

Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA

C.A. Blanchette^{a,*}, B. Helmuth^b, S.D. Gaines^a

^a Marine Science Institute, University of California, Santa Barbara, CA 93106 USA

^b University of South Carolina, Department of Biological Sciences and Marine Science Program, Columbia, SC 29028, USA

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Abstract

The Point Conception, California, USA region (hereafter PC) is one of the most important biogeographic and oceanographic discontinuities on the US west coast. Here we address how mesoscale oceanographic variability in the region around PC affects the growth of the competitively dominant species in the rocky intertidal assemblage: the mussel *Mytilus californianus*. Strong upwelling and high wave exposure dominate the California coast north of PC, and weak, seasonal upwelling and warmer water temperatures are characteristic of the region south/east of PC. We hypothesized that the oceanographic gradients in temperature, upwelling, wave exposure and productivity around PC would exert strong bottom–up influences on growth rates of mussels, potentially underlying large-scale differences in community structure around the PC region. We evaluated these predictions by measuring mussel growth rates across the PC region both in the intertidal and offshore on moorings. Intertidal mussels grew at much higher rates at sites south relative to north of PC and growth rates decreased in a gradient from south to north. The gradient in intertidal mussel growth around PC was uncorrelated with inshore concentrations of chlorophyll-*a*, and was most strongly correlated with the alongshore gradient in wave exposure and intertidal temperature. Mussels on moorings offshore from the intertidal sites grew at much higher rates than those in the corresponding intertidal areas, and mussel growth rates did not differ significantly among moored locations around PC. The gradient of increasing temperature from north to south among mooring sites was correlated with a decreasing gradient in productivity in the same direction, potentially contributing to equal and opposite effects on mussel growth at offshore moorings. This study suggests that environmental factors such as cold temperatures and high wave exposure contribute to the spatial pattern of decreasing mussel growth rates from south to north around PC, underlying large-scale patterns of community structure in this region.

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1. Introduction

Recent studies suggest that nearshore oceanographic conditions can have important effects on the structure of benthic communities, mediating connections between onshore biological communities and offshore water

* Corresponding author. Tel.: +1 805 893 5144; fax: +1 805 893 8062.

E-mail address: blanchet@lifesci.ucsb.edu (C.A. Blanchette).

masses. Variation in the intensity of coastal upwelling has been suggested to play an important role in the recruitment of benthic invertebrates along the US west coast (Hughes, 1984, 1990; Underwood and Denley, 1984; Gaines et al., 1985; Roughgarden et al., 1985; Caley et al., 1996). Variable upwelling and frequent relaxations along the Oregon coast are correlated with high rates of larval arrival and communities dominated by filter-feeding invertebrates (Menge, 1991; Connolly and Roughgarden, 1998; Connolly et al., 2001). Consistently strong upwelling along the northern and central California coast has been proposed to limit invertebrate recruitment, resulting in communities dominated by macrophytes, with relatively low proportional abundances of filter-feeding invertebrates (Gaines et al., 1985; Gaines and Roughgarden, 1985, 1987; Roughgarden et al., 1988). Studies that have incorporated mesoscale oceanographic variability suggest that, in addition to the oceanographic influences on patterns of larval delivery, bottom-up forces (nutrients, phytoplankton, detritus) can be important determinants of rocky intertidal community structure (Bustamante et al., 1995b; Menge et al., 1997b, 1999; Blanchette et al., 2006). For example, in South Africa, decreases in nutrient concentration occurring across scales of 1000's of kilometers from western through southern to eastern South Africa are correlated with decreases in macrophyte biomass and production (Bustamante et al., 1995b). These changes underlie decreases in abundance of both sessile and mobile consumers, suggesting strong bottom-up effects on higher trophic levels (Bustamante et al., 1995a,b). In New Zealand, between-coast differences in top-down (predation and grazing) and bottom-up (prey recruitment, nutrients, filter-feeder growth, macrophyte biomass accumulation) factors were associated with large-scale differences in oceanographic conditions (Menge et al., 1999, 2003).

In the search for general principles to guide our understanding of marine communities, Schiel (2004) argues for a better understanding of the dynamics of key species, particularly habitat-forming foundation species. The dynamics of these dominant space occupiers are likely to be especially important in the absence of strong keystone interactions. Suspension-feeding invertebrates such as barnacles and mussels occupy a central place in the food webs of intertidal communities throughout the world. They provide important links in the energy flow between primary producers and larger consumers including whelks, seastars, and shorebirds (Baird et al., 1985; Menge, 1992; Ricciardi and Bourget, 1999). Mussels in particular are an important ecological component of rocky shore communities throughout the

world, and occupy a central trophic position in intertidal food webs worldwide. The California mussel, *Mytilus californianus* is an abundant member of open-coast rocky intertidal communities along much of the entire west coast of North America. It is an important source of food for higher trophic levels and is a dominant competitor for primary space, and has been shown to out-compete all plant and animal species in an intertidal bed (Paine, 1974; Petersen, 1984; Robles and Robb, 1993; Robles et al., 1995). Given that mussels hold such a central role in these communities, we can learn a great deal about the functioning of the entire community by understanding the factors driving the abundance, growth and production of this ecologically important species.

Several studies have shown that mussels respond to strong “top-down” control, exerted primarily by the seastar predator, *Pisaster ochraceus* (Paine, 1966, 1974; Menge et al., 1994, 2004). However, recent studies have also shown that mussels respond to strong “bottom-up” influences at sites with high offshore productivity (Duggins et al., 1989; Bertness et al., 1991; Thresher et al., 1992; Witman et al., 1993; Bustamante et al., 1995b; Bustamante and Branch, 1996; Menge et al., 1997a,b, 1999). The “bottom-up” hypothesis predicts that high offshore production (e.g. high phytoplankton concentration) fuels onshore production by enhancing food supply to adult filter-feeders leading to higher survival, growth rates and reproductive output. Menge et al. (1992, 1994, 1997b,a) tested these predictions by measuring growth rates of the mussel *M. californianus* at sites along the Oregon coast known to differ in onshore community structure and offshore productivity. The results of these studies showed striking differences in mussel growth among sites that were strongly related to differences in food concentration (indexed by chlorophyll-a measurements). In these studies, enhanced chlorophyll and elevated mussel growth rates were linked to cycles of strong upwelling and relaxation events.

Coastal upwelling processes have been shown to have an important influence on the structure of benthic communities in all of the studies described thus far by effecting the transport of larvae, nutrients and phytoplankton to shore. Although the northern and central California coast is characterized by strong upwelling (Strub et al., 1990; Strub and James, 1995) the prevailing oceanographic regime changes where the California coastline shifts from a north/south to an east/west orientation at Point Conception (hereafter referred to as PC). PC divides the California coast into two regions with very different circulation patterns. This region is one of the most important biogeographic and

oceanographic discontinuities on the US west coast (Valentine, 1966; Briggs, 1974; Newman, 1979; Doyle, 1985; Burton, 1998; Gaylord and Gaines, 2000). The northern region is typified by high wave exposure and consistently strong coastal upwelling bringing cold, nutrient-rich waters to the surface, resulting in both cold sea surface temperatures and high nutrient concentrations along the coast. The region immediately south/east of PC (the Santa Barbara Channel) is largely protected from heavy wave action by the offshore CA Channel Islands, and is typified by weak seasonal upwelling, which tends to occur in the winter months (Harms and Winant, 1998).

These physical gradients around PC are correlated with patterns of intertidal community structure. Macrophytes (algae and surfgrass) dominate space at sites

north of PC, while filter-feeding invertebrates dominate sites south/east of PC (Blanchette and Gaines, in press). This transition mirrors the gradient in community structure between northern/central CA and OR, where filter-feeders dominate space in OR and macrophytes dominate space in CA (Connolly and Roughgarden, 1998). Connolly and Roughgarden (1998) suggest that the OR/CA community structure transition is driven primarily by variation in recruitment of mussels, the competitive dominants. The higher algal abundances in CA are thought to be due to competitive release from mussels, which do not recruit well into the CA sites (Connolly and Roughgarden, 1998). In a recent study of the distribution, recruitment and size of *M. californianus* around PC, we found no evidence of decreased mussel recruitment at the persistent upwelling sites north of PC.

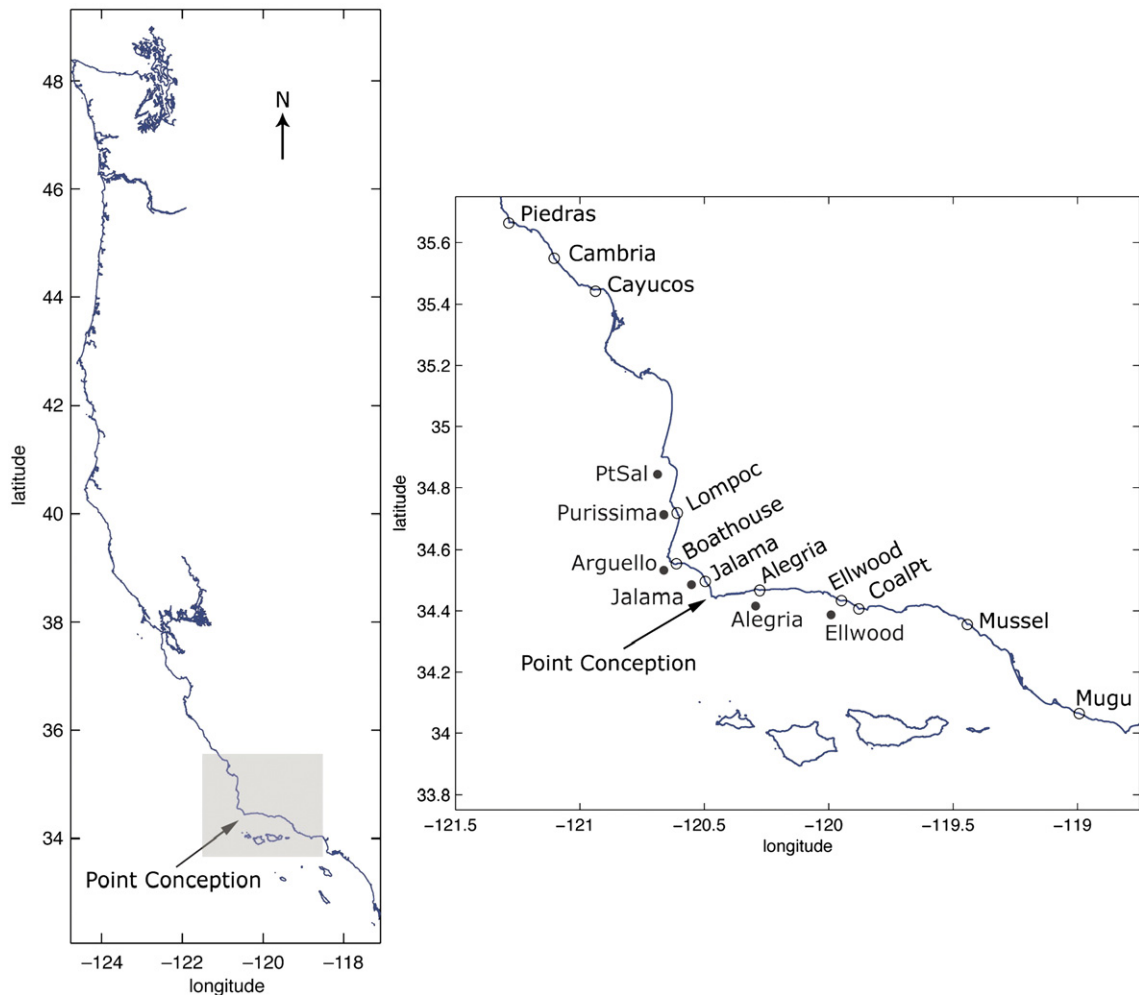


Fig. 1. Regional map of the US west coast highlighting the location of the Point Conception Region: shaded and expanded in the box to the right. Intertidal study locations are depicted with open circles and labeled on the land-side of the map, and mooring locations are depicted with closed circles and labeled on the ocean side of the map.

Mussel beds were thicker and more spatially extensive, and mussels were larger at low upwelling sites south of PC (Blanchette and Gaines, in press). Our findings suggest that unlike other well-studied systems, supply of benthic larvae does not underlie the large-scale gradient in community structure around PC. We suggest that environmental conditions favorable to macroalgal growth north of PC, and conditions favorable to filter-feeder growth south of PC may drive mesoscale patterns of intertidal community structure in this region.

Variation in growth rates among populations of interacting species may greatly alter the nature of community structure and dynamics (Bertness et al., 1991), and variable patterns of growth, have been shown to result from variation in upwelling (Menge et al., 1997a,b, 1999, 2003; Sanford and Menge, 2001; Phillips, 2005). Given the inability of differential recruitment to explain the observed community pattern, our main hypothesis is that environmental conditions favorable to algal growth north of PC and filter-feeder growth south of PC contributes to the shift from algal dominated to filter-feeder dominated from north to south around PC. Support for the first part of this hypothesis comes from previous work documenting a gradient of increasing growth in the kelp *Egregia menziesii*, at a range of sites from south to north around PC correlated with cold water temperatures, high nutrients and enhanced flow due to high wave exposure (Blanchette et al., 2002). Here we predict that mussels will respond in the opposite direction, with an increasing pattern of growth from north to south, enhancing the shift from algal to mussel-dominated communities in the region south of PC. Specifically we test the prediction that the higher abundances of large mussels in the region south of PC are due to elevated growth rates of mussels relative to the high upwelling region north of PC and we explore potential underlying causes (food, temperature, wave exposure) for spatial variability in growth rates of mussels in this region.

2. Methods

2.1. Study regions and sites

Point Conception marks the boundary between two regions with very different circulation patterns. Along the coast north of PC, throughout much of the year, the California Current flows southward, paralleling the shore (Hickey, 1998). At PC, the coastline turns suddenly from a north–south to an east–west orientation, and the California Current largely diverges from the shore as it continues southward (see Fig. 1). The

northern region (north of PC) is characterized by a persistent upwelling regime (Brink et al., 1984; Atkinson et al., 1986). This distinction is suggested by the highly complex thermal structure of the ocean surface along this range of the coast with a very broad band of cold upwelled water along the coast (Fig. 2a). In the northern region, coastal winds are almost always upwelling favorable, bringing cold, nutrient-rich waters to the surface resulting in both cold sea surface temperatures along the coast and high nutrient concentrations (Caldwell et al., 1986; Henderschott and Winant, 1996; Harms and Winant, 1998). The southern region (ranging eastward from PC) is characterized by weak upwelling and intermittent downwelling (Brink and Muench, 1986). This distinction is suggested by the warmer mass of water close to shore in the region

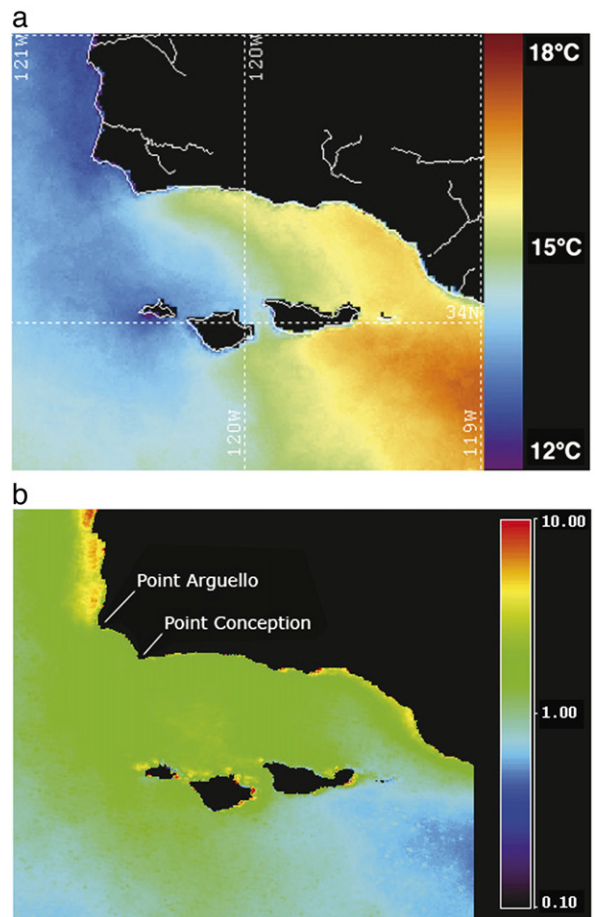


Fig. 2. Representative seasonal composite satellite images of; (a) sea surface temperature and (b) chlorophyll-a (SeaWiFS) from summer 2000. Note the sharp discontinuity in temperature around Point Conception and the high concentration of offshore chlorophyll-a north of Point Arguello relative to the Santa Barbara Channel. Images created by Mark Otero, ICESS, UCSB.

Table 1

Mean tidal elevations (m above MLLW \pm 1 s.e.m.) for the 1999 mussel growth plots in both the mid and low mussel zone at each of the sites around Point Conception

Site	Region	Mid-zone	Low zone
Alegria	South	0.421 \pm 0.022	0.299 \pm 0.021
Jalama	South	0.864 \pm 0.015	0.503 \pm 0.042
Lompoc	North	1.511 \pm 0.050	0.521 \pm 0.070
Piedras	North	1.534 \pm 0.084	1.044 \pm 0.049

between the Channel Islands and the coast of the southern California Bight (Fig. 2a). The Santa Barbara

Channel (the region southeast of PC) is typified by seasonal upwelling, which tends to occur in the winter months (Winant et al., 1999). Along the California coast north of PC, upwelled nutrients are rapidly advected offshore contributing to phytoplankton blooms offshore. These offshore blooms can be seen in satellite images of chlorophyll-a, which is relatively high north of PC compared to offshore waters south of PC (Fig. 2b).

The sites used in this study spanned a total range of \sim 300 km. They were all wave-exposed rocky shores selected within each region to represent the range of variation observed among sites, within the constraints of

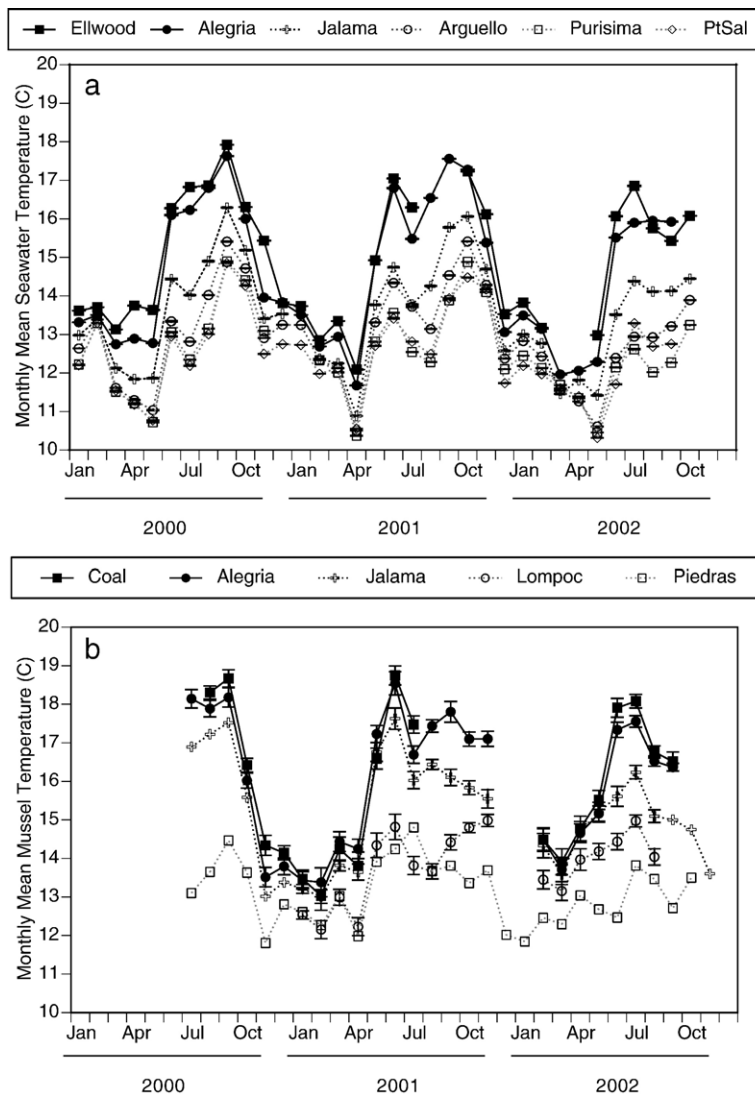


Fig. 3. Monthly mean temperatures from 2000 to 2002: a) seawater temperatures from thermistors mounted 1 m below the surface on each of the six moorings spanning the Point Conception region, and b) mussel body temperature from mussel-shaped, epoxy embedded thermistors in the mid-zone at the 5 main intertidal sites spanning the Point Conception region. Moorings and sites north of the Point Conception region are represented by open symbols and dashed lines. Moorings and sites in the Santa Barbara Channel are represented by solid symbols and solid lines.

feasibility and appropriate access (Fig. 1). The study sites were selected to be relatively uniform in having gently to moderately sloping rocky benches present. Although macro-topographies were similar among sites, meso-topography (degree of heterogeneity from pools, surge channels, outcrops) varied slightly among sites and substratum composition varied among regions. All sites were characterized by mid-intertidal zones dominated by the mussel *M. californianus* as well as other flora and fauna characteristic of wave-exposed rocky shores.

2.2. Site and mussel-related measurements

2.2.1. Seawater temperature

We recorded seawater temperature at a 2-min resolution using tidbit thermistors (Optic Stowaway, Onset computer Corp). Tidbits were mounted 1 m below surface level on buoys offshore from the intertidal sites moored in 15 m water depth spanning the PC region (see Fig. 1 for mooring locations).

2.2.2. Wave exposure

We measured wave energy impacting the shoreline at each of our main intertidal study areas using predictions derived from the “Southern California Swell Model” (<http://cdip.ucsd.edu/models/wave.model.shtml>). The swell model is based on wave refraction–diffraction simulations and simulates wave arrival at periods of 8 s and longer (O’Reilly and Guza, 1993). For the model, deep-water wave data are collected by a datawell buoy

in 549 m of water, about 19 km west of Pt. Arguello. These data are transferred to the Coastal Data Information Program at Scripps Institution of Oceanography (La Jolla, CA) at approximately 30-min intervals. The buoy data are processed to produce an estimate of the deep-water directional spectrum. The data presented here are estimations of mean significant wave height (roughly the average height of the 1/3rd highest waves) based on the swell model for inshore locations at each of our main study sites.

2.2.3. Chlorophyll-a

We estimated concentration of phytoplankton, a primary component of the food of mussels, by quantifying the concentration of chlorophyll-a (Chl a) in bottle samples taken from shore at each site (Menge et al., 1997a). Replicate seawater samples ($n=3-5$) were collected from each site in acid-washed opaque plastic 250-mL bottles (HDP). Depending on site, region and prior sampling done to determine the most appropriate volume, 100–500 mL of water were filtered through 22-mm Whatman glass-fiber filters. Chlorophyll-a was measured with a Turner Model 10 fluorometer following acetone extraction (Parsons et al., 1984).

2.2.4. Mussel body temperature

We deployed a series of temperature loggers modified to thermally match living mussels in mussel beds at each of the five main intertidal sites (Coal Oil Point, Alegria, Jalama, Lompoc and Piedras) spanning

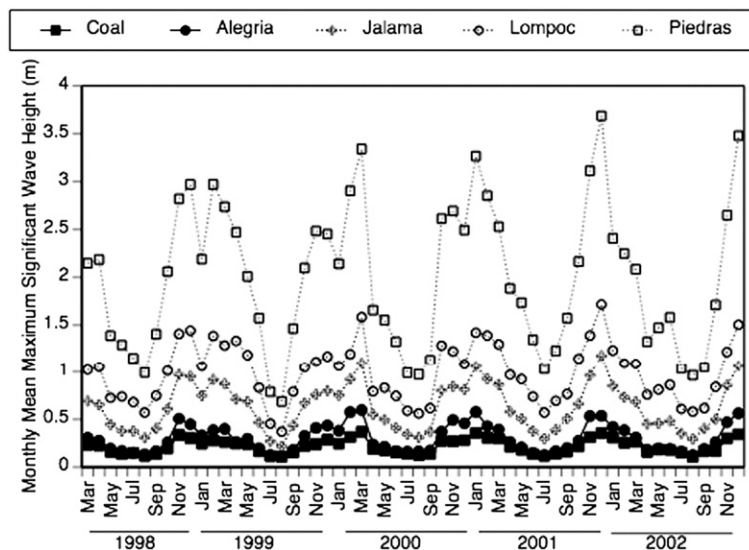


Fig. 4. Predicted monthly mean significant wave height from 1998 to 2002 based on the southern California swell model. Predictions represent inshore wave heights at each of the 5 main intertidal sites spanning PC. Sites north of PC are represented by open symbols and dashed lines. Sites in the Santa Barbara Channel are represented by solid symbols and solid lines. Data are monthly means ± 1 s.e.m.

Point Conception. The mussel-based loggers consisted of a thermistor-based temperature recorder (Tidbit logger, Onset computer Corp. Pocasset, MA) fitted inside an epoxy shell with a morphology and color similar to that of an 8 cm mussel. At this size, the product of mass*specific heat of the instrument closely approximates that of a living animal, and therefore has similar thermal properties (Fitzhenry et al., 2004). Tests of the instrument indicate that it records temperatures that are within approximately 2 °C of living animals in the field (Helmuth and Hofmann, 2001; Fitzhenry et al., 2004). Between 4–6 instruments were deployed at a fixed mid-tidal elevation (1.13 ± 0.29 m above Mean Lower Low Water [MLLW]) at all sites. The loggers were deployed in approximate growth position (posterior end upward) in mussel beds at each site (Helmuth et al., 2002). The instruments recorded temperature

averages at 10 min intervals, with a resolution and accuracy of ~ 0.3 °C, and were in place nearly continuously from July 2000–December 2002.

2.2.5. Effective shore level

We used the intertidal mussel-based temperature loggers at each of the five main intertidal sites to calculate the effective shore level (ESL) of each logger throughout the year (Harley and Helmuth, 2003). In brief, the method relies on recording the timing of sudden temperature drops, which are diagnostic of the first instance of wave splash during the return of the tide. For example, if a point on the shore at an absolute shore level (ASL) of MLLW + 1.0 m is wetted by waves when the water level is at only MLLW + 0.25 m, then the “effective” shore level (ESL) of that point is MLLW + 0.25 m. The difference between ASL and

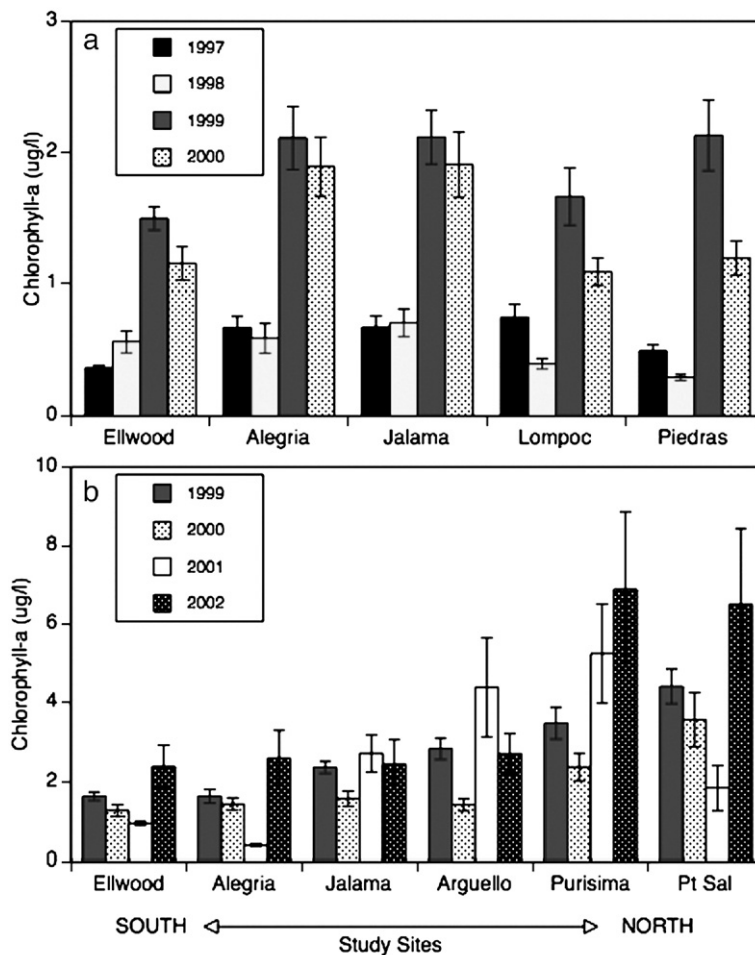


Fig. 5. Yearly mean chlorophyll-a ($\mu\text{g/L}$) from 1997 to 2000 (shaded bars) from: (a) intertidal sites and (b) mooring sites spanning the Point Conception region arranged from the southernmost sites on the left to the northernmost sites on the right. Data are yearly means ± 1 s.e.m.

Table 2

Results of two-way ANOVA for the effects of year and site on chlorophyll-a abundance across a range of (a) intertidal sites and (b) mooring sites

Source of variation	df	SS	MS	F	P
<i>a) Intertidal Chl-a (log)</i>					
Year	3	50.43638400	16.81212800	26.301	<0.0001
Site	4	4.40111200	1.10027800	1.721	0.1434
Site × year	12	10.05476600	0.83789717	1.311	0.2069
Residual	715	457.03555000	0.63921056		
<i>b) Mooring Chl-a (log)</i>					
Year	3	8.27930900	2.75976967	3.770	0.0107
Site	5	25.71028200	5.14205640	7.024	<0.0001
Site × year	15	22.80743200	1.52049547	2.077	0.0098
Residual	546	399.73237000	0.73211057		

ESL (in this example, 75 cm) represents the “run-up” of the wave, and is an estimate of the degree of wave splash at the site. We used these site-specific estimates

of wave run-up and records of sudden temperature drops from the intertidal loggers to calculate ESLs for upper, lower and mid-mussel zone mussels at each site.

2.2.6. Predicted submergence time

To estimate the potential amount of time available for feeding for mussels located at the upper, mid and lower mussel zones at each site, we estimated the submergence time for mussels in each of these areas based ESL. We calculated the total amount of time that the tidal elevation, as estimated from tide tables was above the ESL for mussels in each of the zones.

2.3. Mussel growth experiments

2.3.1. Intertidal mussel growth experiments

To quantify growth rates of mussels, we collected small (~3 cm) *M. californianus* from each study site and translocated them into plots in the elevational middle of the mussel zone at each site using methods

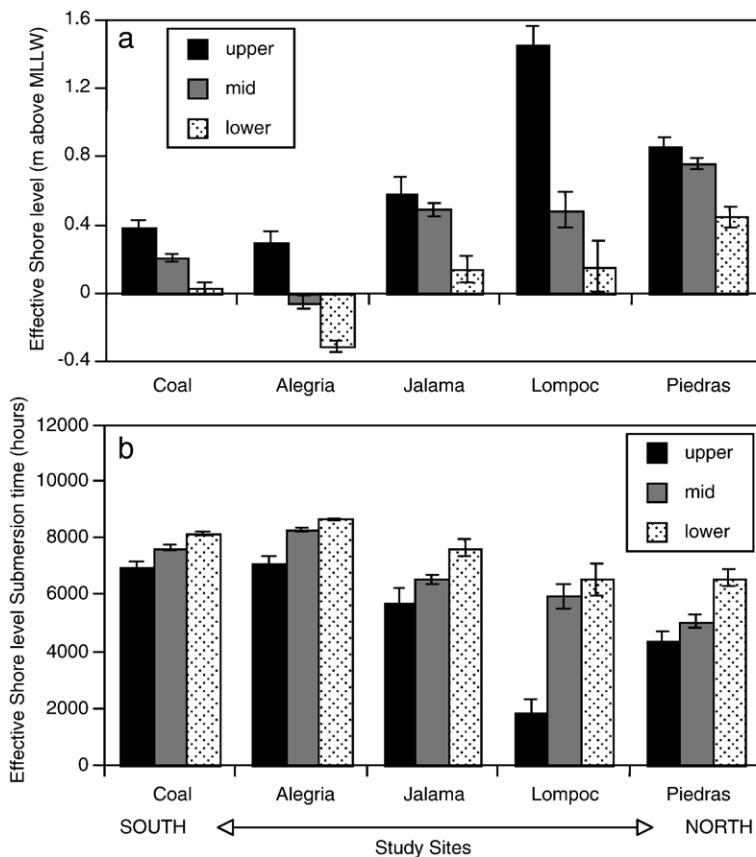


Fig. 6. (a) Mean Effective Shore Level (m above MLLW); (b) Predicted yearly submergence time at Effective Shore Level (h) for mussel bed upper and lower limits and mussel growth plots at each of the 5 main intertidal sites spanning the Point Conception region arranged from the southernmost site on the left to the northernmost site on the right. Data are site means ± 1 s.e.m.

Table 3

Results of two-way ANOVA for the effects of site and zone (mid and low) on mussel growth plot elevations

Source of variation	df	SS	MS	F	P
<i>Growth plot elevation</i>					
Site	4	45.63251100	11.40812775	38.265	<0.0001
Zone	1	24.10476600	24.10476600	80.852	<0.0001
Site × zone	4	9.79588600	2.44897150	8.214	<0.0001
Residual	126	37.56495000	0.29813452		

described in detail in Menge et al., 1997b,a; Phillips, 2005. We marked mussels by filing a small (~1 mm) triangular notch on the posterior shell edge of each mussel without disturbing the soft tissue (see also; Dehnel, 1956; Seed, 1976). Mussels were placed ventral side down in their natural position in groups of

50 and covered with plastic mesh cages to allow them to reattach to the rock with their byssal threads. We had observed in earlier experiments that few byssal threads are produced if the cages remain snug, so to encourage the more rapid production of threads, we loosened the cages (i.e., increased the space between the mussels and the mesh) after two weeks. After six to eight weeks under the mesh, we removed the cages to initiate the experiments. Mussel growth was estimated as the shell added since translocation, quantified as the increment between the notch and the new shell edge. Marked mussels were recovered and collected after 6 to 10 months and brought to the laboratory. The shell length (i.e. the anatomical height) of the mussels was measured to the nearest 0.1 mm with Vernier calipers from the umbo to the initial ventral margin (marked by the notch) and from the umbo to the final ventral margin of the shell. The distance from the umbo to the notch

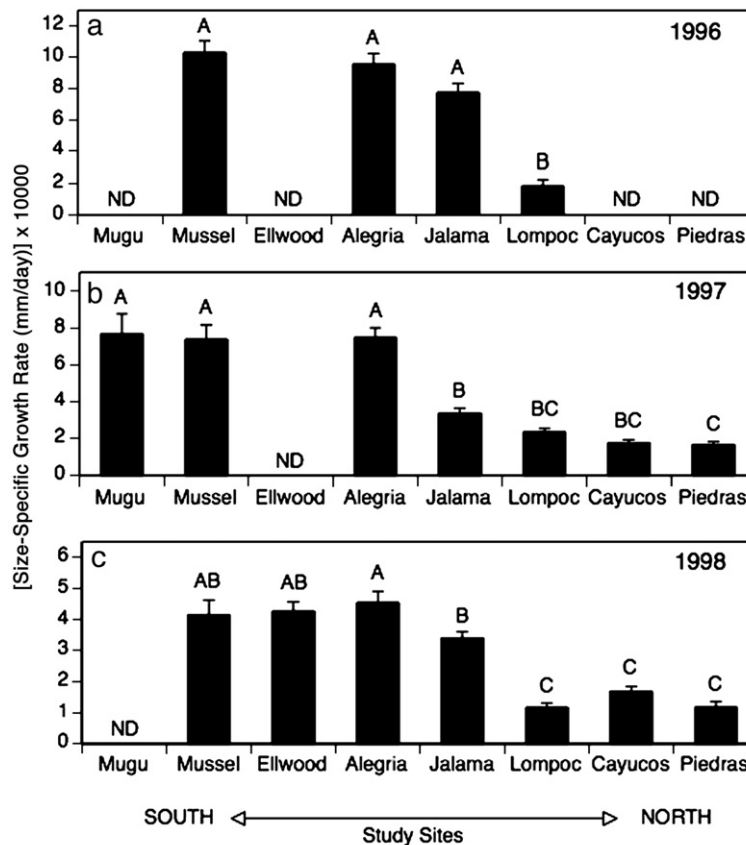


Fig. 7. Size specific growth rates ($[\text{mm/day}] \times 10,000$) for mussels from mussel growth experiments in (a) 1996 (b) 1997 and (c) 1998 at several intertidal sites spanning the Point Conception region arranged from the southernmost site on the left to the northernmost site on the right. ND = No Data for some sites/years. Data are site means \pm 1 s.e.m. Means with different letters are significantly different from one another at $\alpha = 0.05$ based on a Tukey–Kramer multiple comparison.

Table 4
Results of ANOVA among sites on mussel growth rates in (a) 1996, (b) 1997 and (c) 1998

Source of variation	df	SS	MS	F	P
<i>a) 1996 Intertidal</i>					
Site	3	0.00001721	0.00000574	28.081	<0.0001
Residual	191	0.00003902	0.00000020		
<i>b) 1997 Intertidal</i>					
Site	6	0.00002969	0.00000495	46.102	<0.0001
Residual	439	0.00004712	0.00000011		
<i>c) 1998 Intertidal</i>					
Site	6	0.00000926	0.00000154	38.481	<0.0001
Residual	471	0.00001889	0.00000004		

represents the initial length at the time when the mussels were marked. The second measurement incorporates the shell length increment during time of deployment. To compare growth across sites and over time, we calculated size specific growth rates as the change in shell length divided by the total mussel length per day.

2.3.2. Effects of tidal elevation

In 1999 we added a variation to the basic experimental design described above to evaluate the effects of tidal elevation on mussel growth. For this experiment we translocated and marked mussels using the method described above into both the middle and lowest edges of the mussel zones at each site. Average tidal elevations for these plots are shown in Table 1.

2.3.3. Effects of mussel source location

In 2000 and 2001 we again added a variation to the basic experimental design described above to evaluate the potential for local adaptation in mussels at each site. For this experiment we collected and notched 20 mussels from a common source site near Santa Cruz, CA and 20 mussels from each of the transplant sites. We transplanted 20 common source and 20 local source mussels into each of the 5 plots in the elevational middle of the mussel zone at each site using the method described above.

2.3.4. Mooring-based mussel growth experiments

To more directly evaluate the effects of regional oceanographic variability on mussel growth, we translocated mussels from a common source near Santa Cruz, CA to each of six moorings arrayed slightly offshore (within 1 km from shore) from many of the intertidal

study locations around PC (see Fig. 1). All moorings were fixed at a depth of 15 m with a subsurface buoy. Ten notched mussels were placed in each of four 0.5 cm vexar mesh bags affixed to each of the moorings at 1 m below the water surface. We collected mussels from each of the moorings after 6 to 10 months and measured growth using the techniques described above.

2.4. Data analysis

All analyses were performed using JMP statistical software (v5.0 SAS Institute). We examined probability plots of residuals for the assumption of normality, and plots of residuals vs. estimated values for independence of error terms. Data not meeting these assumptions were appropriately transformed. We analyzed data on chlorophyll-a, and mussel growth using ANOVA and performed post-hoc tests Tukey–Kramer tests to test for differences among sites.

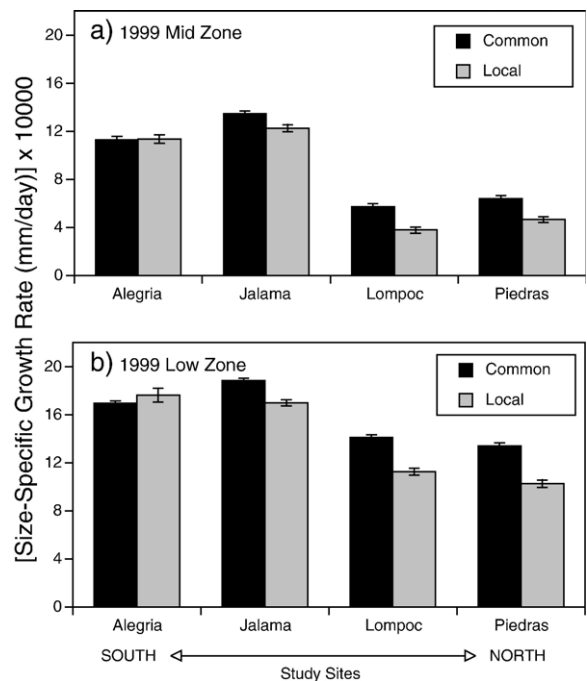


Fig. 8. Size specific growth rates ($[\text{mm/day}] \times 10,000$) for mussels from the 1999 mussel growth experiment in (a) mid-zone and (b) low zone at several intertidal sites spanning the Point Conception region arranged from the southernmost site on the left to the northernmost site on the right. Black bars represent mussels collected from a common intertidal source near Santa Cruz, CA and gray bars represent mussels collected locally. Data are site means ± 1 s.e.m.

Table 5

Results of three-way ANOVA for the effects of site and zone (mid and low), and mussel source (common and local) on mussel growth rates in 1999

1999 Intertidal					
Source of variation	df	SS	MS	F	P
Site	3	0.00028057	0.00009352	738.949	0.0000
Zone	1	0.00023139	0.00023139	1828.264	<0.0001
Site × zone	3	0.00000875	0.00000292	23.045	<0.0001
Source	1	0.00001307	0.00001307	103.269	<0.0001
Site × source	3	0.00000543	0.00000181	14.301	<0.0001
Zone × source	1	0.00000052	0.00000052	4.109	0.0429
Site × zone × source	3	0.00000058	0.00000019	1.528	0.205
Residual	2854	0.00036121	0.00000013		

Evaluation of the environmental factors contributing to variation in mussel growth around PC was confounded by high spatial correlations among several environ-

mental factors along this gradient. In the intertidal, temperature, wave exposure and tidal elevation were all highly correlated with each other and with spatial

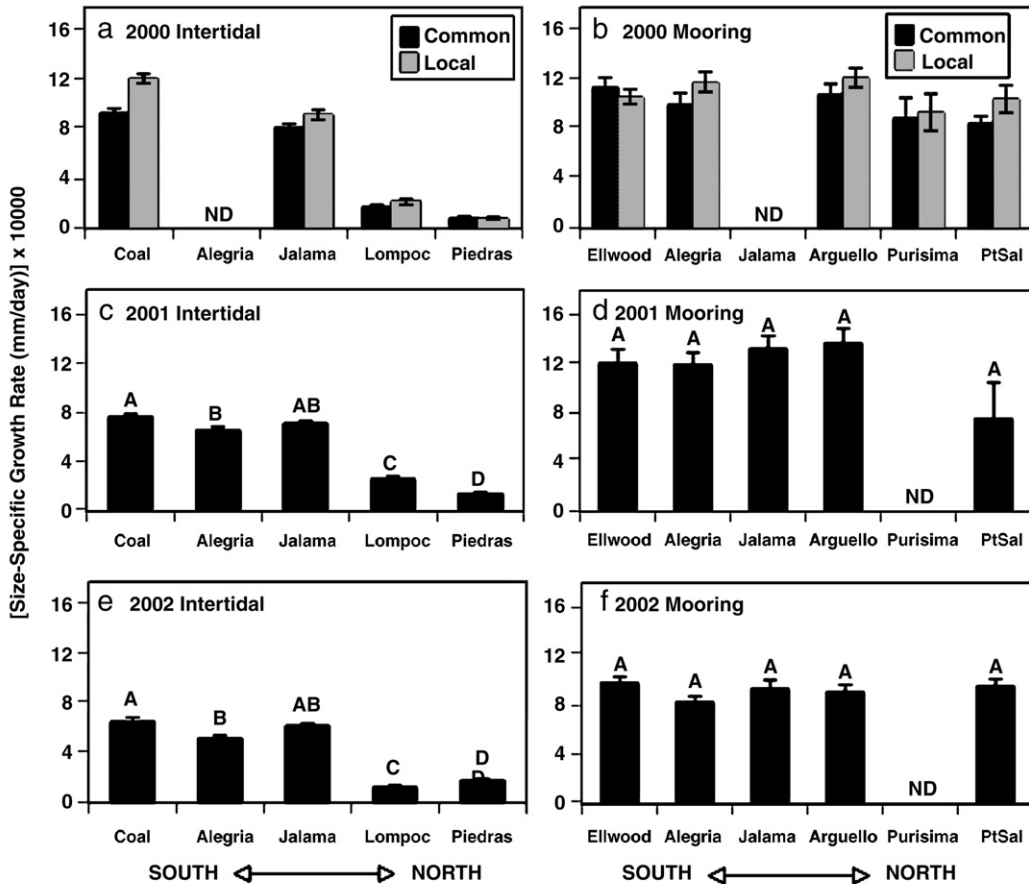


Fig. 9. Size specific growth rates ([mm/day] × 10,000) for mussels from mussel growth experiments in (a and b) 2000 (c and d) 2001 and (e and f) 2002 from (a, c and e) intertidal sites and (b, d and f) mooring sites. Black bars represent mussels collected from a common intertidal source near Santa Cruz, CA and gray bars represent mussels collected locally. Intertidal and mooring sites are arranged from the southernmost site on the left to the northernmost site on the right. ND = No Data for some sites/years. Data are site means ± 1 s.e.m. Means with different letters are significantly different from one another at $\alpha=0.05$ based on a Tukey–Kramer multiple comparison.

Table 6

Results of two-way ANOVA for the effects of site and mussel source (common and local) on mussel growth rates in 2000 from (a) intertidal sites and (b) mooring sites

Source of variation	df	SS	MS	F	P
<i>a) 2000 Intertidal</i>					
Site	3	0.00011946	0.00003982	380.122	<0.0001
Source	1	0.00000185	0.00000185	17.660	<0.0001
Site × source	3	0.00000210	0.00000070	6.682	0.0002
Residual	717	0.00007511	0.00000010		
<i>b) 2000 Mooring</i>					
Site	4	0.00000286	0.00000072	2.229	0.0662
Source	1	0.00000007	0.00000007	0.218	0.1383
Site × source	4	0.00000114	0.00000029	0.888	0.4703
Residual	369	0.00011839	0.00000032		

position. At the moorings chlorophyll-a concentration and water temperature were inversely correlated with each other and correlated to the spatial gradient.

We used a partial regression approach in an attempt to understand the relative contributions of different environmental factors after “partialing out” the spatial components of variation (Thomson et al., 1996; Meot et al., 1998; Legendre, 2000). We used this partial correlation approach to analyze mussel growth patterns in the intertidal and at the moorings over three years (2000, 2001 and 2002). For the intertidal, we removed the effects of spatial variation by regressing mean mussel growth and the two environmental variables hypothesized to contribute most to patterns of growth

Table 7

Results of ANOVA among sites on mussel growth rates in (a) 2001 intertidal, (b) 2001 mooring (c) 2002 intertidal and (d) 2002 mooring

Source of variation	df	SS	MS	F	P
<i>a) 2001 Intertidal</i>					
Site	4	0.00004691	0.00001173	186.724	<0.0001
Residual	734	0.00004610	0.00000006		
<i>b) 2001 Mooring</i>					
Site	4	0.00000176	0.00000044	1.274	0.2847
Residual	113	0.00003903	0.00000035		
<i>c) 2002 Intertidal</i>					
Site	4	0.00003618	0.00000905	171.365	<0.0001
Residual	665	0.00003510	0.00000005		
<i>d) 2002 Mooring</i>					
Site	4	0.00000071	0.00000018	1.125	0.3441
Residual	232	0.00003660	0.00000016		

Table 8

Associations among mean intertidal mussel growth from 2000 to 2002 and means of potential physical driving forces (mussel body temperature, mean significant wave height and tidal elevation) over the growth period

	Growth	Temperature	Waves	Elevation
Growth	1.0000			
Temperature	0.9292*	1.0000		
Waves	-0.8260**	-0.8851**	1.0000	
Elevation	-0.8350**	-0.9279**	0.9595**	1.0000

Values are Spearman's Rank Correlations (r_s) across the six study sites (*= $p < 0.05$; **= $p < 0.01$).

(yearly mean mussel body temperature and yearly mean wave exposure) against mean tidal elevation and the third degree polynomial of the latitude and longitude of each site based on Trend Surface Analysis (Legendre, 1993; Legendre et al., 1997). The residuals of this regression represent the part of the variation not attributable to spatial position. We used these residuals to examine the potential effects of temperature and wave exposure on growth in a way that was un-confounded with spatial position. Similarly, we examined the relative effects of the two environmental factors hypothesized to contribute most to patterns of growth on the moorings (yearly mean mooring-based water temperature and yearly mean chlorophyll-a) by examining residuals from the regressions of these variables against spatial position.

3. Results

3.1. Water temperature

Mean monthly seawater temperatures reflect the seasonal gradient in water temperature around PC and were on average 2–4 °C higher at moored locations in the Santa Barbara Channel than at sites north of PC (Fig. 3a). The temperature differentials were greatest in the summer months due to the difference between the seasonal warming of waters south of PC where upwelling is weak, and the consistently strong upwelling throughout most of the year north of PC. Monthly mean seawater temperatures at sites north of PC rarely reach above 15 °C, while mean summer temperatures at sites in the SB Channel are often in the range of 17–18 °C.

3.2. Mussel body temperature

Monthly mean intertidal mussel body temperatures were on average 2–4 °C higher at intertidal sites in the

Table 9

Associations among mean mooring mussel growth from 2000 to 2002 and means of potential physical driving forces (chlorophyll-a, seawater temperature) over the growth period

	Growth	Chl-a	Temperature
Growth	1.0000		
Chl-a	-0.3518	1.0000	
Temperature	0.2853	-0.7195**	1.0000

Values are Spearman's Rank Correlations (r_s) across the six study sites (*= $p < 0.05$; **= $p < 0.01$).

Santa Barbara Channel than at sites north of PC (Fig. 3b). Mean mussel body temperatures are largely reflective of the seasonal warming of waters in the SB Channel in the summer where differences among sites are greatest. Mussels at the 2 southernmost sites reached mean monthly body temperatures of 18 °C, where summer body temperatures of mussels north of PC were consistently 3–4 °C cooler, and mean monthly temperatures never exceeded 15 °C. These differences reflect the geographic pattern of sites from north to south where mean body temperatures at the northernmost site, Piedras, were consistently colder than at the southernmost site, Coal Oil Point.

3.3. Wave exposure

The geographical pattern of variation among sites is strongly reflected in the wave exposure gradient around PC, where sites north of PC were consistently more exposed to swells than sites south of PC (Fig. 4). The magnitude of the differences among sites was greatest in the winter months, when northern hemisphere swells were largest.

3.4. Chlorophyll-a concentration

Mean annual chlorophyll-a values were relatively low at all intertidal sites (Fig. 5a). These values were well below 3 µg/L at all sites over a 4-year period and were considerably lower than values reported for Oregon (Menge et al., 1997a, 2004). Although chlorophyll-a did vary across the years, there were no significant differences among sites and no pattern in this measure of food availability along the geographic gradient from north to south (Table 2). Chlorophyll-a was considerably higher at the offshore mooring sites north of PC than at the intertidal sites, or the mooring sites south of PC (Fig. 5b). Offshore chlorophyll-a abundance varied significantly over time and space

(Table 2), and was greatest at the northern moorings presumably due to the high intensity upwelling along the coast north of PC. Upwelled water is rapidly advected offshore in this region, resulting in a low chlorophyll zone nearshore, and elevated chlorophyll levels offshore (Brink et al., 1984; Caldwell et al., 1986). The weaker upwelling in the Santa Barbara Channel results in low chlorophyll both inshore and offshore.

3.5. Tidal elevation

There was significant spatial variation in mussel bed tidal elevations across PC. Spatial variation in ESL indicated that mussels ranging from north to south around PC were effectively shifted lower into the intertidal zone at southern sites (Fig. 6a, Table 3). The consequence of this shifted zonation pattern of mussels from the north to south is that for a given level relative to the bed, mussels have the potential to spend more time underwater and feeding at the southern sites (Fig. 6b).

3.6. Patterns of mussel growth

Intertidal mussel growth rates consistently declined from southern to northern sites in 1996, 1997 and 1998 (Fig. 7a–c). In all cases the site effect was significant and the pattern was consistent among years (Table 4). The pattern of decreasing growth from south to north was consistent with the results of the mussel growth

Table 10

a) Results of ANOVA on the residuals from regressions of temperature and wave exposure against spatial location on patterns of mussel growth in the intertidal; and b) results of ANOVA on the residuals from regressions of temperature and chlorophyll against spatial location on patterns of mussel growth on moorings

Source of variation	df	SS	MS	F	P
<i>a) Intertidal</i>					
Residual temperature	1	2.69148350	2.69148350	5.154	0.0465
Residual wave exposure	1	0.19955610	0.19955610	0.382	0.5503
Residual	10	5.22170000	0.52217000		
<i>b) Mooring</i>					
Residual temperature	1	19.68730200	19.68730200	21.456	0.0006
Residual chlorophyll-a	1	5.62500600	5.62500600	6.130	0.0292
Residual	12	11.01095800	0.91757983		

experiment in both the mid and low intertidal in 1999 (Fig. 8a and b). For all sites mussels grew at significantly higher rates in the low than in the mid-zone, and in most cases common source mussels grew at higher rates than local mussels, although this effect varied depending on site (Table 5). The results of the intertidal mussel growth experiments from 2000, 2001 and 2002 were consistent with the previous results that showed a decline in growth from southern to northern sites (Fig. 9a,c,e). There was a significant effect of source location on growth rates in 2000, however this effect varied depending on site (Table 6). Contrary to the spatial patterns of growth in intertidal mussels, mussel growth rates on the moorings across a similar spatial extent around PC did not differ significantly across sites in any of the years of these experiments (Fig. 9b,d,f; Table 7) and within any given year, mussel growth rates were higher on the moorings than those from the nearest intertidal site.

3.7. Environmental correlates of mussel growth

Out of several factors hypothesized to contribute to mussel growth (food, temperature, wave exposure, tidal elevation) the spatial pattern of intertidal mussel growth around PC is consistent with mean intertidal temperature, wave exposure and tidal elevation as possible driving factors. Inshore chlorophyll-a concentrations were uncorrelated with mussel growth in any year. For the years from 2000–2002, mussel growth was highly correlated with mussel body temperature, wave exposure and tidal elevation (Table 8). However, caution is necessary in interpreting these results, since all of these factors are highly correlated with each other. Since wave exposure and tidal elevation were effectively eliminated as possible driving factors for mussel growth on moorings, we examined relationships between chlorophyll-a and seawater temperature, since each of these factors exhibits a strong spatial pattern around Point Conception. Neither chlorophyll nor water temperature, per se were significantly correlated with mooring-based mussel growth; however, these factors were strongly inversely correlated with each other (Table 9). The results of the partial regression analysis suggest that the residual variability in temperature is significantly correlated with the pattern of intertidal mussel growth once the effects of spatial position have been accounted for in the model (Table 10a). The residuals of wave exposure were no longer significant, although these results are difficult to interpret, since most of the variation in wave exposure was so strongly correlated to spatial position. At the moorings, both the residuals of

temperature and chlorophyll-a remained highly correlated with the spatially-partialed pattern of mooring mussel growth (Table 10b).

4. Discussion

The results of this study support our prediction that growth rates of mussels increase from north to south around PC coincident with the prevailing oceanographic gradient in upwelling intensity. Gradients in size, abundance and distribution of *M. californianus* around PC documented in Blanchette and Gaines (in press) are strongly correlated with a gradient in mussel growth documented here. The results of previous research have documented important roles for several factors in regulating the growth rates of mussels. These factors include water temperature (Hickman, 1979), food quality and quantity (Frechette and Bourget, 1885; Widdows et al., 1979; Incze et al., 1980; Ceccherelli and Rossi, 1984), wave exposure (Harger, 1970) density (Seed, 1968, 1969; Kautsky, 1982) and genotypic characteristics (Diehl and Koehn, 1985). Physiological studies have shown that growth may be regulated by the interaction of several environmental factors (Thompson and Bayne, 1974; Bayne et al., 1976). These synergistic interactions can complicate our understanding of the relative importance of any single factors to growth in the field. Additionally, as described above for the PC region, many of these factors covary in nature (e.g. water temperature, food availability, wave exposure, etc.). Our approach here has been to try to tease apart the combined influence of some of these factors by examining patterns of mussel growth among different experimental situations (i.e. intertidal vs. mooring, mid vs. low zone) to elucidate the single and combined influence of some of the major factors to mussel growth. In the following sections we discuss some of the major factors contributing to the observed patterns of size and growth of *M. californianus* around PC.

4.1. Food availability

Food availability is obviously an important factor influencing mussel growth (Page and Hubbard, 1987; Smaal and Vanstralen, 1990). The primary diet of *M. californianus* consists of a wide range of phytoplankton, algal spores, flagellates, ciliates, other protozoa, organic debris, diatoms, and bacteria (Coe and Fox, 1942; Shaw et al., 1988). Although mussels will consume a great range of seston and particulates, Page (1997) has shown a high degree of selectivity for phytoplankton, which provides the highest quality food. Sanford and Menge

(2001) found that growth of the barnacle *Balanus glandula* in Oregon was correlated over the long-term with a site with higher levels of phytoplankton. Bertness et al. (1991) also documented significantly higher growth and reproductive output in the barnacle *Semi-balanus balanoides* in locations with higher food and higher net flux of food. Menge et al. (1992, 1994, 1997b,a) found striking differences in the growth rates of *M. californianus* at sites along the Oregon coast to be strongly related to the persistent differences between the sites in food concentration (indexed by chlorophyll-a measurements). However, not all studies support food availability as a major factor influencing growth. Phillips (2005) found significant differences in the growth of intertidal *M. californianus* at a range of sites around PC similar to the pattern seen in this study. In contrast to other studies supporting a strong influence of food on filter-feeder growth, but similar to the results of this study, Phillips (2005) found the differences in mussel growth to be completely unrelated to any corresponding variability in food supply as measured by chlorophyll-a, POC or PON. Additionally Phillips (2005) measured the C/N ratio of the seston as an index of food quality, hypothesizing that if C/N reflects food quality, then a lower ratio implies better food quality. However mussel growth was highest at sites south of PC where values of C/N were highest, completely opposite to predictions. Thus, sites with the two highest growth rates had the poorest quality phytoplankton. Notably, there were compositional differences among sites in the phytoplankton. The southern sites were dominated by flagellates, and the northern sites were dominated by diatoms. Although this difference in phytoplankton composition was consistent with the observed growth pattern, it remains uncertain as to the relative nutritional contribution of these different types of phytoplankton to growth. Page and Hubbard (1987) found that regional differences in food availability (indexed by chlorophyll-a) were the most important factor explaining offshore versus onshore mussel growth rates between an oil platform in the Santa Barbara Channel and an intertidal site. However, Page and Richard (1990) compared growth rates of *M. edulis* between a pier at Avila beach (north of PC) and Platform Holly in the Santa Barbara Channel (offshore from Santa Barbara). They found no significant differences in growth over time despite the higher seston concentrations (both chlorophyll-a and particulates) at the site north of PC. The results of these studies are consistent with the patterns in mussel growth relative to food availability documented here. Either mussel growth is unrelated to food availability in this region or perhaps other factors such as temperature, tidal

elevation and wave exposure have more of an overriding influence on growth in this system.

There is increasing evidence that larval nutritional history may influence the condition of larvae at settlement and ultimately affect juvenile growth rates and survivorship (Jarrett and Pechenik, 1997; Moran and Emler, 2001; Phillips, 2002b). We attempted to address differences in the condition of our transplanted mussels by selecting both local and common source cohorts to be transplanted in each of the locations in 1999 and 2000. There were significant effects of the source location on growth in the intertidal experiments in both years and significant interactions between the effects of the transplant and source sites, suggesting that early mussel life history may have an important influence on later performance. The performance of common source mussels relative to local mussels was highly dependent on the location. The source site effect was non-significant for the mussels placed on the moorings where the environment for growth was seemingly optimal and mussels grew at such high rates that source effects became irrelevant. Although mussel source had a significant influence on growth, this effect did not influence the larger spatial scale trends in growth in either 1999 or 2000.

4.2. Temperature

Results of many studies support the general expectation that marine invertebrate growth increases with water temperature over a species' range (Newell, 1979). Coe and Fox (1942) suggest that mussel growth should increase over a range of temperatures (14–20 °C). Water temperatures much above 20 °C have been shown to be detrimental, but in fact the most rapid mussel growth rates occur between 17–20 °C. Several studies note positive relationships between growth and temperature. Yamada and Peters (1988) and Yamada and Dunham (1989) observed a decreasing pattern of growth from south to north along the US west coast presumably due to lower temperatures in the northern regions. Growth rates for all species of mussels decrease in the winter months as a result of cooler water temperatures (Seed, 1976; Yamada and Dunham, 1989; Seed and Suchanek, 1992). Bayne et al. (1976) found that in laboratory experiments that *M. californianus* had an increasing positive scope for growth with increasing temperatures between 13–17.5 °C. The water temperatures experienced by the mussels in this study generally fall within the range of temperatures used in the experiments referenced above, but it is difficult to interpret the effects of water temperature alone here, due to covariation in time and space with other factors.

Considerably less is known about the physiological effects of aerial body temperature on mussel growth. Several recent studies have shown that significant physiological damage can occur after exposure to temperature extremes experienced during aerial exposure at low tide, and that the resulting stress response can consume a very significant portion of an intertidal organism's metabolic energy, especially for animals in high intertidal regions (Hofmann and Somero, 1995; Hofmann, 1999; Somero, 2002). Interestingly, while we found no significant correlation between water temperature and growth of subtidal mussels, we did find a strong positive correlation between growth and mean intertidal body temperature. These results are intriguing, but need to be interpreted with caution. Mean intertidal temperature reflects both the influence of water temperature (during submersion at high tide) as well as body temperature during aerial exposure at low tide, which is generally much more extreme (Helmuth, 2002). As we have previously described, summertime aerial body temperatures at Piedras and Lompoc are cooler than those at Alegria and Jalama (Helmuth, 2002; Helmuth et al., 2002), effectively mirroring patterns in water temperature at these 4 sites. It is therefore difficult to decouple the effects of aerial vs. aquatic temperature on growth using the correlational approach taken by our study.

Since we found no significant spatial variation in chlorophyll-a around PC, it is possible that the growth differences observed could be attributed solely to the influence of water temperature on mean intertidal temperature, and that differences in aerial temperature had no effect on growth. In other words, at sites with warmer water temperatures (south of PC), mussels grew faster regardless of temperatures experienced during aerial exposure at low tide. However, it is equally possible that chronic exposure to cooler intertidal temperatures resulted in slower growth rates north of PC. The physiological basis of the observed pattern, however, remains enigmatic, as most studies have focused on the negative role of elevated body temperatures during aerial exposure (Somero, 2002). While preliminary, our results suggest that at the mid-tidal elevations investigated here, there could potentially be a positive effect of increased body temperature on mussel growth, although without detailed experimentation the relative roles of food, water temperature and aerial temperature remain unresolved.

4.3. Wave exposure

Several studies have recorded faster growth and better physiological condition of mussels and other

intertidal filter-feeders in exposed compared to sheltered situations (Bertness et al., 1991; Robles and Robb, 1993; Sanford et al., 1994; Dahlhoff and Menge, 1996; Leichter and Witman, 1997; Sanford and Menge, 2001). In South Africa, growth of the indigenous mytilids *Aulacomya ater*, *Choromytilus meridionalis* and *Perna perna* and of the alien *Mytilus galloprovincialis* is faster in areas of high water circulation than in areas with restricted circulation (Schurink and Griffiths, 1993). Steffani and Branch (2003) found that *M. galloprovincialis* grew faster and had higher condition values at moderately exposed sites than at sheltered sites. This was most likely related to greater food availability at sites with greater water flow. However, at extremely exposed sites both growth rate and condition values were diminished. Similarly Westerborn and Jattu (2006) found that peak biomass of *Mytilus edulis* occurred at sites of intermediate exposure, independent of food concentrations. Decreases in growth of mussels and other bivalves on shores with heavy wave impact or in areas with very high water velocities have been reported elsewhere (Fox and Coe, 1943; Harger, 1970; Wildish and Saulnier, 1992). Ackerman and Nishizaki (2004) also report maximal clearance rates and growth of *M. californianus* at intermediate water velocities ($\sim 10\text{--}12\text{ cm s}^{-1}$). Rate of ingestion by mussels increases with food availability until a threshold concentration of food particles is reached, above which the ingested ration remains relatively constant, and the 'surplus' filtered material is bound with mucus to form pseudofaeces that are expelled (Griffiths and King, 1979b; Griffiths and Griffiths, 1987; Hawkins and Bayne, 1992). Furthermore, at very high water velocities the filtration rate of bivalves is inhibited by hydrodynamic effects on the functioning of the bivalve pump (Wildish et al., 1992; Wildish and Saulnier, 1992; Newell and Wildish, 1997; Newell et al., 2001). It seems entirely plausible that the efficiency of mussel feeding in these northern sites could be hampered by the intensity of flow. Quantifying flow rates over time at these sites was outside the scope of this study, and linking field flow measurements to laboratory results is difficult due to the difficulty in simulating realistic "wave-exposed, intertidal flows" in laboratory flow tanks. However, wave exposure remains as one of the most plausible physical factors restricting growth of intertidal mussels in the region north of PC.

Hydrodynamic forces can also alter the energy budget of mussels by increasing demands for byssus production or renewal of shell material, reducing the energy available for growth and production of mussels living on shores with heavy wave surge (Carrington, 2002a,b; Carrington and Gosline, 2004). Above certain

thresholds, increases in water flow and food supply are therefore unlikely to have further positive effects on mussel growth, and may even have negative effects (Prins and Smaal, 1989). Additionally, intense wave action imposes high hydrodynamic forces on mussels and puts them at risk of dislodgement and damage to their shells (Paine and Levin, 1981; Denny, 1987; Carrington, 2002b). Mussels can respond to the risk of dislodgement by increasing their attachment strength at wave-exposed shores (Price, 1982; Witman and Suchanek, 1984; Hunt and Scheibling, 2001; Carrington, 2002a; Carrington and Gosline, 2004). Attachment strength depends on the number and size of byssus threads anchoring mussels to the substratum (Bell and Gosline, 1997). These threads decay over time and must be replaced to maintain attachment, and the process of replacement can form 8 to 15% of a mussel's total energy expenditure (Griffiths and King, 1979b; Hawkins and Bayne, 1985). An increase in shell thickness can protect mussels from the destructive effects of wave action (Fox and Coe, 1943; Raubenheimer and Cook, 1990). This is also metabolically costly, since 25 to 50% of the total body energy can be tied up in the shell (Jorgensen, 1976; Griffiths and King, 1979a; Gardner and Thomas, 1987). At wave-exposed sites, such as those found north of PC, trade-offs probably exist between positive effects of reductions in thermal stress from increased wave splash and increased food availability due to increased flow and the negative effects of increased risk of dislodgement and increased energy invested in byssus production. In contrast, south of PC sites are more likely to be food limited and thermally stressed due to reduced water motion, but mussels are less likely to experience mortality from wave-generated forces and may therefore need to invest less metabolic energy in resisting dislodgement. These trade-offs are likely to result in differences in the availability of surplus energy and in the partitioning of this energy into byssus, shell and/or flesh production at sites along the wave exposure gradient.

4.4. Tidal elevation

One of the most striking distributional patterns in this region is the elevational shift in zonation of mussel beds around PC. Both upper and lower bed limits are shifted upwards in the region north of PC associated with increased wave exposure, predation pressure and decreased temperature (Blanchette and Gaines, *in press*). This variability is consistent with what we would expect based on factors we know to influence the upper and lower edges of the mussel zone (e.g.

predation, wave exposure and temperature). There is limited information from the literature on the vertical distribution of *M. californianus*, but estimates range from 3.0 m above Mean Lower Low Water (MLLW; (Paine, 1974)) to 1.0 m above MLLW (Paine, 1966, 1974; Suchanek, 1981; Seed and Suchanek, 1992; Menge et al., 1994; Robles et al., 1995).

The upward shift in the lower limits of mussel beds from south to north around PC is consistent with both the densities of the primary predator, *P. ochraceus* and the gradient in predation intensity (Menge et al., 2004). Predation intensity was evaluated across the same range of sites by transplanting mussels to the lowest edge of the mussel bed and recording the number of mussels consumed by predators over time. As expected, predation was highest at the northern sites (Piedras and Lompoc), lowest at the southern sites (Ellwood and Alegria) and intermediate at Jalama (Menge et al., 2004). This gradient in predation intensity is likely to be extremely important in regulating the lower limit of mussel beds around PC. Here we also document a strong gradient in wave exposure around PC that could significantly influence the upper mussel bed limits by providing wave splash and preventing desiccation and temperature extremes. Wave exposure has been demonstrated to extend upper intertidal zonal limits; the greater the wave action, the further the zonal boundaries are pushed upshore (Stephenson and Stephenson, 1949; Lewis, 1964; Benson, 2002). Temperature and desiccation may be jointly influential in setting upper distributional limits (Dahlhoff and Menge, 1996). Body temperature is a more effective measure of the thermal tolerance or "stress" of an intertidal organism than traditional measures of water or air temperature (Helmuth and Hofmann, 2001; Helmuth, 2002; Helmuth et al., 2002). The results of this study show that mid-zone mussels at the southern sites experience higher mean body temperatures than those at the northern sites, and we have previously shown (Helmuth et al., 2002) that temperature extremes at Jalama and Alegria are higher than those at Piedras and Lompoc. Thus, intertidal temperature extremes may potentially limit the upper distributions of the mussel beds in these areas where thermal stresses are higher. Overall, the elevated gradient in the vertical distribution of *M. californianus* around PC reflects a balance between the increased physical stresses (temperature, desiccation due to lack of wave splash) limiting the upper distributions in the southern region, and the ecological impacts of predation restricting the lower distributions in the northern region.

The gradient in elevation of mussel beds around PC is reflected in the elevational positions of the mid-zone

mussel growth experiments. Several studies have found that tidal elevation plays an important role in growth of intertidal organisms. Individuals lower on the shore, with longer submersion times typically have higher growth rates than those higher on the shore (Barnes and Powell, 1953; Dehnel, 1956; Seed, 1969; Rodhouse et al., 1984). Mussel growth rates decrease with an increase in emersion time (Seed, 1968; Harger, 1970; Griffiths, 1981; Rodhouse et al., 1984) and subtidal *M. californianus* have been observed to grow at faster rates than intertidal animals (Yamada and Peters, 1988; Yamada and Dunham, 1989; Buschbaum and Saier, 2001). Additionally, animals higher in the intertidal zone may grow more slowly than lower zone animals due to the reductions in time spent undergoing aerial respiration (Bayne et al., 1976; Dittman and Robles, 1991), and/or due to increases in the amount of energy allocated to stress responses (Hofmann and Somero, 1995; Roberts, 1997; Somero, 2002). The largest animals are prevalent in the low intertidal, and sizes tend to decrease going up the shore (Paine, 1974; Suchanek, 1992; Marsden and Weatherhead, 1999).

The 1999 growth experiment provides support for the importance of tidal elevation on growth within a site. Within each site, low zone mussels grew significantly larger than mid-zone mussels exposed to similar site conditions (seawater temperature, food, wave exposure, etc.). This effect is most likely due to greater feeding time as a result of greater submersion time. The relationship between growth and tidal elevation across sites is more difficult to interpret. Although there is a highly significant relationship across sites between mussel growth and tidal elevation ($R^2=0.76$, $p<0.001$) tidal elevation is not necessarily the driving factor per se. Although growth is greatest at sites where the tidal elevation of mussel growth plots is lowest, there may not be a simple relationship between tidal elevation and submersion time, particularly if shifts in tidal elevation are related to variation in wave exposure, and both are likely to have independently strong influences on growth.

Results from the 2000, 2001 and 2002 mussel growth experiments provide evidence for the importance of tidal elevation on growth. First, mooring-based mussels generally grew at much higher rates than intertidal mussels across a similar spatial scale presumably due to constant submergence and therefore feeding time. Second, if we compare the spatial patterns in growth between the intertidal and mooring-based mussels, we see that once mussels are all at the same effective elevational level (i.e. 1 m below surface on the moorings) the spatial pattern in growth disappears. This finding holds across 3 consecutive years and suggests that there

are spatial gradients in some factors unique to the intertidal situation that may have a large influence on growth (i.e. submersion time, wave exposure, aerial body temperature, etc.). There are, however, a few factors complicating our interpretation of the mooring-based mussel growth experiments. Unlike the intertidal, chlorophyll-a is significantly elevated at the northern moorings relative to both the southern moorings and the northern intertidal sites. So, although mooring-based mussels are growing at similar rates around PC, food availability is potentially higher in the northern region. It is possible that the positive effects of elevated food in the north are offset by low water temperatures due to the strong inverse relationship between chlorophyll-a and temperature at the moorings. Thus the positive effects on growth via enhanced food are diminished by negative influences of low temperature on growth in the north, and negative effects of lower food on growth in the south are enhanced by the positive effects of increased water temperatures at the southern sites resulting in equal but opposite effects on growth and an overall lack of spatial pattern. Similar interactions between food and temperature have been observed to influence growth rates of barnacles, whelks and seastars (Sanford and Menge, 2001; Sanford, 2002).

4.5. Nearshore oceanography and upwelling intensity

Menge et al. (1997b) found that patterns of intertidal community structure were strongly linked to variation in nearshore pelagic productivity, which occurred due to differences in the strength and nature of upwelling. Higher abundances and growth of filter-feeders were found at sites with consistently higher levels of upwelling and phytoplankton. These differences were correlated with variation in the width of the continental shelf offshore. Because high nutrients in upwelled water can stimulate phytoplankton productivity, upwelling coupled with relaxation can result in high productivity (due to upwelling) and delivery of this phytoplankton to benthic filter-feeders (due to relaxation) can result in positive effects on growth. The role of relaxation events is critical in this scenario, allowing the highly productive blooms to be delivered to shore. This is the key difference between the Oregon upwelling system and Californian system studied here. The intermittent upwelling characteristic of the Oregon system provides delivery of phytoplankton inshore during periods of relaxation. In the California system, upwelled nutrients are rapidly advected away from the coast contributing to phytoplankton blooms offshore. These offshore blooms can be seen in satellite images of chlorophyll-a, which is relatively high north of PC compared to offshore waters

south of PC (Fig. 2b). Productivity that results from upwelling develops well offshore (Abbott and Zion, 1985; Pelaez and McGowan, 1986) and because relaxations are infrequent in this system, the enhanced production rarely becomes available to coastal benthic organisms (Dugdale and Wilkerson, 1989; Dugdale et al., 1997). This effect is evidenced in the relatively low growth rates of intertidal mussels in the northern region. The strong upwelling north of PC produces the classic conveyor-belt effect where nutrients are carried up from depth along the coast and upwelled water is rapidly advected offshore as the phytoplankton bloom develops. The elevated levels of chlorophyll-a offshore at sites north of PC relative to inshore are evidence of this upwelling effect. Sites south of PC typically only experience weak, brief periods of upwelling relative to the north. The lack of differences between offshore and onshore chlorophyll-a is evidence of this weak upwelling.

4.6. Consequences to community structure

Mussels occupy a central trophic role in the structure of intertidal communities along the US west coast (Paine, 1966, 1971; Dayton, 1971). Paine's formulation of the keystone concept (Paine, 1966, 1974) was based on the idea that the seastar *P. ochraceus* could exert an inordinate influence on the diversity and structure of the entire community through preferential predation on *M. californianus*. The role of *Pisaster* as a keystone is manifested through its influence on *Mytilus* (Paine, 1966, 1969). Mussels define an entire zone of the intertidal and provide food for a range of organisms from anemones to otters and support a diverse community of small invertebrates within the bed (Seed and Suchanek, 1992). Processes contributing to variation in the abundance of mussels can have cascading influences throughout the community. We see evidence of this in the patterns of community structure around PC. Intertidal communities south of PC are dominated by filter-feeding invertebrates (mussels and barnacles) and communities north of PC are dominated by macrophytes. The findings of Blanchette and Gaines (in press) suggest that the gradient in mussel abundance around PC is not driven by larval settlement. Sites north of PC have recruitment rates equal to or higher than southern sites across several years. Mussel beds are smaller, less spatially extensive and have lower overall biomass at the northern sites, however they are composed of a high density of relatively small individuals. This is likely a reflection of moderate recruitment and slow growth. The rapid growth of mussels at the southern intertidal sites is facilitated by the relative absence of seastar predators, allowing the

mussels to expand into the low intertidal, potentially increasing feeding time and growth. These differences in growth can have important consequences to community structure, affecting susceptibility to physical stress, reproductive output, competition and predation. Reproductive output in mussels is known to scale approximately with biomass and the elevated growth rates and large individual sizes and biomass of mussels from the sites south of PC translates into a large potential reproductive output. Phillips (2002a) has also shown that over time the proportion of reproductively mature mussels is higher at sites south of PC than those to the north. Although these spatial differences in reproductive output do not seem to be linked to recruitment in the local region, this great potential variability in reproduction has large implications for source/sink dynamics and conservation of spawning stock in the context of marine protected areas.

4.7. Conclusions

The results presented here fill a spatial and conceptual gap in our understanding of the benthic/pelagic connections, and environmental influences on community structure along the Pacific coast of North America. The oceanographic shift from consistently strong upwelling to weak upwelling around Point Conception is correlated with gradients in several environmental and ecological variables (temperature, wave exposure and productivity) and a shift in mussel abundance, vertical distribution and growth. Unlike the Oregon system, the gradient in intertidal mussel growth around Point Conception is unrelated to food availability, and seems to be most strongly influenced by wave exposure and temperature. Furthermore, high mussel growth rates south of Point Conception may also be facilitated by the lack of predators, allowing mussels to occupy relatively low intertidal habitats. These results provide a clear example of the interaction of physical (temperature, wave exposure) and ecological (predation) factors in determining the distribution, size, and growth of this dominant intertidal organism, and ultimately influencing large-scale patterns of intertidal community structure in this region.

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