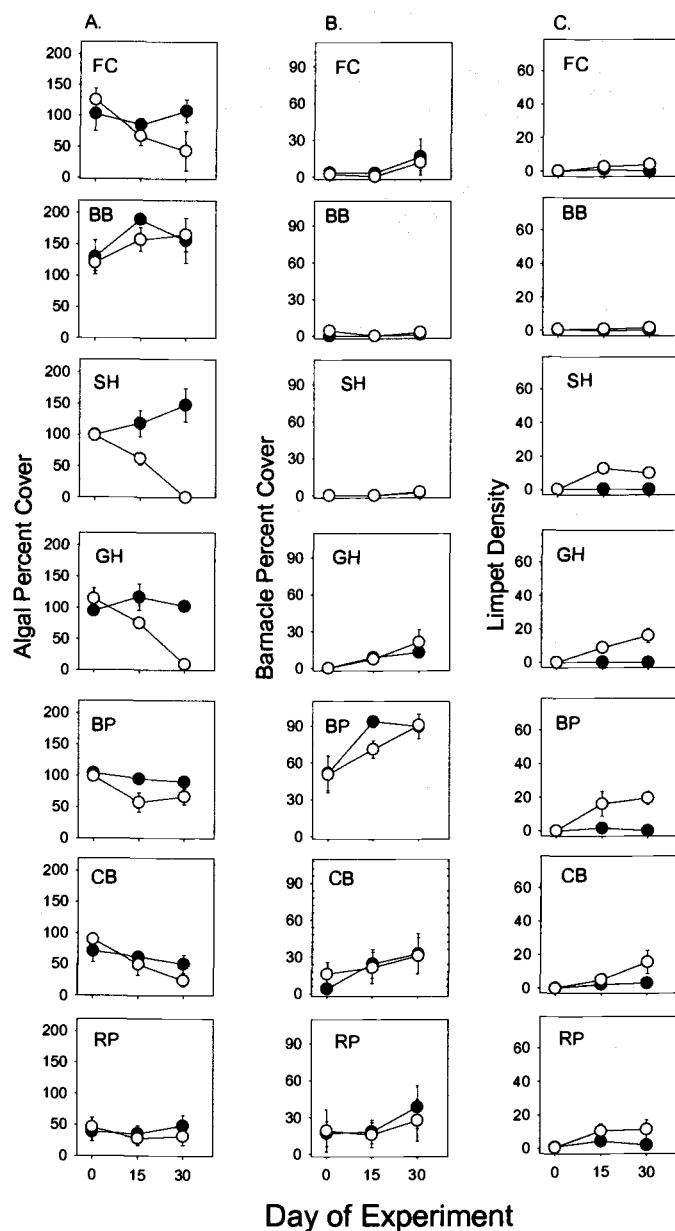


Figure 4.10. Results of the low zone herbivore rate experiment in 2000. Column (A) is the rate of algal consumption by limpets, column (B) is the effect of limpets on barnacle cover and column (C) is the density of limpets (herbivores) over 30 days at seven sites on the Oregon coast. Filled dots indicate -limpet treatment, open dots indicate + limpet treatments. Sites are arranged in latitudinal order with the northernmost site, FC, at the top and the southernmost site, RP, at the bottom. BB and FC are in the Cape Foulweather region, SH and GH are in the Cape Perpetua region, BP, CB and RP are in the Cape Blanco region.

Mid zone 2000 – The daily change in algal cover in the mid zone in 2000 differed among sites (one-way ANOVA, $P < 0.0001$, Figure 4.11A). Unlike the previous comparisons, in 2000 grazing rates in the mid zone in the Cape Foulweather region did not differ from the Cape Perpetua region ($P = 0.52$), while in both the Cape Foulweather and Cape Perpetua regions, grazing rates were greater than in the Cape Blanco region ($P < 0.0001$, $P = 0.0003$, respectively). As in the other rate experiments, the daily rate of change in algal cover was greater in the central coast than in the southern coasts ($P < 0.0001$).

We conclude that in both years and zones, rates of grazing were highest on the central Oregon coast (Table 4.2). In 2000 in the low zone, grazing rates were higher in the Cape Perpetua region than in either the Cape Foulweather or Cape Blanco regions. In the mid zone, rates were higher in both the Cape Perpetua and Cape Foulweather regions than in the Cape Blanco region (Table 4.2).

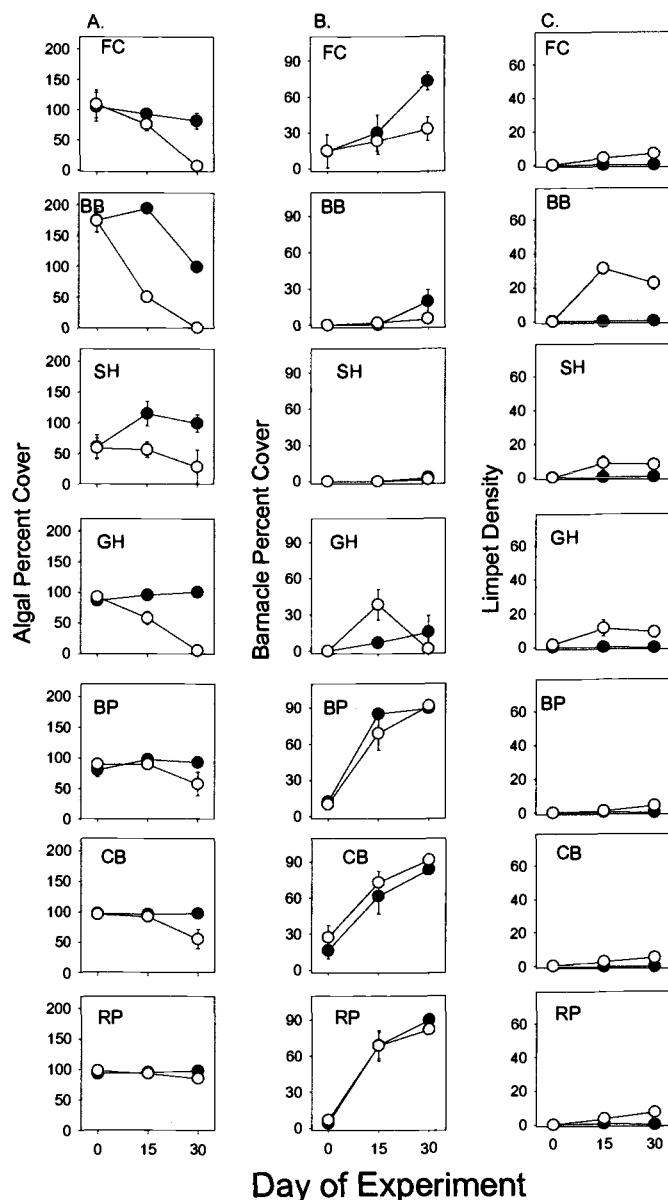


Figure 4.11. Results of the mid zone herbivore rate experiment in 2000.

Column (A) is the rate of algal consumption by herbivores, column (B) is the effect of herbivores on barnacle cover and column (C) is the density of limpets (herbivores) over 30 days at seven sites on the Oregon coast. Filled dots indicate - herbivore treatment, open dots indicate + herbivore treatments. Sites are arranged in latitudinal order with the northernmost site, BB, at the top and the southernmost site, RP, at the bottom. BB and FC are in the Cape Foulweather region, SH and GH are in the Cape Perpetua region, BP, CB and RP are in the Cape Blanco region.

Barnacle Cover

Low zone 2000 – In the low zone rate experiment, as in the low zone effect experiments, barnacle cover varied among sites and through time (time by site interaction, Table 4.5). Barnacle cover tended to increase with time and was highest at sites on the southern coast (Figure 4.10B). Results were consistent with those from the low zone effect experiment: the Cape Perpetua region did not differ from the Cape Foulweather region ($P=0.74$), while the Cape Blanco region differed from both the Cape Perpetua and Cape Foulweather regions ($P<<0.0001$ for both comparisons). Barnacle cover was lower on the central coast than on the southern coast ($P<<0.0001$)

Table 4.5. Results of repeated-measures ANOVA testing the effect of site on barnacle cover in the herbivore rate experiments.

Source	Univariate analysis				Multivariate Analysis			
	df	MS	<i>F</i>	<i>P</i>	Wilks ' λ	df	<i>F</i>	<i>P</i>
<i>Low rate 2000</i>								
Between subjects								
Site	6	9986.0638	13.93	<<0.0001				
Error	28	716.8433						
Within subjects								
Time	2	2192.2645	24.79	<<0.0001	0.4315	2, 27	17.79	<<0.0001
Time X Site	12	288.9642	3.27	0.001	0.3213	12, 54	3.44	0.0009
Error	56	88.4250						
<i>Mid rate2000</i>								
Between subjects								
Site	6	10342.7622	62.46	<<0.0001				
Error	28	165.6038						
Within subjects								
Time	2	115811.6239	73.71	<<0.0001	0.1111	2, 27	108.03	<<0.0001
Time X Site	12	1787.8258	8.33	<<0.0001	0.1330	12, 54	7.84	<<0.0001
Error	56	214.5203						

Mid zone 2000 – As in the low zone, barnacle cover varied among sites and through time (time by site interaction, Table 4.5). As in the low zone, barnacle cover increased with time and was highest at the three sites on the southern coast (Figure 4.11B). Barnacle abundance was lowest at Cape Perpetua, higher at Cape Foulweather, and highest at Cape Blanco ($P < 0.0001$ for all comparisons). Barnacle cover was lower at central coast sites than at southern coasts ($P < 0.0001$).

In summary, in both the mid and low zones in 2000, barnacle cover was dramatically lower on the central than on the southern coasts. In the low zone on the southern coast, average barnacle cover was 42% higher while in the mid zone cover was 69% higher (Table 4.2). In both zones there were consistent differences between both the Cape Foulweather and Cape Perpetua regions and the Cape Blanco region (Table 4.2).

Per capita effects

Mid zone 1999 – In 1999, the per capita effect of herbivores varied among sites (one-way ANOVA, $P = 0.019$) and the differences were consistent with the rate of change in algal cover (Figure 4.12A). Per capita effects were lower at the Cape Foulweather region than at both the Cape Perpetua region ($P = 0.050$) and the Cape Blanco region ($P = 0.0057$). The per capita effect of herbivores did not differ

between the Cape Perpetua and Cape Blanco regions ($P=0.47$). Per capita effects were lower on the central coast than on the southern coasts ($P=0.033$).

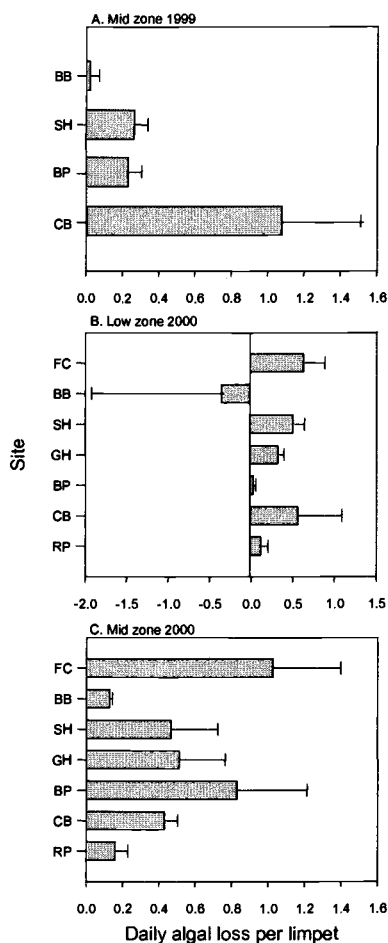


Figure 4.12. Per capita grazing rates (+ SE) by limpets on early colonizing algae in (A) the mid zone 1999, (B) the low zone 2000 and (C) the mid zone 2000. The per capita grazing rate estimates the daily loss of algal cover due to grazing by a single limpet (see Methods).

Low zone 2000 – While sites differed in the daily rate of change of algal cover in the low zone in 2000, there was no variation in the per capita effect of herbivores among sites (one-way ANOVA, $P=0.63$, Figure 4.12B).

Mid zone 2000 – In the mid zone in 2000 the per capita effect of herbivores varied among sites (one-way ANOVA, $P=0.013$, Figure 4.12C). Interestingly, while there were overall differences among sites, there was no evidence that per capita effects differed between regions ($P>0.25$ for all comparisons).

In conclusion, although there were regional differences in the per capita effect of herbivores in the mid zone in 1999, there was no such regional variation in the mid zone in 2000. In the low zone in 2000, per capita effect did not vary among sites or regions (Table 4.2).

Zone, barnacle cover and limpet density affected the cover of algae in both the effect and the rate experiments, and these relationships varied among sites. In the effect experiment, zone ($P=0.0002$), barnacle cover ($P=0.031$), limpet density ($P<0.0001$) and site ($P=0.0011$) all contributed to variation in algal cover, explaining 40.9% of the variance. In the rate experiment, zone ($P=0.0052$), barnacle cover ($P=0.026$), limpet density ($P<0.0001$) and site ($P<0.0001$) explained 47.9% of the variance in algal cover.

DISCUSSION

Effect of herbivory

The impact of grazers on the recolonization of bare space by algae varied between oceanographic regions in ways that were generally consistent with our hypotheses. Based on previous studies (Menge 1995), we predicted that in regions with high cover of algae (i.e., Cape Foulweather and Cape Blanco), the top-down effects of herbivores would be weaker than in the region with low cover of algae (i.e. Cape Perpetua). As predicted, in the low zone limpets generally had similar and relatively small effects on algal cover in the Cape Foulweather and Cape Blanco regions and relatively large effects in the Cape Perpetua region. However, this pattern was not apparent in the mid zone where grazing impacts were all relatively large. Why did the patterns of grazer effects differ between the mid and low zones? The multiple regression analysis and careful study of the results in Figs. 7 and 8 suggest that at least proximately, the answer lies in the three-way interaction between algae, limpets and barnacles and how this varies with time of immersion (level on the shore) and possibly, oceanographic conditions.

In general, strong limpet effects on algal abundance occurred at site * zone combinations where limpet abundance was relatively high and either barnacle abundance was relatively low (e.g., SH and GH in low and mid zones, BB in mid zone; Fig. 4.7, 4.8) or where algal colonization was relatively slow regardless of

barnacle abundance (e.g., BP, CB, RP mid zones; Fig. 4.8). In contrast, weak limpet effects on algal abundance occurred at site * zone combinations where either limpet abundance was low (e.g., FC, BB in the low zone) or where barnacle abundance was relatively high (e.g., BP, CB, RP in the low zone). The exception to these groupings is the FC mid zone, where low densities of limpets had a relatively strong effect on algae despite relatively high abundance of barnacles.

What are the mechanisms underlying these groupings? We consider four factors: direct effects of limpets, direct and indirect effects of barnacles, effects of immersion time, and possible interactions between benthic microalgae and shading by phytoplankton. The most straightforward factor, and the one tested explicitly by our experimental design, was the effect of grazing by limpets. As has been demonstrated in previous studies (Dayton 1971, Underwood 1980, Branch 1981, Hawkins and Hartnoll 1983, Cubit 1984, Dungan 1986), limpet grazing can control microalgal abundance, maintaining rock surfaces free of algae, and this was consistently observed at SH and GH. Limpets can interact with barnacles in at least two ways. During settlement of barnacles, limpets reduce barnacle abundance through bulldozing (Dayton 1971, Underwood et al. 1983), Foley et al. unpublished data). After barnacles have established and grown to occupy a significant fraction of the space, they can inhibit limpet foraging (Choat 1977) and provide safe microsites for algal colonization, thus indirectly increasing algal abundance despite the presence of a dominant grazer (Farrell 1991). Adult barnacles can also compete directly with algae for access to bare rock. These latter effects seem most likely to

be important determinants of the weak limpet effect in the low zone on the southern coast. Barnacle cover reached the highest levels in the low zone at these three sites, and limpet effects were weak even at BP where limpet densities were high (Figure 4.7).

Physical environmental factors seem likely to come into play when mid and low zone results are considered. Low zone habitats are immersed for significantly greater amounts of time than are mid zone habitats, meaning that low zone algae experience longer exposures to nutrients and less exposure to desiccating conditions, and are thus likely to grow faster. Evidence of this can be seen in low and mid zone changes in algal abundance during the first two weeks of the experiments (Figures 4.7, 4.8). In the mid zone, algal cover did not change from 0 during the first two weeks, while in the low zone, algal cover was > 0 , sometimes substantially so, at all but Cape Perpetua sites. Qualitative field observations over many years are consistent with these differences; we have repeatedly observed rapid (but usually brief, lasting only a week or two) increases in microalgae, particularly benthic diatoms in low zone habitats that were not matched by similar increases in the mid zone. Under this scenario, bottom-up processes influencing algal abundance are generally likely to be stronger in the low zone than the mid zone. If so, then mid zone limpets may be more able to keep pace with algal colonization and growth, suggesting that top-down effects may dominate relatively uniformly in the mid zone, as was observed (Figures 4.5, 4.8). If greater immersion time led uniformly to a predominance of bottom-up effects over top-down effects,

that is, if algal production outpaced the ability of limpets to consume them, then limpet effects would be uniformly weak in the low zone. Although such an effect may underlie the weak grazing effects seen at Cape Foulweather and Cape Blanco region, our data show that grazing effects were consistently strong at sites in the Cape Perpetua region. Why did we obtain variable results in the low zone? Above, we discussed the contributions of limpet density and barnacle interference to variation in the low zone, but here we suggest that another factor, variable oceanographic conditions favoring algal growth, is also at work. As we have noted, initial algal growth in our experiments at SH and GH was slow compared to other low zone sites. The explanation for this difference has long puzzled us, but recent studies (K. Nielsen et al. unpublished data) suggest that dense phytoplankton blooms at SH and GH might shade benthic algae, slowing their growth. Simultaneous *in situ* quantification of phytoplankton concentration (using continuously measuring fluorometry) and of light (photosynthetically active radiation) at SH, FC and CB indicate that when submerged, light levels can drop to 0 when phytoplankton blooms occur at SH. Such drops in light were not observed at FC. Although similar attenuation of light occurred at CB where dense phytoplankton blooms were also observed (and where initial growth of algae was similar to that at SH and GH), high barnacle cover probably interfered with limpet grazing to weaken top-down effects at this site. We note that under this interpretation, 1999 results are not consistent with 2000 results (Figure 4.6). The lack of data on barnacle cover in 1999 makes interpretations of these results

difficult, however, as do the lack of frequent observations at CB on phytoplankton. A decade of observation (B. Menge unpublished data, personal observations) indicates that dense phytoplankton blooms are a common occurrence during the upwelling (summer) season at Cape Perpetua sites, but are rare in the Cape Foulweather region. Although these observations suggest that variable bottom-up effects may result from interactions between phytoplankton and benthic algae, further research is needed to test this hypothesis.

Temporal variation

We observed strong inter-annual variation in the effect of grazers on the central and southern coast. While there were large differences in herbivore effects between the central and southern regions in 2000, there were no such differences in 1999. The most likely explanation for this lack of difference is simply low statistical power. Experiments were done at only one southern site in 1999, CB, while experiments were done at four central coast sites. Certainly the patterns of grazer effect we saw at each site in 1999 were similar to those observed for the same sites in 2000. This disparity in regional representation was the reason for adding two additional southern sites in 2000.

Recruitment of mussels and barnacles was strikingly different between the central and southern coasts in 1998 and 1999 (see Chapter 2). Rates of recruitment

were higher on the central coast, where upwelling is intermittent, than on the southern coast, where upwelling is more persistent. Therefore, we were surprised to observe high cover of barnacles in our experimental plots on the southern coast relative to the central coast in 2000. However, subsequent analysis of recruitment data for 2000 revealed unusually high recruitment on the southern coast (see Chapter 2). This reversal suggests a shift in the processes that drive recruitment between years.

Limpet density increased with time in both years and zones, but densities did not vary consistently among sites. In the low zone, limpet abundance was generally lower in 1999 than in 2000. These differences in abundance between years may be due to interannual variation in recruitment, such as we observed for barnacles. In earlier studies at SH and BB, Menge (unpublished data) observed similar interannual variation in limpet recruitment. Although limpet recruitment was not quantified, prior observations suggest that the increase in abundance through each summer is probably related to on-going recruitment. Additional research on recruitment limpet patterns, heretofore largely ignored, would be useful in helping to understand variation in limpet density.

Rate of herbivory

These experiments were carried out in an effort to reduce the effect of differential rates of colonization and growth that can occur in the limpet grazing effect experiments. We reasoned that by starting all experiments with similarly high initial algal cover (instead of starting at zero algal cover), differences in grazing would more truly reflect variation in top-down effects unconfounded by bottom-up differences.

In the low zone, rates of grazing were generally consistent with results from the grazing effect experiments (Figures 4.9-4.11). Sites that had the strongest effects of herbivores (SH, GH) also had the highest rates of grazing. In this case, either low limpet density (FC, BB) or interference with grazing by barnacles (BP, CB, RP) seemed most closely associated with low grazing rates. High grazing rates at the Cape Perpetua sites were associated with relatively high limpet densities and low barnacle cover, thus presumably allowing relatively unimpeded limpet foraging.

In the mid zone grazing rate patterns differed between 1999 and 2000. In 1999, rates of herbivory were relatively high at Cape Blanco and Cape Perpetua sites and low at the Cape Foulweather site (BB). In addition, the grazing rate experiments gave results at one site, CB, which contrasted with the results of the grazing effect experiments (high rate, low effect). Examination of per capita rates helps to understand this difference (Figure 4.12). Although limpet densities were

relatively low in 1999 at CB (Figure 4.9), per capita rates were high, suggesting that per individual, CB limpets were more effective grazers than were SH and BP limpets.

In contrast, in 2000, mid zone grazing rates were low at south coast sites and high at central coast sites (Figure 4.11). As mentioned above, it is likely that the high cover of barnacles on the southern coast in 2000 inhibited grazing by limpets. Although limpets can reduce barnacle cover by bulldozing newly settled cyprids (Farrell 1991), in our rate experiments limpets were excluded from the plots for approximately one month. By the time the copper paint barriers were removed, barnacles had settled and grown to a size that afforded a refuge from bulldozing. Diatoms and algal sporelings that settled and grew on the barnacle tests were thus less accessible to limpets. The unusually strong grazing rates at FC seemed due to high per limpet grazing effectiveness (Figure 4.12), while the comparably high rate at BB apparently resulted from the exceptionally high limpet density that occurred at this site in this year (Figure 4.11).

Resolving the paradox: Complex relationships between limpet grazers, barnacles and bottom-up influences

We believe that our results provide insight into the factors underlying the different food chain dynamics in predator-prey vs. herbivore-plant interactions

along the Oregon coast. As mentioned in the Introduction, predator-prey (sea star-mussel) interactions along the Oregon coast seem strongly influenced by variation in two bottom-up processes: recruitment of mussels and particulate food supply for filter feeders (mussels and barnacles) (Menge 1992, Menge et al. 1994, Menge 2000b). Sites where both processes are high (SH, GH) have high densities of sea stars (and whelks), and field experiments have repeatedly demonstrated that predation rates are high at such sites (Menge et al. 1994, Menge et al. 1996, Navarrete 1996, Menge 2000b, B. Menge et al. unpublished data).

Previous grazer-algal studies, however, suggested that grazing was also strong at the sites where predation was strong, but in contrast to the predator-prey results, food abundance was relatively low at the high grazing sites. Quantification of growth rates of a dominant intertidal kelp at these sites (*Hedophyllum sessile*) revealed no between-site differences (BB = SH), suggesting that macrophyte productivity was comparable at these sites, and thus could not account for between-site differences in algal abundance (BB > SH). In contrast, field observations made during intensive study at these sites beginning in 1989 indicated that relatively brief (1-2 weeks) blooms of microalgae, primarily benthic diatoms and sporelings of rapidly-colonizing algae such as *Enteromorpha* spp., *Petalonia fasciata*, and *Ulva* spp., occur each spring (May, June) at the Cape Foulweather sites but not at the Cape Perpetua sites. These are the algae that colonized during our short-term grazer exclusion experiments, and that appeared to generate the among-site

differences in bottom-up inputs that we postulate are largely responsible for the among-site differences in bottom-up effects in the low zone.

The present study sheds some light on how bottom-up and top-down processes interact to produce structure in low zone algal assemblages. However, the mechanisms we propose remain largely unexplored and will require further research. In particular, we need a better understanding of several processes. Limpet recruitment seemed quite variable, both among sites and over time, and remains poorly understood. Studies of the reproductive cycles, larval production, larval transport, and recruitment of limpets in these oceanographically and ecologically distinct regions are badly needed. The dynamics of microalgal blooms are also relatively unstudied, at least in the context of species interactions and community dynamics. Such an investigation would require examining nutrient dynamics, benthic diatom and algal spore blooms, and the effects of light attenuation by phytoplankton. Our results also indicate that interactions with barnacle recruits and metamorphs are important, and thus that incorporating the interactions of barnacles with limpets and algae in differing oceanographic contexts will be necessary for full understanding.

CHAPTER FIVE: GENERAL CONCLUSIONS

The studies presented in Chapters 2-4 point to the importance of investigating the role of large-scale processes affecting rocky intertidal communities. Our results indicate that regional variation in upwelling regimes can affect recruitment rates of invertebrates with planktonic larvae, growth rates of intertidal kelps and can influence the strength of the interaction between herbivorous limpets and microalgae.

In Chapter 2 we examined how variation in nearshore oceanographic patterns affects recruitment and growth rates of invertebrates along the Oregon coast. We found generally consistent variation in recruitment and growth rates between the central Oregon coast, where upwelling is relatively intermittent, and the southern Oregon coast, where upwelling is more persistent. With the exception of barnacle recruitment in 2000, recruitment and growth rates were higher in central Oregon where more frequent relaxation events presumably led to higher rates of delivery of larvae and phytoplankton (a primary food source for filter-feeding invertebrates) to onshore communities. While we observed striking differences between the central and southern coasts, we did not observe consistent differences between regions within the central Oregon coast. Therefore, it appears likely that variation in local features may be more important in structuring communities at the mesoscale.

In Chapter 3 we focused on how large-scale variation in upwelling patterns affected intertidal kelp communities along the Oregon coast. We were especially interested in how areas of persistent upwelling may modify the impact of El Niño events. Our results indicate that at Cape Blanco kelps were not as strongly affected by the 1997-98 El Niño as were kelps on the central Oregon coast. However, in the two years following the El Niño, kelps had recovered such that there were no longer differences between regions.

In Chapter 4 we investigated how top-down and bottom-up processes along the Oregon coast varied in response to regional differences in upwelling patterns. We designed experiments to measure the strength of the interaction between limpet grazing on algae and how it varied in response to differences in nearshore oceanographic patterns. Our results indicate that the effects of limpet grazing were highest at sites in the Cape Perpetua region, where bottom-up influences tend to be weaker than at either Cape Foulweather or Cape Perpetua.

Each of these chapters addresses the factors that drive both spatial and temporal variability in the dynamics and structure of rocky intertidal communities. When looking at these chapters together, several general patterns emerge. First, we observed strong interannual variation in a host of parameters. For example, the effects of the 1997-98 El Niño were evident at sites along the entire Oregon coast. Higher temperatures in 1997 and 1998 coincided with poor conditions for growth of intertidal kelps, although kelps were less impacted on the southern Oregon coast. The El Niño did not appear to strongly affect the growth or recruitment of intertidal

invertebrates. However, we did observe interannual variation in these parameters. For example, we observed anomalously high recruitment of barnacles to sites on the southern coast in 2000. These results indicate that large-scale processes that underlie factors such as the growth and recruitment of intertidal organisms can vary substantially among years.

Second, we did not always observe striking differences between the Cape Foulweather and Cape Perpetua regions as has been described in previous studies. Menge and colleagues (Menge 1992, Menge et al. 1997a) found that SH, a site in the Cape Perpetua region, had consistently higher recruitment and growth rates of mussels than BB, a site in the Cape Foulweather region (Menge 2002). While this is in contrast to our results, we found that the effects of grazing by limpets among regions were consistent with previous studies that found that top-down influences (i.e. predation and grazing) were demonstrated to be greater at SH (Menge et al. 1997a, Menge 2000b). Menge and colleagues (Menge et al. 1997b) have implicated variation in the width of the continental shelf between these regions as the likely cause of differences in onshore communities. If these bathymetric differences do indeed underlie regional variation in community structure, they may be strongly modified by local factors with sites.

These first two points suggest that the Oregon coast is both a spatial and temporal mosaic where large-scale fluctuations in the structure and dynamics of intertidal communities stem from a suite of factors that vary substantially among years and sites. However, despite this strong temporal and spatial variation, we

observed a third general pattern among studies: there were large and consistent differences between the central and southern coasts. These regions appear to be oceanographically distinct with Cape Blanco marking a transition between upwelling regions. Recruitment of barnacles and mussels were consistently lower at sites in the Cape Blanco region, with the exception of barnacle recruitment in 2000. Growth rates of mussels were also lower on the southern than the central coast. We observed striking between-region differences in the response of intertidal kelps to conditions associated with the 1997-98 El Niño, although these differences did not persist in subsequent years. Finally, even though the effects of grazers were complex and variable, they were consistently different between the central and southern coasts. Thus, while a complex set of factors drive the structure and dynamics of intertidal communities, regional differences in oceanographic conditions underlie a substantial proportion of this variability.

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