

Distribution, abundance, size and recruitment of the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA

C.A. Blanchette*, S.D. Gaines

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

Received 15 July 2006; received in revised form 15 September 2006; accepted 22 September 2006

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 and environmental variability in the region around PC, CA may influence the distribution, abundance and size of the mussel *Mytilus californianus*, a competitively dominant species in rocky intertidal assemblages along the northeast Pacific. 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 gradient in temperature, upwelling, and wave exposure around PC would greatly influence patterns of recruitment and abundance of mussels, potentially underlying large-scale differences in community structure. We evaluated these predictions by surveying intertidal community structure, mussel distribution, size, abundance and recruitment at a range of intertidal sites around PC. We found that intertidal communities north of PC were dominated mainly by macrophytes, while mussels and barnacles were relatively scarce. Intertidal communities south of PC were dominated by mussels and barnacles, with a low abundance of macrophytes. Mussels were larger and mussel beds were more expansive and extended lower in elevation at sites ranging from north to south around PC. At northern sites, high abundances of sea star predators and elevated wave exposure effectively displaced the entire mussel zone upwards. We found no differences in the numbers of mussel recruits to sites around PC, suggesting that spatial patterns of mussel abundance were not driven by differential recruitment. These results suggest that unlike other well-studied systems, supply of benthic larvae does not underly 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 underly mesoscale patterns of intertidal community structure in this region.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Benthic–pelagic coupling; Community ecology; Intertidal; Marine invertebrates; Mesoscale; Mussel; *Mytilus californianus*; Point Conception; Recruitment; Upwelling

1. Introduction

A major goal in ecology is to understand the forces contributing to the structure and dynamics of ecological communities through time and space. Characterizing how these processes operate across different scales has become an increasingly key area of ecological research

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

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

(Denny et al., 2004). Small-scale experimentation has provided considerable insight into local ecological dynamics (Connell, 1985; Paine et al., 1985; Menge, 1992; Navarrete and Menge, 1996), while biogeographic studies at much larger scales have provided perspectives of the processes influencing whole assemblages (Santelices, 1980; Gaines and Lubchenco, 1982; Brattstrom and Johanssen, 1983; Bustamante and Branch, 1996). Mesoscale processes (those operating across scales of 10s to 100s of km) have recently begun to receive the attention of marine ecologists (Menge and Olson, 1990; Connolly and Roughgarden, 1998; Broitman et al., 2001; Menge et al., 2004; Nielsen and Navarrete, 2004) and may provide a useful framework with which results of local scale studies can be used to make predictions about community responses across large-scale environmental gradients.

Recently, mesoscale studies from the rocky intertidal zone have begun to provide valuable insights into community-structuring processes. Marine ecologists have made great advances in understanding the connections between onshore benthic communities and offshore water masses. The concept of “supply-side ecology” recognizes the role that variable larval input can play in determining the size of local adult populations (Hughes, 1984, 1990; Underwood and Denley, 1984; Gaines et al., 1985; Roughgarden et al., 1985; Caley et al., 1996). Oceanographic variability has been shown to be extremely important for the delivery of larvae to shore through upwelling-relaxation mechanisms, and thus latitudinal 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. 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). This large-scale variation in recruitment from Oregon to central California has been proposed to drive variation in post-settlement processes such as competition and predation and ultimately community structure (Connolly and Roughgarden, 1998; Menge, 2000; Connolly et al., 2001).

Filter-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, sea stars, 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.

Cycles of coastal upwelling and relaxation have been shown to have an important influence on the structure of benthic communities in all of the studies described thus far by affecting the transport of larvae and nutrients 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, CA (see Fig. 1). The Point Conception region (hereafter referred to as PC) – the section of coast between Points Arguello and Conception – is a major oceanographic transition zone and divides the California coast into two regions with very different circulation patterns (Cudaback et al., 2005). This area 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 (Caldwell et al., 1986; Henderschott and Winant, 1996; Harms and Winant, 1998). 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.

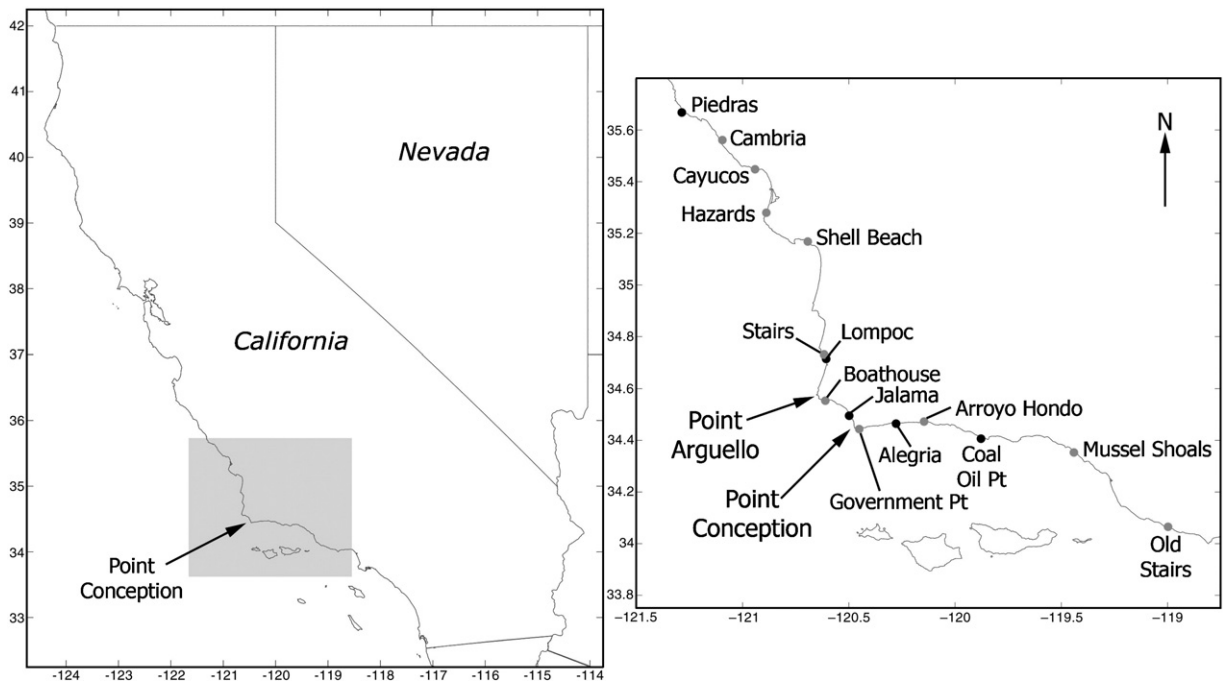


Fig. 1. Regional map of the California coast highlighting the location of the Point Conception Region (shaded) and expanded in the box to the right. Locations of Point Arguello and Point Conception are indicated with arrows. Main intertidal study sites are depicted with black dots and additional community survey sites are depicted with gray dots.

Macrophytes (algae and surfgrass) dominate space at sites north of PC, while filter-feeding invertebrates dominate sites south/east of PC (personal observations). 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).

Here we explore how the competitively dominant mussel, *M. californianus*, responds to mesoscale oceanic variability across the region spanning PC. We document spatial variation in size and spatial coverage of mussel beds and patterns of recruitment, size and abundance of mussels around PC. Similar to the community structure transition described above for the OR/CA region (Connolly and Roughgarden, 1998) we predict that the strong upwelling in the region north of PC limits mussel recruitment, leading to communities dominated by macrophytes and reduced mussel cover, relative to the region south of PC, where mussel beds dominate space.

2. Methods

2.1. Study region

Point Conception marks the boundary between two regions with very different circulation patterns (Cudaback et al., 2005). Water temperature is the most notable and often studied physical difference between these two regions (Valentine, 1966). The temperature shift at PC is on the order of 4 °C with warmer waters occurring to the south and cold waters driven by coastal upwelling occurring to the north (Blanchette et al., 2002). A steep gradient in wave exposure occurs around PC due to a change in orientation of the coastline from predominantly North/South north of PC to East/West south of PC (Blanchette et al., 2002). Sites north of PC are fully exposed to large ocean swells and storms generated in the North Pacific, whereas sites to the south of PC are relatively protected from heavy wave action (O'Reilly and Guza, 1993).

The sites used in this study spanned a total range of ~ 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 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. Community Structure

Benthic species abundance. We used a stratified point-intercept sampling method to quantify percentage cover of sessile invertebrate and macrophyte species at each site. A representative shore section 30 m long was designated as the site. A 30-m baseline tape was laid out along the upper edge of the highest intertidal barnacle zone, parallel to the shore. A point-intercept transect was then surveyed perpendicular to the horizontal tape at each 3-m interval, for a total of 11 transects per site. These vertical transects extended from the upper edge of the barnacle zone to about the 0.0 m MLLW level predicted by the tide tables (generally the surfgrass zone). Along each vertical transect, the species or taxon located under each point at a pre-determined interval along the tape was scored sequentially. The transect sampling interval at each site depended on the size and topography of the bench and was calculated to provide at least 100 points sampling points per transect. For example, if a vertical transect extended 20 m, the transect sampling interval would be 20 cm. For each point, we sampled the taxa directly under the point, then additionally the two nearest taxa within a radius equivalent to half the sampling interval from that point. Percentage cover estimates reported here are based on the primary taxa attached to rock located directly under each point. Following the approach of Connolly and Roughgarden (1998) and to facilitate comparisons among studies, here we quantify broad compositional patterns of intertidal assemblages across the region by examining species abundances pooled into functional groups (macrophytes, mussels, barnacles, and bare rock). Macrophytes (macroalgae and surfgrasses), mussels and barnacles are by far the dominant invertebrate space occupiers in the community.

Predator Densities. The experiments in this study were conducted concurrently with a large-scale experiment designed to evaluate geographic variability in predation intensity (Menge et al., 2004). In 1999 and 2000 we estimated predator densities at each site by counting the numbers of sea stars (*Pisaster ochraceus*) in four quadrats

in a grid (2×4 m) centered over each replicate of the predation experiment at the lowest edge of the mussel zone at each site. In 2001 and 2002 we estimated densities of *Pisaster* at each site by counting the total numbers of *Pisaster* along 1 to 3 band transects centered along the lowest edge of the mussel zone at each site.

2.3. Mussel-related measures

Mussel Recruitment. Potential mussel recruitment rates were quantified using standardized plastic mesh ball collectors or Tuffys™ (Menge, 1992; Menge et al., 1994, 1999; Leonard et al., 1998). The plastic mesh filaments of these collectors mimic the preferred filamentous substrata of mussel larvae such as finely branched algae and mussel byssus (Paine, 1971, 1974). Five replicate collectors were fastened to the rock in the mid-zone of each site and replaced monthly to bimonthly. In the laboratory, mussel recruits were detached from the mesh, counted and identified to genus under a dissecting microscope. Although two species of *Mytilus* occur

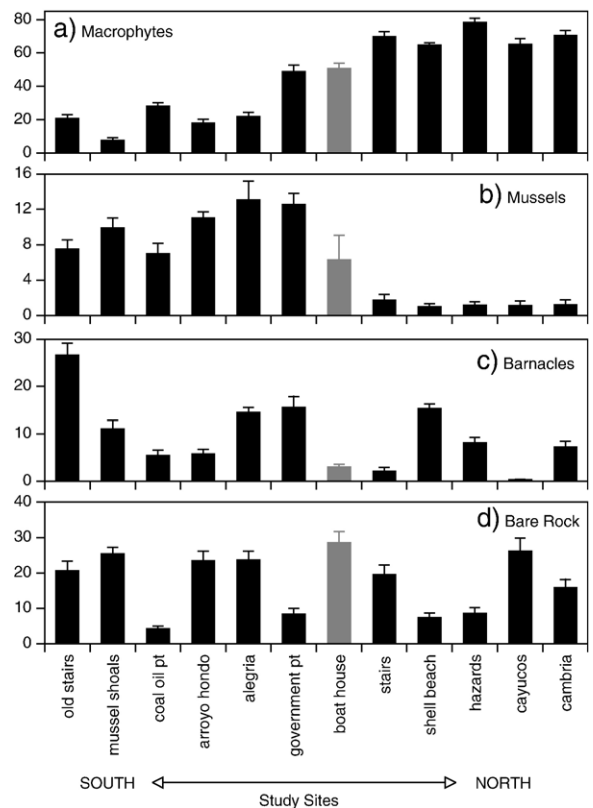


Fig. 2. Mean (± 1 s.e.m.) percent cover of a) macrophytes; b) mussels; c) barnacles and d) bare rock space at a range of sites spanning PC arranged from the southernmost site on the left to the northernmost site on the right. The shaded site (Boathouse) lies at the center of the PC region. Site locations are shown in Fig. 1.

within this region (*M. californianus* and *M. galloprovincialis*) the California mussel, *M. californianus* is by far the most abundant *Mytilus* species at all the open coast rocky intertidal sites (Johnson and Geller, 2006). For approximately 1 year, we attempted to identify *Mytilus* recruits to species using morphological characters (Martel et al., 1999). However this was extremely labor intensive, and across all sites we found that 90% or more of the mussel recruits were *M. californianus*, which was confirmed using genetic techniques (C. Blanchette and L. Miller, unpublished data). This is consistent with findings from further north along the coast at a range of similar open coast rocky intertidal sites near Santa Cruz, CA where 80–90% of recruits are *M. californianus* (P. Raimondi, unpublished data).

Mussel Abundance. To quantify mussel abundance at each site, we established 3 horizontal 30-m transects in both the middle and lower portions of the mussel zone at each site. For small sites or sites where we could not establish a contiguous 30-m transect, we sampled at least 3 shorter transects in each zone. We defined the mid mussel zone at each site as the elevational middle of the mussel bed. The low mussel zone transects were placed along the lower limit of the mussel bed at each site. We randomly placed ten 0.25 m² quadrats along each of the transects, but only in locations where either

Table 1

Results of a nested ANOVA for the effects of region (north vs. south of PC) and sites nested within regions on the average percent cover of a) macrophytes, b) mussels, c) barnacles and d) bare rock space at a range of sites spanning PC

	df	SS	MS	F	p
a) Macrophytes					
Region	1	398.19616000	398.19616000	597.483	0.0001
Site	10	132.49749000	13.24974900	19.881	0.0001
{region}					
Residual	120	79.97476000	0.66645633		
b) Mussel					
Region	1	149.09172000	149.09172000	178.515	0.0001
Site	10	20.31149000	2.03114900	2.432	0.0113
{region}					
Residual	120	100.22103000	0.83517525		
c) Barnacle					
Region	1	59.42813000	59.42813000	101.234	0.0001
Site	10	155.18618000	15.51861800	26.435	0.0001
{region}					
Residual	120	70.44445000	0.58703708		
d) Rock					
Region	1	0.00702000	0.00702000	0.008	0.9306
Site	10	158.49327000	15.84932700	17.200	0.0001
{region}					
Residual	120	110.57814000	0.92148450		

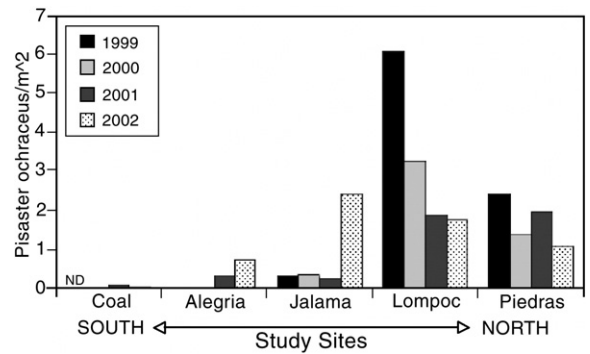


Fig. 3. *Pisaster ochraceus* density (individuals/m²) from 1999 to 2002 (shaded bars) at each of the 5 main intertidal sites spanning PC arranged from the southernmost site on the left to the northernmost site on the right. Jalama lies at the center of the PC region. ND=No Data for Coal Oil Point in 1999.

mussels already occurred or where they could potentially occur (this excludes sandy stretches, pools, surge channels, etc.). In each quadrat we measured the percent cover of mussels and depth of the mussel bed. We took 5 depth measurements in each quadrat, one in each of the 4 quadrants and one in the middle using rulers or rods marked off to the nearest 0.5 cm.

Mussel morphology and Condition Index. To estimate the allometric relationship between shell length and biomass, we haphazardly collected 30–40 mussels greater than 1 cm in length from each site. We measured the length of each mussel from the umbo to the ventral margin and the total wet weight of each individual before dissection. We then removed all epibionts from each mussel shell and dissected the tissue from the shell. The flesh and the shell were oven dried for several days at 50° until the weight was constant. We measured dry weight of both

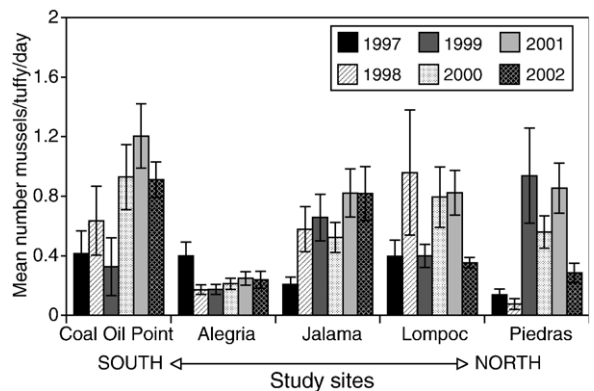


Fig. 4. Yearly mean mussel recruitment rates from 1997 to 2000 (shaded bars) at each of the 5 main intertidal sites spanning PC arranged from the southernmost site on the left to the northernmost site on the right. Jalama lies at the center of the PC region. Data are yearly means \pm 1 s.e.m.

Table 2

Results of two-way ANOVA for the effects of year and site on mussel recruitment rates

Recruitment					
Source of variation	df	SS	MS	F	p
Site	4	1.98945100	0.49736275	0.578	0.6783
Year	5	16.96133300	3.39226660	3.945	0.0015
Site × year	20	35.33745100	1.76687255	2.055	0.0042
Residual	985	846.94264000	0.85984024		

shell and tissue from each mussel. The Condition Index (CI) was calculated based on the following equation (Davenport and Chen, 1987; Steffani and Branch, 2003):

$$CI = [\text{dry flesh weight}(\text{mg}) / \text{shell weight}(\text{mg})] \cdot 100$$

Biomass. In conjunction with another experiment designed to study mid-zone succession, we cleared five 0.25 m² plots in the middle of the mussel zone at each of 3 sites around PC (Coal Oil Pt, Jalama and Lompoc). Prior to clearing, we quantified percent cover of the dominant organisms. In each plot we carefully removed and collected all organisms and brought them back to

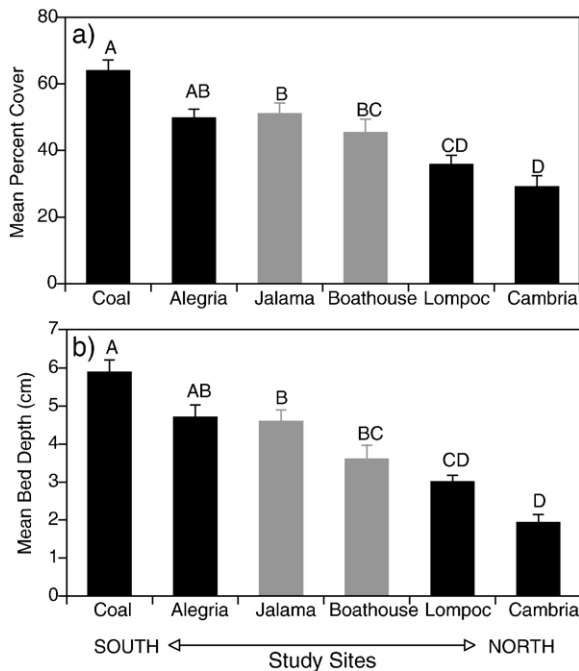


Fig. 5. Mussel bed size at each of 6 main intertidal sites spanning PC arranged from the southernmost site on the left to the northernmost site on the right; (a) mean mid zone percent cover of mussels and (b) mean mussel bed depth in the mid zone. The shaded sites (Jalama and Boathouse) lie at the center of the PC region. Data are site means ± 1 s.e.m. Means with different letters are significantly different from one another at α=0.05 based on a Tukey–Kramer multiple comparison.

Table 3

Results of ANOVA among sites on (a) mussel bed percent cover and (b) depth

Source of variation	df	SS	MS	F	p
a) Mussel bed % cover					
Site	5	39632.6500	7926.5300	13.289	<0.0001
Residual	336	200420.9300	596.4909		
b) Mussel bed depth					
Site	5	520.8655	104.1731	21.240	<0.0001
Residual	336	1647.9646	4.9047		

the laboratory to measure biomass of the major functional groups. Here we report on biomass and density of *M. californianus* from these plots.

Tidal Elevation. We measured the tidal elevation of the mussel zone at each site along 20 vertical transects spaced 3 m apart running from the upper limit of the barnacle zone to the middle of the surfgrass zone. Along

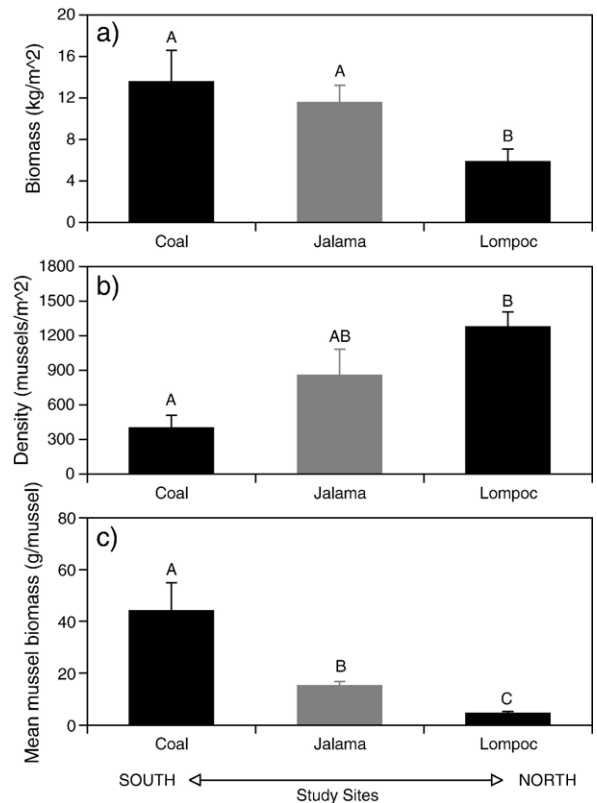


Fig. 6. Mussel size and abundance; (a) mean density (individuals/m²), (b) mussel bed biomass (kg/m²) and (c) individual biomass (g) at 3 sites spanning PC arranged from southernmost site on the left to the northernmost site on the right. The shaded site (Jalama) lies at the center of the PC region. Data are site means ± 1 s.e.m. Means with different letters are significantly different from one another at α=0.05 based on a Tukey–Kramer multiple comparison.

Table 4
Results of ANOVA among sites on (a) mussel bed biomass, (b) density and (c) individual biomass

Source of variation	df	SS	MS	F	p
<i>a) Total biomass</i>					
Site	2	2.09103070	1.04551535	5.742	0.0178
Residual	12	2.18512340	0.18209362		
<i>b) Density</i>					
Site	2	4.71592370	2.35796185	7.159	0.009
Residual	12	3.95235970	0.32936331		
<i>c) Individual biomass</i>					
Site	2	12.16764400	6.08382200	30.975	<0.0001
Residual	12	2.35689100	0.19640758		

each transect we measured the upper elevation defined as the highest location along each transect where mussels were found. Similarly we recorded the elevations at the lowest edge of the mussel zone along each transect. All elevation surveys were conducted using standard survey equipment using a laser-leveler system. Elevations were referenced to mean lower low water (MLLW) by measuring a reference height of sea level at the time of lowest tide as predicted for each location using the xtide (<http://www.flaterco.com/xtide>) tidal prediction software. Tidal predictions were based on an average from survey measurements of sea level conducted on several different days in an attempt to even out the variability due to climate and swell.

2.4. Data analysis

All analyses were performed using JMP statistical software (v5.0 SAS Institute). We examined probability

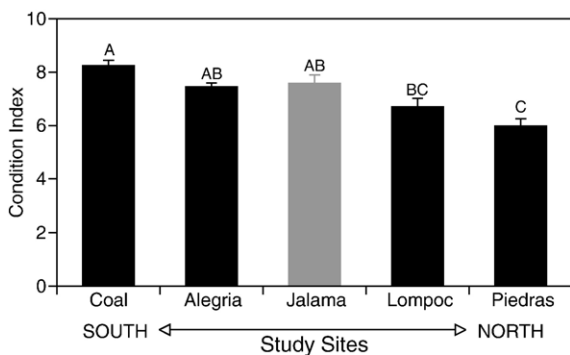


Fig. 7. Mussel condition ($[\text{flesh weight}/\text{shell weight}] \times 100$) at each of 5 main intertidal sites spanning PC arranged from the southernmost site on the left to the northernmost site on the right. The shaded site (Jalama) lies at the center of the PC region. Data are site means \pm 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 5
Results of ANOVA among sites on mussel condition

Condition Index					
Source of variation	df	SS	MS	F	p
Site	4	93.15967000	23.28991750	10.793	<0.0001
Residual	161	347.40805000	2.15781398		

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. Proportional or percent cover data were arcsin-transformed, and all other data were log-transformed ($\ln(x+1)$). We analyzed data on mussel abundance and condition, tidal elevation and using ANOVA and performed post hoc tests Tukey–Kramer tests to test for differences among sites.

3. Results

Community Structure Patterns. Two of the dominant occupiers of space in these rocky intertidal communities are macrophytes and mussels, which transition in abundance sharply in the PC region (Fig. 2). Macrophyte abundance generally increased in a gradient from south to north around PC, and macrophyte cover was significantly higher at sites north of PC, while mussels displayed the opposite pattern of decreasing cover in a gradient from south to north around PC, and were significantly more abundant at sites south of PC (Table 1a, b). Barnacle cover was much more variable among sites, but barnacle cover was significantly higher at sites south of PC. The amount of bare rock space

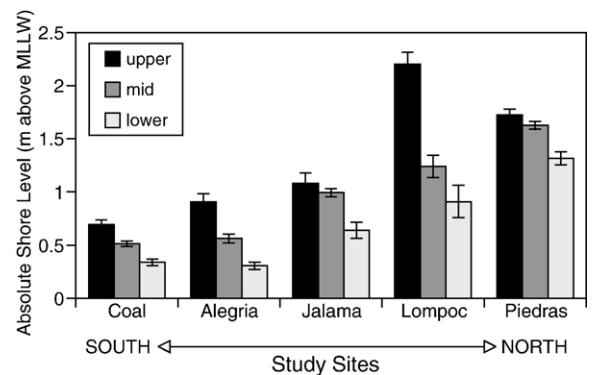


Fig. 8. Mean Absolute Shore Level (m above or below MLLW) for mussel bed upper and lower limits at each of the 5 main intertidal sites spanning PC arranged from the southernmost site on the left to the northernmost site on the right. Jalama lies at the center of the PC region. Data are site means \pm 1 s.e.m.

Table 6
Results of two-way ANOVA for the effects of site and zone (mid and low) on mussel bed upper and lower limits

Mussel bed elevation					
Source of variation	df	SS	MS	F	p
Site	3	9.95110180	3.31703393	96.946	<0.0001
Zone	1	4.18873660	4.18873660	122.423	<0.0001
Site × Zone	3	0.92682200	0.30894067	9.029	<0.0001
Residual	44	1.50547500	0.03421534		

varied greatly among sites and there was no significant difference in the amount of bare rock space between regions to the north and south of PC (Table 1c, d).

Predator density. *P. ochraceus*, the primary predator of *Mytilus* was most abundant at sites north of PC across all years (Fig. 3). *Pisaster* ranged from scarce to absent at sites in the SB Channel in most years.

Mussel Recruitment. Mussel recruitment rates varied greatly over time and space around PC (Fig. 4). There was no significant variation among sites, and no gradient in recruitment rates around PC either across years or in any particular year. There was, however significant variation in recruitment among years, and a significant interaction among sites and years (Table 2).

Mussel Size and Abundance. Mussel bed size consistently decreased in terms of both percentage cover and depth across a range of sites from south to north around PC (Fig. 5a and b; Table 3). The total biomass of mussels from a subset of these sites was also consistent with this decline from south to north (Fig. 6a). Although total mussel biomass was lowest at the northernmost site (Table 4), the density of mussels was significantly highest in this site (Fig. 6b) due to the significantly reduced size of mussels from south to north (Fig. 6c). This gradient in mussel size around PC is also reflected in the Condition Index (Fig. 7). Values of the condition index steadily decreased from south to north across a range of sites around PC, reflecting a greater biomass of tissue per gram of shell for the southern mussels (Table 5).

Tidal elevation. There was significant spatial variation in mussel bed tidal elevations (both upper and lower limits) across PC (Fig. 8, Table 6). Spatial variation in elevational limits indicated that mussels ranging from north to south around PC were effectively shifted lower into the intertidal zone at southern sites.

4. Discussion

The results of this study reveal a strong geographic gradient in the distribution, abundance, and size of

M. californianus around PC linked to the larger scale shift in community structure in this region. Contrary to our original predictions, mussel recruitment was not reduced in the high upwelling region north of PC relative to the Santa Barbara Channel sites. Mussel beds were thicker, more spatially extensive and higher in biomass in a gradient from north to south around PC. Mussel beds south of PC were occupied by larger, less densely packed mussels. The elevational zones occupied by mussel beds were also shifted upwards in a gradient from south to north around PC. These results suggest that post-settlement processes such as differences in growth and mortality drive the pattern of mussel abundance and size around PC and contribute to the overall shift in community structure in this region.

4.1. Supply-side ecology and 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 sea star *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 are dominated by filter-feeding invertebrates (mussels and barnacles) in the south and large macrophytes north of PC. The spatial pattern in mussel recruitment rates documented here does not support the idea that the gradient in mussel abundance around PC is driven by larval settlement. Sites north of PC have recruitment rates equal to or higher than southern sites across several years. It is notable that recruitment rates across this region are at least an order of magnitude lower than those observed in Oregon (Menge et al., 1997; Connolly et al., 2001).

Similar to the findings of Connolly and Roughgarden (1998) we observed a sharp gradient in intertidal community structure coincident with a major oceanographic transition region. The pattern of community structure that we observed around PC is consistent with the findings of Connolly and Roughgarden (1998) for the

CA/OR region with one exception. Both of our studies show higher abundances of macrophytes in the region of high upwelling and high abundances of filter-feeders in the region of limited upwelling, however Connolly and Roughgarden (1998) report a sharp difference in the abundance of bare rock space between regions correlated with a gradient in recruitment of mussels and barnacles (Connolly et al., 2001), while we find no difference in bare space across the PC region. This difference may be significant in light of our findings that differential patterns of recruitment did not seem to underlie patterns of community structure. As demonstrated in their mathematical model, variability in recruitment of a competitive dominant should directly influence the amount of available bare space (Connolly and Roughgarden, 1998). This is consistent with both their findings and our findings where we observe no spatial variation in either recruitment or in bare space.

4.2. Zonation and elevational shifts

There are several factors known to influence intertidal mussel zonation; predation has been demonstrated to determine the lower limit of the mussel zone, while desiccation and temperature are primarily thought to influence upper limits (Stephenson and Stephenson, 1949; Dayton, 1971; Paine, 1974). 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. The strong gradient in wave exposure around PC could also 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). 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.

4.3. Regional differences in growth and performance

Around the PC region, we found mussel beds to be smaller, less spatially extensive and have lower overall biomass at the northern sites. These sites contained a high density of relatively small individuals. These differences in size and abundance of mussels are likely due to differential growth rates correlated with the oceanographic transition at PC. Although recruitment rates are similar, mussels may be able to grow more rapidly in the southern region where water temperatures are warmer, and wave exposure is reduced (see Blanchette et al., in press). The higher abundance of large mussels at the southern intertidal sites is also facilitated by the relative absence of sea star predators, allowing the mussels to expand into the low intertidal, potentially increasing feeding time and growth. Mussel growth at northern sites may be limited by cold water temperatures and decreased feeding time due to upward shifts in elevation and extremely high water motion. Increased intra-specific competition at southern sites with fast growing mussels may also be responsible for higher mortality rates of small individuals and may explain the trend of low densities of large individuals. Density-dependent effects of intra-specific competition on growth have been shown for *M. californianus* on the Oregon coast (Yamada and Peters, 1988).

Menge et al. (1997) 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. 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 California system studied here. The intermittent upwelling characteristic of the Oregon system provides delivery of phytoplankton inshore during periods of relaxation. In the California system,

upwelling is consistently strong north of PC and these blooms of phytoplankton are continually advected offshore, as opposed to the Oregon system where upwelling relaxations transport blooms inshore. Along the California coast north of PC, upwelled nutrients contribute to phytoplankton blooms that are rapidly advected offshore as they develop. Thus, productivity resulting 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 may contribute to the potentially low growth rates of intertidal mussels in the northern region, and high densities of small individuals.

The overall community pattern of macrophyte dominance in the northern region may reflect enhanced growth and performance of macrophytes in the cold, nutrient-rich water north of PC. Macrophytes are clearly the dominant space occupiers in these communities and factors influencing algal productivity may also strongly influence the structure of the entire community (Bustamante et al., 1995; Wootton et al., 1996; Foster et al., 2003; Nielsen and Navarrete, 2004). The strong relationship between temperature and nutrient availability is well established (Jackson, 1977; Wheeler and North, 1980; Zimmerman and Kremer, 1984; Dayton et al., 1999). Numerous studies have shown that most macrophytes, particularly kelps, thrive in cold, nutrient-rich water, and growth, reproduction, and propagule survival of many species are all enhanced under cold water, nutrient-rich conditions (Luning and Freshwater, 1988; Nielsen and Navarrete, 2004). In a previous study (Blanchette et al., 2002) we demonstrated a strong gradient in growth of the intertidal kelp *Egregia menziesii* around PC. Growth of *Egregia* was strongly increased in a gradient from south to north around PC correlated with cold water, increased flow and nutrient availability. This gradient of algal growth around PC in combination with a proposed gradient in mussel growth could account for the observed shift in dominance from algae to filter-feeders in the observed community pattern.

5. 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 PC is correlated with gradients in several environmental and ecological variables (upwelling, temperature, wave exposure and predation intensity) and a coincident shift in community structure and mussel abundance, size and vertical distribution. Unlike the OR/CA region, where a similar shift in community structure occurs due to a dramatic increase in mussel recruitment in OR, we found no evidence of variation in recruitment rates of mussels around PC. Instead, the shift in community structure around PC seems to be driven by oceanographic conditions favorable to macroalgal growth and dominance north of PC, and conditions favorable to mussel growth and dominance south of PC.

Acknowledgments

This project has been funded by the Partnership for Interdisciplinary Studies of Coastal Oceans, and the Andrew W. Mellon Foundation. We appreciate the support of the Coal Oil Point Natural Reserve, Vandenberg Air Force Base, Piedras Blancas Lighthouse Station, Hollister Ranch, Jalama Beach County Park and helpful reviews by B. Broitman. The following contributed greatly to field data collection: C. Svedlund, C. Mangiardi, C. Gottschalk, J. Kovach, A. Wyndham, T. Jenkins, C. Krenz, B. Miner and the PISCO SWAT team. This is contribution 234 of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO): A Long-Term Ecological Consortium funded by the David and Lucille Packard Foundation. [SS]

References

- Abbott, M., Zion, P., 1985. Satellite observations of phytoplankton variability during an upwelling event. *Cont. Shelf Res.* 4, 661–680.
- Baird, D., Evans, P., Mile, H., Pienkowski, M., 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. *Oceanogr. Mar. Biol. Annu. Rev.* 23, 573–597.
- Benson, K.R., 2002. The study of vertical zonation on rocky intertidal shores—a historical perspective. *Integr. Comp. Biol.* 42, 776–779.
- Blanchette, C.A., Miner, B.G., Gaines, S.D., 2002. Geographic variability in form, size and survival of *Egregia menziesii* around Point Conception, California. *Mar. Ecol. Prog. Ser.* 239, 69–82.
- Blanchette, C.A., Helmuth, B., Gaines, S.D., in press. Patterns of growth of the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA.
- Brattstrom, H., Johanssen, A., 1983. Ecological and regional zoogeography of the marine benthic fauna of Chile. *Sarsia* 68, 289–339.
- Briggs, J.C., 1974. *Marine Zoogeography*. Mc Graw–Hill, New York.
- Broitman, B.R., Navarrete, S.A., Smith, F., Gaines, S.D., 2001. Geographic variation of southeastern Pacific intertidal communities. *Mar. Ecol. Prog. Ser.* 224, 21–34.

- Burton, R.S., 1998. Intraspecific phylogeography across the Point Conception biogeographic boundary. *Evolution* 52, 734–745.
- Bustamante, R.H., Branch, G.M., 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *J. Exp. Mar. Biol. Ecol.* 196, 1–28.
- Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Keats, D., Jurd, M., McQuaid, C., 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* (Berlin) 102, 189–201.
- Caldwell, P.C., Stuart, D.W., Brink, K.H., 1986. Mesoscale wind variability near Point Conception, California during spring 1983. *J. Clim. Appl. Meteorol.* 25, 1241–1254.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. In: Fautin, D.G. (Ed.), *Annual Review of Ecology and Systematics*, vol. 27. Annual Reviews Inc., Palo Alto, California, USA, pp. 477–500.
- Connell, J.H., 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* 93, 11–45.
- Connolly, S.R., Roughgarden, J., 1998. A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *Am. Nat.* 151, 311–326.
- Connolly, S.R., Menge, B.A., Roughgarden, J., 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific ocean. *Ecology* 82, 1799–1813.
- Cudaback, C.N., Washburn, L., Dever, E., 2005. Subtidal inner-shelf circulation near Point Conception, California. *J. Geophys. Res., [Oceans]* 110.
- Dahlhoff, E.P., Menge, B.A., 1996. Influence of phytoplankton concentration and wave exposure on the ecophysiology of *Mytilus californianus*. *Mar. Ecol. Prog. Ser.* 144, 97–107.
- Davenport, J., Chen, X., 1987. A comparison of methods for the assessment of condition in the mussel (*Mytilus edulis* L.). *J. Molluscan Stud.* 53, 293–297.
- Dayton, P.K., 1971. Competition, disturbance, and community organization—provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351–389.
- Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol. Monogr.* V69, 219–250.
- Denny, M., Helmuth, B., Leonard, G., Harley, C., Hunt, L., Nelson, E., 2004. Quantifying scale in ecology, lessons from a wave-swept shore. *Ecol. Monogr.* 74, 513–532.
- Doyle, R.F., 1985. *Biogeographical Studies of Rocky Shores Near Point Conception, California*, Biology. University of California, Santa Barbara, California.
- Dugdale, R.C., Wilkerson, F.P., 1989. New production in the upwelling center at Point Conception, California—temporal and spatial patterns. *Deep-Sea Res.* 36, 985–1007.
- Dugdale, R.C., Davis, C.O., Wilkerson, F.P., 1997. Assessment of new production at the upwelling center at Point Conception, California, using nitrate estimated from remotely sensed sea surface temperature. *J. Geophys. Res., [Oceans]* 102, 8573–8585.
- Foster, M.S., Nigg, E.W., Kiguchi, L.M., Hardin, D.D., Pearse, J.S., 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. *J. Exp. Mar. Biol. Ecol.* 289, 15–39.
- Gaines, S., Lubchenco, J., 1982. A unified approach to marine plant–herbivore interactions. II. Biogeography. *Ann. Rev. Ecol. Syst.* 13, 111–138.
- Gaines, S., Roughgarden, J., 1985. Larval settlement rate—a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl. Acad. Sci. U. S. A.* 82, 3707–3711.
- Gaines, S., Roughgarden, J., 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science* 235, 479–481.
- Gaines, S., Brown, S., Roughgarden, J., 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67, 267–272.
- Gaylord, B., Gaines, S., 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* 155, 759–789.
- Harms, S., Winant, C.D., 1998. Characteristic patterns of the circulation in the Santa Barbara channel. *J. Geophys. Res., [Oceans]* 103, 3041–3065.
- Henderschott, M.C., Winant, C.D., 1996. Surface circulation in the Santa Barbara channel. *Oceanography* 9, 114–121.
- Hughes, T.P., 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *Am. Nat.* 123, 778–795.
- Hughes, T.P., 1990. Recruitment limitation, mortality, and population regulation. *Ecology* 71, 12–20.
- Jackson, G.A., 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off southern California. *Limnol. Oceanogr.* 22, 979–995.
- Johnson, S.B., Geller, J.B., 2006. Larval settlement can explain the adult distribution of *Mytilus californianus* Conrad but not of *M. galloprovincialis* Lamarck or *M. trossulus* Gould in moss landing, central California: evidence from genetic identification of spat. *J. Exp. Mar. Biol. Ecol.* 328, 136–145.
- Leonard, G.H., Levine, J.M., Schmidt, P.R., Bertness, M.D., 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79, 1395–1411.
- Lewis, J., 1964. *The Ecology of Rocky Shores*. English Universities Press, London.
- Luning, K., Freshwater, W., 1988. Temperature tolerance of northeast Pacific marine algae. *J. Phycol.* 24, 310–315.
- Martel, A.L., Robles, C., Beckenbach, K., Smith, M.J., 1999. Distinguishing early juveniles of eastern Pacific mussels (*Mytilus* spp.) using morphology and genomic DNA. *Invertebr. Biol.* 118, 149–164.
- Menge, B.A., 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *J. Exp. Mar. Biol. Ecol.* 148, 89–100.
- Menge, B.A., 1992. Community regulation under what conditions are bottom-up factors important on rocky shores? *Ecology* 73, 755–765.
- Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *J. Exp. Mar. Biol. Ecol.* 250, 257–289.
- Menge, B.A., Olson, A.M., 1990. Role of scale and environmental factors in regulation of community structure. *Trends Ecol. Evol.* 5, 52–57.
- Menge, B., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept—variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.* 64, 249–286.
- Menge, B., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997. Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proc. Natl. Acad. Sci. U. S. A.* 94, 14530–14535.
- Menge, B.A., Daley, B.A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G., Burnaford, J.L., 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecol. Monogr.* 69, 297–330.

- Menge, B., Blanchette, C., Raimondi, P., Freidenburg, T., Gaines, S., Lubchenco, J., Lohse, D., Hudson, G., Foley, M., Pamplin, J., 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecol. Monogr.* 74, 663–684.
- Navarrete, S.A., Menge, B.A., 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecol. Monogr.* 66, 409–429.
- Newman, W.A., 1979. Californian transition zone: Significance of short-range endemics. In: Gray, J., Boucot, A.J. (Eds.), *Historical Biogeography, Plate Tectonics, and the Changing Environment*. Oregon State University Press, Corvallis, Oregon, pp. 399–416.
- Nielsen, K.J., Navarrete, S.A., 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. *Ecol. Lett.* 7, 31–41.
- O'Reilly, W.C., Guza, R.T., 1993. A comparison of two spectral wave models in the southern California bight. *Coast. Eng.* 19, 263–282.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65–75.
- Paine, R.T., 1969. A note on trophic complexity and community stability. *Am. Nat.* 103, 91–93.
- Paine, R.T., 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* 52, 1096–1106.
- Paine, R.T., 1974. Intertidal community structure— experimental studies on relationship between a dominant competitor and its principal predator. *Oecologia* 15, 93–120.
- Paine, R.T., Castillo, J.C., Cancino, J., 1985. Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand, and Washington state. *Am. Nat.* 125, 679–691.
- Pelaez, J., McGowan, J.A., 1986. Phytoplankton pigment patterns in the California current as determined by satellite. *Limnol. Oceanogr.* 31, 927–950.
- Petersen, J.H., 1984. Establishment of mussel beds— attachment behavior and distribution of recently settled mussels (*Mytilus californianus*). *Veliger* 27, 7–13.
- Ricciardi, A., Bourget, E., 1999. Global patterns of macroinvertebrate biomass in marine intertidal communities. *Mar. Ecol. Prog. Ser.* 185, 21–35.
- Robles, C., Robb, J., 1993. Varied carnivore effects and the prevalence of intertidal algal turfs. *J. Exp. Mar. Biol. Ecol.* 166, 65–91.
- Robles, C., Sherwoodstephens, R., Alvarado, M., 1995. Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* 76, 565–579.
- Roughgarden, J., Iwasa, Y., Baxter, C., 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66, 54–67.
- Roughgarden, J., Gaines, S., Possingham, H., 1988. Recruitment dynamics in complex life-cycles. *Science* 241, 1460–1466.
- Santelices, B., 1980. Phylogeographic characterization of the temperate coast of Pacific south america. *Phycologia* 19, 1–12.
- Seed, R., Suchanek, T., 1992. Population and community ecology of *Mytilus*. In: EM, G. (Ed.), *The Mussel Mytilus: Ecology, Physiology, Genetics and Culture*. Elsevier, Amsterdam, pp. 87–169.
- Steffani, C.N., Branch, G.M., 2003. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Mar. Ecol. Prog. Ser.* 246, 197–209.
- Stephenson, T.A., Stephenson, A., 1949. The universal features of zonation between tide-marks on rocky coasts. *J. Ecol.* 37, 289–305.
- Strub, P.T., James, C., 1995. The large-scale summer circulation of the California current. *Geophys. Res. Lett.* 22, 207–210.
- Strub, P.T., James, C., Thomas, A.C., Abbott, M.R., 1990. Seasonal and nonseasonal variability of satellite-derived surface pigment concentration in the California current. *J. Geophys. Res., [Oceans]* 95, 11501–11530.
- Underwood, A.J., Denley, E., 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong, D.R., Simberloff, D., Abele, L., Thistle, A. (Eds.), *Ecological Communities*. Princeton University Press, Princeton, pp. 151–180.
- Valentine, J.W., 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. *Limnol. Oceanogr.* 11, 198–211.
- Wheeler, P.A., North, W.J., 1980. Effect of nitrogen supply on nitrogen content and growth rate of juvenile *Macrocystis pyrifera* (phaeophyta) sporophytes. *J. Phycol.* 16, 577–582.
- Wootton, J.T., Power, M.E., Paine, R.T., Pfister, C.A., 1996. Effects of productivity, consumers, competitors, and El Nino events on food chain patterns in a rocky intertidal community. *Proc. Natl. Acad. Sci. U. S. A.* 93, 13855–13858.
- Yamada, S.B., Peters, E.E., 1988. Harvest management and the growth and condition of submarket-size sea mussels, *Mytilus californianus*. *Aquaculture* 74, 293–299.
- Zimmerman, R.C., Kremer, N.J., 1984. Episodic nutrient supply to a kelp forest ecosystem in southern California. *J. Mar. Res.* 42, 591–604.