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Intertidal community structure and oceanographic patterns around Santa Cruz Island, CA, USA

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Abstract Recent studies suggest that nearshore oceanographic conditions can have important effects on the structure of benthic communities. On Santa Cruz Island (SCI), CA, USA there is a persistent difference in mean annual sea surface temperature (SST) around the island due to its location at the confluence of opposing cold and warm ocean current systems. Over the course of a 4-year study (1997–2001) seawater nutrient and chl-*a* concentrations, algal tissue C:N ratios, recruitment and growth of filter-feeders (barnacles and mussels), and intertidal community structure were measured at six intertidal sites around the island. There were strong associations between remotely sensed SST and patterns of community structure. Macrophyte abundance was highest at sites with persistently low SST, while recruitment, abundance, and growth of filter-feeding invertebrates were strongly, positively correlated with SST. The cold-water sites were associated with higher nutrient concentrations and lower algal C:N ratios, particularly in the winter months. Values of chl-*a* were generally low and variable among sites, and were not correlated with the predominant SST gradient. Recruitment of barnacles and mussels was positively correlated with adult abundance across all sites. While detailed experimental studies are needed to further evaluate the mechanisms underlying community dynamics, these results indicate that the confluence of cold- and warm-water masses around SCI may determine the contrasting patterns of intertidal community structure.

Introduction

A major focus of current ecological research is to understand the factors producing variation in community structure at a variety of spatial and temporal scales. Traditional marine ecological studies have focused on processes operating at relatively small spatial scales (1–10 m), but the generality of these findings is increasingly being challenged (Dayton and Tegner 1984; Carpenter 1996; Polis and Hurd 1996; Menge et al. 1997b, Schiel 2004). As broad scale issues are increasingly dominating questions in conservation and management, marine ecologists have been pressed to examine linkages between patterns and processes operating at larger spatial scales. In marine systems, this “scaling-up” has resulted in a significant conceptual shift in our understanding of the connections among populations and communities and the importance of benthic–pelagic linkages. Benthic communities are inextricably linked to the oceanic environment through the delivery of food, nutrients, and propagules. The oceanographic processes driving the delivery of these constituents span large spatial scales and thereby connect distant communities (Gaines et al. 1985; Roughgarden et al. 1988; Bustamante et al. 1995b; Menge et al. 1997b; Schiel 2004).

Recent ecological studies from eastern boundary upwelling ecosystems around the world support a strong coupling between nearshore oceanographic patterns and intertidal benthic community structure. In South Africa, it has been established that large-scale (100's of km) patterns of intertidal community structure covary with nearshore productivity and wave exposure (Bustamante et al. 1995b; Bustamante and Branch 1996). Along the coast of Chile, several studies provide evidence that the abundance of dominant intertidal functional groups is strongly correlated to persistent differences in nearshore sea surface temperatures (SSTs; Broitman et al. 2001; Nielsen and Navarrete 2004). Around the south island of New Zealand, community structure and dynamics in

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the rocky intertidal have been shown to be related to island-scale differences in upwelling intensity around the south island (Menge et al. 1999, 2003). Similarly, on the US West coast, nearshore oceanographic conditions have been shown to determine community structure along the coast of Oregon where enhanced chlorophyll and elevated mussel growth rates are linked to coastal upwelling (Menge et al. 1997a, b).

One major mechanistic hypothesis linking nearshore oceanography to community pattern relates to the spatial and temporal variability in coastal upwelling. Latitudinal variation in the upwelling intensity has been suggested to play an important role in the recruitment of benthic invertebrates along the US West coast. The upwelling/relaxation model is based on the idea that planktonic larvae are swept offshore by Ekman transport where they accumulate along coastal fronts and are occasionally returned to shore when upwelling-favorable winds relax (Roughgarden et al. 1988; Shanks et al. 2000). Variable upwelling and frequent relaxations along the Oregon coast are correlated with high rates of larval arrival in barnacles and mussels (Menge 1991; Connolly et al. 2001). In contrast, consistently strong upwelling along much of the California coast has been proposed to limit invertebrate recruitment (Gaines et al. 1985; Gaines and Roughgarden 1985; Roughgarden et al. 1988; Strub and James 1995). This large-scale variation from Oregon to central California in the recruitment of competitively dominant invertebrates such as mussels and barnacles has been proposed to underlie variation in post-settlement processes such as competition and predation and ultimately community structure (Connolly and Roughgarden 1998). Regions of strong coastal upwelling may also influence community structure through positive direct effects on macroalgae, which compete for space with mussels and barnacles (Schiel 2004). Coastal upwelling delivers cold, nutrient-rich water to shore, and locations of strong upwelling are characterized by high nutrient concentrations which have been shown to affect the abundance (Bustamante et al. 1995b; Broitman et al. 2001) and growth rates (Blanchette et al. 2002; Nielsen and Navarrete 2004) of benthic macroalgae.

Persistent upwelling does not describe the entire California coast. Point Conception (34.5°N) divides the coast into two regions with very different nearshore circulation patterns. The northern region is typified by consistently strong coastal upwelling bringing cold, nutrient-rich waters to the surface resulting in both cold SSTs along the coast and high nutrient concentrations (Brink et al. 1984; Abbott and Zion 1985). The Santa Barbara Channel, immediately southeast of Point Conception is typified by weak and infrequent seasonal upwelling, which tends to occur in the winter months (Hickey 1993; Blanchette et al. 2002; Winant et al. 2003). The California Channel Islands, just offshore from Point Conception lie within this oceanographic transition region. These islands have recently received attention as a focal region of biological and oceanographic diversity (Airame et al. 2003). The broad range of SSTs and

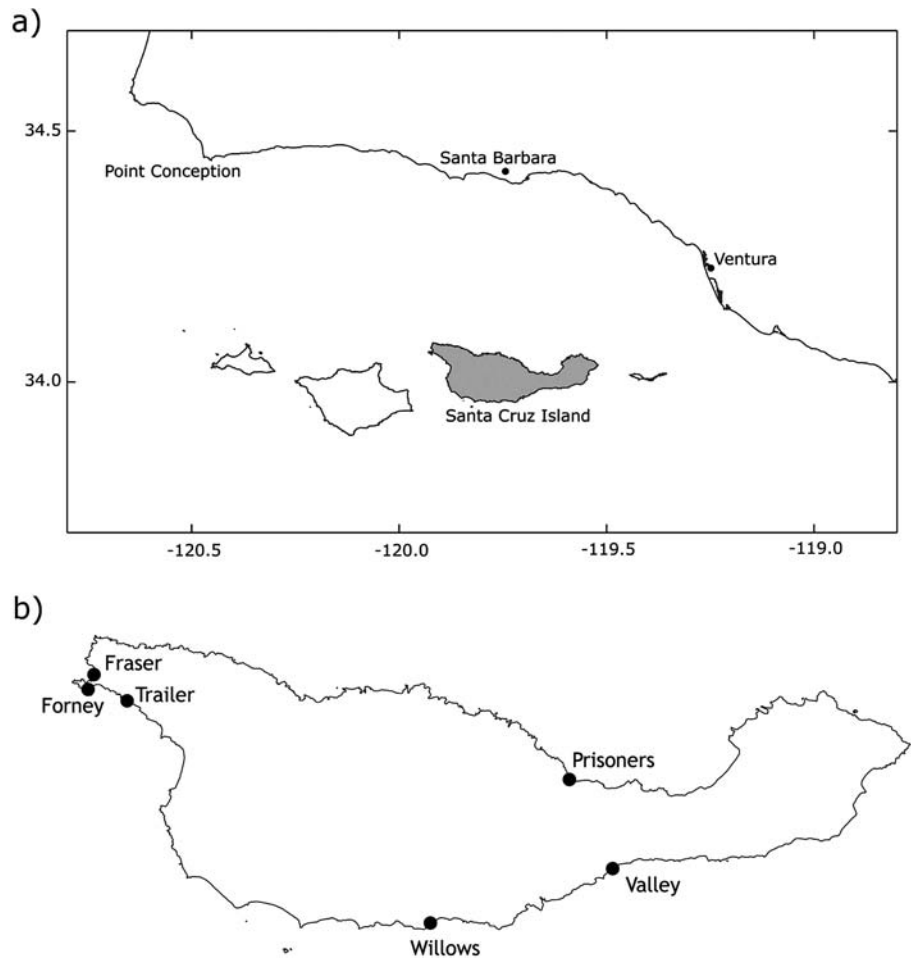
oceanographic variability found across the entire Point Conception region is found at a much smaller geographic scale within this island group. These islands experience variable mixing between the cold waters of the California current and warmer, nearshore waters of the Southern California Countercurrent (Huyer 1983; Hickey et al. 2003) Santa Cruz Island (SCI) is the largest of the California Channel Islands and lies directly in the center of this transition region (Fig. 1a).

The biogeographical significance of the exposure of these offshore islands to different temperature regimes and distinctive water masses was recognized early by Hewatt (1946) who was among the first to describe the marine invertebrate faunas around SCI and their biogeographical affinities with the faunal elements characteristic of mainland intertidal habitats north and south of Point Conception. Although this early documentation was mainly descriptive and contains only single point measures of seawater temperature, Hewatt (1946) noted the potential importance of ocean temperature differences across the island to variability in assemblages of invertebrates around the island. Hewatt's biogeographic observations were later supported through quantitative studies of macroalgal communities across the Southern California Bight (Neushul et al. 1967; Murray and Littler 1981).

Recent work has shed some light on potential mechanisms linking oceanographic variability to larval delivery around SCI. Broitman et al. (2005) examined the connections between long-term mean SST and recruitment of mussels and barnacles around SCI. Sites located on the west end of the island experienced low, but variable SSTs, while eastern sites were warmer (by 1–1.5°C) and less variable. This oceanographic variability was linked to the dynamics of recruitment of mussels and barnacles around the island. Recruitment of both barnacles and mussels was highest at the eastern, warm-water sites. Western sites were dominated by an energetic flux of cold, recently upwelled water relatively depleted of larvae, while eastern sites received high numbers of larvae associated with the influx of warm surface waters (Broitman et al. 2005).

The spatial gradient in ocean temperatures around SCI provides a unique opportunity to examine the relationship between nearshore oceanographic conditions and biological community structure at a relatively small spatial scale. Here, we examine the potential community-level consequences of the documented gradient in recruitment of barnacles and mussels at six intertidal sites spanning the major oceanographic gradient across SCI (Broitman et al. 2005). Our aim in this paper is to document patterns of intertidal community structure across the oceanographic transition zone spanning SCI. We evaluate our main hypothesis, which is that the competitively dominant invertebrate filter-feeders (barnacles and mussels) are favored under warm-water conditions, and macrophytes (seaweeds and surfgrass) are favored under cold-water conditions. We discuss several potential mechanisms to link observed

Fig. 1 **a** Map of greater northern California Channel Islands region. Santa Cruz Island (*shaded gray*) is at the center of the map. **b** Locations of six intertidal study sites around SCI



patterns of community structure to the prevailing oceanographic conditions around the island.

Methods

Physical and oceanographic setting

Santa Cruz Island is the largest of the northern California Channel Islands and is located approximately 35 km south of Santa Barbara, CA, USA (Fig. 1a). Six rocky intertidal sites distributed around SCI (Fig. 1b) were chosen as study locations. Three sites were located on the

northwest of the island (Forney, Fraser, and Trailer), two on the southeastern shore (Willows and Valley) and one in the Santa Barbara Channel on the northeastern shore of SCI (Prisoners). These sites were all gently sloping (0–20°) rocky benches and were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type. Steep cliffs and sandy beaches dominate much of the coast between study sites. The number and locations of field sites were therefore limited by appropriate habitat availability, accessibility, property restrictions, and other logistical constraints. The Channel Islands are located in an extremely dynamic oceanographic setting (Fig. 2). The westernmost Channel

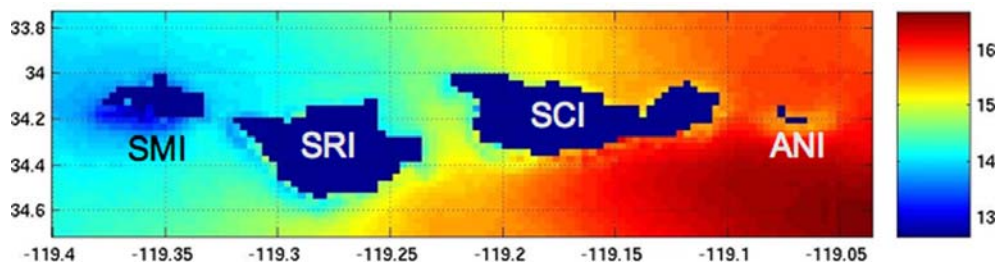


Fig. 2 Map of northern California Channel Islands. *SMI* San Miguel Island, *SRI* Santa Rosa Island, *SCI* Santa Cruz Island, *ANI* Anacapa Island. *Color scale* represents mean smoothed SST from 6-year AVHRR time series of weekly means (January 1997–December 2002). Nominal pixel resolution is 1.1 km

Islands, San Miguel, Santa Rosa, and the western region of SCI are highly influenced by cold waters originating in the Point Conception upwelling center. Anacapa Island and the eastern and southeastern shores of SCI are bathed by warmer subtropical waters of the Southern California Countercurrent.

Sea surface temperature analyses

We followed the approach of Broitman et al. (2005) and characterized oceanographic conditions through spatial and temporal patterns of SST from the advanced very-high resolution radiometer (AVHRR) of a nominal resolution of 1.1 km averaged over 5 days. The dataset examined here comprises 438 observations spanning 6 years, from January 1997 to December 2002. From the AVHRR dataset, we selected the pixels corresponding to the locations of our field study and averaged the first three cross-shelf pixels to obtain time series with 80–97% of valid observations. Cross-shelf averaging was imposed to improve temporal coverage; missing pixels were common in the nearshore. Seasonal and long-term means were derived directly from the resulting time series. Satellite-based SSTs at several sites around the island were significantly positively correlated with both surface temperatures from offshore moorings (mounted at 3 m depth) and high tide temperatures from intertidally mounted temperature data loggers (Onset Corp., C.A. Blanchette and B.R. Broitman, unpublished data). We chose to use satellite-based SST for this analysis due to the comprehensive long-term data for all of our study locations. We were unable to mount and maintain offshore moorings at several sites (Fraser and Prisoners) and we lost intertidal data loggers and data (due to logger malfunctions) from many of the sites for large periods of time over the course of the study.

Nutrient and chlorophyll-*a* sampling

To examine the suitability of different intertidal sites for macroalgal and filter-feeder growth, we measured seawater nutrient and phytoplankton concentrations. We collected samples of seawater ($n = 3-5$) from each of the intertidal sites approximately every 3 months from 1997 to 2000. Seawater nutrient samples were immediately frozen and were analyzed for nitrates and nitrites following standard methods (Wheeler 1985). To assess phytoplankton concentration, we filtered 100–500 ml of water onto Whatman GF/F glass-fiber filters and measured chl-*a* on a Turner Model 10 fluorometer following acetone extraction (Parsons et al. 1984). We selected the co-located AVHRR SST data from the SST time series described above for each site over a 5-days interval including the date the water samples were collected to examine the relationship between SST and nutrient availability, and SST and chl-*a* around the island.

Algal tissue C:N ratios

To evaluate the potential for nitrogen limitation in seaweeds around SCI, we collected algal tissue samples at each site from five haphazardly chosen individuals of *Egregia menziesii* seasonally between January 2000 and December 2001. *E. menziesii* is a relatively eurythermal kelp found from Alaska to Baja (Abbott and Hollenberg 1976; Blanchette et al. 2002) and common to all island sites. We collected a 10-cm section of tissue from each individual centered at the meristem. Clean algal material was oven dried at 80°C and ground to a fine powder using liquid N and a pestle and mortar. Total C and total N were determined using an Automated Organic Elemental Analyzer (Dumas combustion method). The percent tissue C and percent tissue N were standardized to algal dry weight (g) and C:N ratios were determined on an atomic weight basis.

Study system and taxonomic groupings

To quantify broad compositional patterns of intertidal assemblages around SCI we surveyed all six sites around SCI in the winter of 2000 and recorded percent covers of sessile species and densities of mobile species using the methods detailed below. The majority of primary space in these communities was occupied by a mixture of macroalgae, surfgrasses (*Phyllospadix* sp.), and filter-feeding invertebrates (mussels and barnacles). To evaluate our main hypothesis regarding the relationship between filter-feeder or macrophyte domination and oceanographic regime, we examined species abundances pooled into functional groups (Table 1). Sessile and mobile invertebrates were classified as in Murray and Littler (1981). Algal classification mainly followed Steneck and Dethier's (1994) "functional form" scheme. Invertebrates and macroalgae from around SCI were initially described by Hewatt (1946). Many of the dominant taxa in each group have ranges that extend broadly to both the north and south of SCI (e.g., *Mytilus californianus*, *Balanus glandula*, *Pisaster ochraceus*, *Nucella emarginata/ostrina*, most *Lottia* sp., *Strongylocentrotus* sp.). The mussel, *M. californianus* is the competitively dominant species in this and many intertidal communities along the US West coast, and is a common intertidal species ranging from Alaska to Baja (Gosling 1992; Seed and Suchanek 1992). The seastar, *P. ochraceus* also commonly occurs from Alaska to Baja and is the primary predator on *M. californianus*. Whelks (*Nucella* sp., *Acanthina* sp., and *Ocenebra* sp.) are all common predators on small mussels and barnacles. The whelks lay eggs directly in the intertidal and have no planktonic larval phase. A variety of snails, chitons, and limpets form the main guild of grazers, mostly on microalgae, and urchins feed mainly on algal drift.

Table 1 List of identified genera assigned to the different functional and trophic groups considered

| Macrophytes | | Invertebrates | |
|-------------------------|------------------------|--------------------|-----------------|
| <i>Corticated algae</i> | <i>Ephemeral algae</i> | <i>Barnacles</i> | <i>Snails</i> |
| Bossiella | Bryopsis | Balanus | Amphissa |
| Calliarthron | Callithamnion | Chthamalus | Littorina |
| Chondracanthus | Ceramium | Pollicipes | Tegula |
| Codium | Chaetomorpha | Tetraclita | <i>Chitons</i> |
| Colpomenia | Cladophora | Semibalanus | Cryptochiton |
| Corallina | Ectocarpus | <i>Mussels</i> | Cyanoplax |
| Cryptopleura | Enteromorpha | Mytilus | Mopalia |
| Cystoseira | Nemalion | Septifer | Nuttalina |
| Egregia | Petalonia | <i>Limpets</i> | <i>Whelks</i> |
| Eisenia | Polysiphonia | Acmaea | Acanthina |
| Endocladia | Porphyra | Fissurella | Ceratostoma |
| Gastroclonium | Scytosiphon | Lottia | Kelletia |
| Gelidium | Ulothrix | Macclintoclia | Nucella |
| Gracilaria | Ulva | Notoacmaea | Ocenebra |
| Halidrys | <i>Crustose algae</i> | Tectura | <i>Seastars</i> |
| Hesperophycus | Cylindrocarpus | <i>Urchins</i> | Leptasterias |
| Hymenena | Pseudolithoderma | Strongylocentrotus | Pisaster |
| Laminaria | Hildenbrandia | | |
| Leathesia | Ralfsia | | |
| Lithothrix | Petrocelis | | |
| Mastocarpus | Pseudolithophyllum | | |
| Mazzaella | | | |
| Osmundea | <i>Surfgrass</i> | | |
| Pelvetia | Phyllospadix | | |
| Plocamium | | | |
| Prionitis | | | |
| Rhodoglossum | | | |
| Rhodymenia | | | |
| Sargassum | | | |

Benthic community structure sessile species sampling

In the winter of 2000, we surveyed benthic community patterns using stratified point-intercept sampling to quantify percentage cover of sessile invertebrate and macrophyte species at the six SCI sites. A representative shore section 60 m long was designated as the site. A 60-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 20 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 every 10-cm point adjacent to the tape was scored sequentially. At sites where the topography was relatively flat, we sampled every 20 cm, and not every 10 cm since there was very little change from point to point at that scale. For each point, we sampled the taxa directly under the point, then additionally the two nearest taxa within approximately 5 cm of that point.

Benthic community structure mobile species sampling

Mobile invertebrate taxa (e.g., limpets, snails, whelks) were scored by direct counts within thirty 0.25-m² quadrats along ten of the vertical transects during the

benthic surveys. Quadrats were sampled along every other vertical transect (6-m intervals) over the 60-m length of the site. At each transect, the total length was noted and divided by 4. Quadrats were surveyed at 0.25, 0.5, and 0.75 transect length positions in order to capture representative abundances from species in the high, mid, and low zones. Because the seastar (*P. ochraceus*) is much larger than most other intertidal invertebrates, and primarily occurs in channels and crevices, we counted the number of seastars within a 2-m swath centered along each of 11 vertical transects at each of the sites as described above.

Recruitment sampling

Mussel recruitment rates were quantified using standardized plastic mesh collectors or Tuffys™, and barnacle recruitment rates were quantified using 10×10 cm² ceramic plates (Menge et al. 1994; Leonard et al. 1998; Broitman et al. 2001). Details regarding recruitment data collection can be found in (Connolly et al. 2001; Navarrete et al. 2002; Menge et al. 2003; Broitman et al. 2005). Five replicate collectors were fastened to the rock in the mid-intertidal zone of each site, where mussels and barnacles were most abundant, and replaced roughly every 2–3 months from 1997 to 2000. We identified recruits to genus for both mussels (*Mytilus* spp.) and barnacles (*Chthamalus* spp. and *B. glandula*) in the lab under a dissecting microscope. Mussel recruitment rates were standardized

to number of individuals per tuffy ($\sim 100 \text{ cm}^3$) per day and barnacle recruitment rates were standardized to number of individuals per plate (100 cm^2) per day.

Mussel growth rates

To quantify growth rates of mussels, we translocated small (2–4 cm), marked *M. californianus* into plots in the elevational-middle of the mussel zone at each site using methods described elsewhere (Menge et al. 1997a; Phillips 2005). We marked mussels by filing a small ($\sim 1 \text{ mm}$) triangular notch on the posterior shell edge of each mussel without disturbing the soft tissue (Seed 1976). Five groups of 50 mussels were placed ventral side down in their natural position and covered with plastic mesh cages ($\sim 500 \text{ cm}^2$) to allow them to reattach to the rock with their byssal threads. After 6–8 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 6–10 months and brought to the laboratory. The shell height of each mussel was measured to the nearest 0.1 mm with Vernier calipers from the umbo to the initial posterior margin (marked by the notch) and from the umbo to the final posterior margin of the shell. The distance from the umbo to the notch represents the length at deployment and the second measurement incorporates the shell-length increment during deployment. To compare growth among sites, we calculated size-specific growth rates as the change in shell length divided by total mussel length per day. We measured mussel growth at five sites around the island (Fraser, Trailer, Prisoners, Willows, and Valley) in 1997/1998 and 2000/2001. Here, we compare site-specific mussel growth rates (averaged across years) to the long-term mean SST.

Statistical analyses

In order to explore the associations between long-term mean SST, percent cover of major functional groups, algal C:N ratios, and filter-feeder growth and recruitment rates we utilized linear regression and Spearman's rank correlation analysis (Zar 1996). As it was not possible to establish a large number of sites around the island, the degrees of freedom of our analyses were severely constrained, and thus we restrict our interpretation of correlation largely to the direction of the trend rather than the absolute magnitude (Sokal and Rohlf 1981). To explore seasonal and spatial variation in seawater temperature, nutrient concentrations, chl-*a*, and algal tissue C:N ratios among sites, we used a nested ANOVA design with sites nested within regions (west–east) based on the predominant SST differences among sites.

Results

Relationships between chl-*a* and nutrient concentration and SST

The long-term mean of the 6-year time series of AV-HRR SST is characterized by a significant temperature difference across the shores of SCI (Fig. 3a). A persistent 1–2°C gradient in SST exists between the sites in the western and eastern ends of the island. Summertime SSTs were significantly higher by several degrees than those in winter, and temperatures at eastern sites were significantly higher by 1–2°C in winter and summer than those at western sites (Table 2). Seawater nutrient concentrations were significantly higher at western sites and higher in winter than in summer (Fig. 3b; Table 2). There was a significant inverse relationship between water temperature and nutrient concentration ($R^2=0.38$, $p<0.0001$). There was no significant seasonal variability and no significant regional difference in chl-*a* concentration among the sites, although there was significant variability among sites (Fig. 3c; Table 2). We found a weak inverse relationship between water temperature and chl-*a* ($R^2=0.15$, $p<0.0002$).

Patterns of community structure

Patterns of space occupancy and mobile species densities showed differences in the community composition between the three western sites (Forney, Fraser, and Trailer) and the three eastern sites (Prisoners, Willows, and Valley; Fig. 4). In terms of sessile species abundance, macrophytes dominated space at the western sites, primarily corticated and ephemeral algae and surfgrass. Crustose algae tended to be slightly more common at the eastern sites (Fig. 4a–d). Filter-feeders (barnacles and mussels) were most abundant at eastern sites (Fig. 4e, f). Large predators (seastars) were far more abundant at eastern sites and nearly absent at western sites (Fig. 4g). Small predators (whelks) were common at only two of the eastern sites (Prisoners and Willows) and one of the western sites (Fraser; Fig. 4h). Herbivores (limpets, urchins, and chitons) were all much more abundant at eastern sites than at western sites (Fig. 4i–k). Snails were common at only two eastern sites (Willows and Valley) and one western site (Trailer; Fig. 4l).

Relationships between community patterns and SST

The dominant sessile functional groups were tightly coupled to the gradient in SST. The abundance of invertebrate filter-feeders and macroalgae were both strongly correlated with water temperature. Macrophytes were more abundant in the cold-water western

Fig. 3 Seasonal mean values for **a** long-term mean AVHRR SST, **b** seawater nutrient concentrations [nitrate + nitrite (μM)], and **c** chl-*a* ($\mu\text{g l}^{-1}$) at six study sites around SCI. *Black bars* represent data from summer (April–September) and *gray bars* represent winter (October–March)

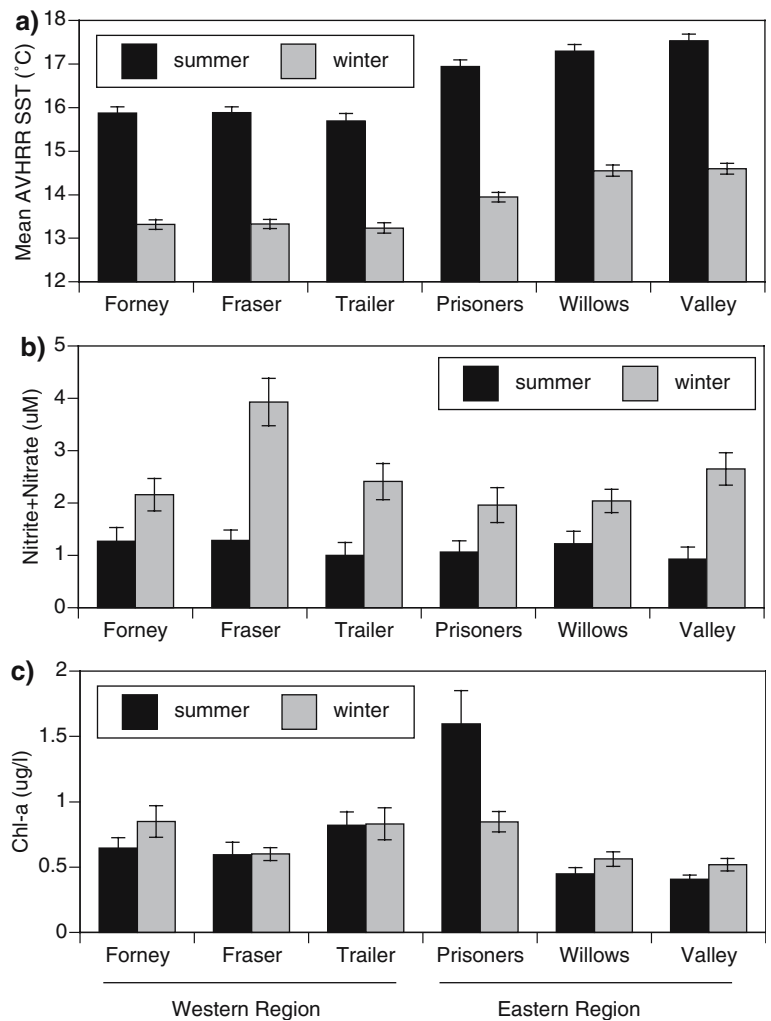


Table 2 Results of nested ANOVA based on differences among seasons (summer, winter), regions (west, east) and sites nested within regions [Forney, Fraser, Trailer (west); Prisoners, Willows, Valley (east)] for long-term mean AVHRR SST; seawater nutrient concentrations [nitrate + nitrite (μM)]; and chl-*a* ($\mu\text{g l}^{-1}$)

| Source | <i>df</i> | SS | MS | <i>F</i> | <i>P</i> |
|------------------------------|-----------|-----------|-----------|-----------|----------|
| AVHRR SST temperature | | | | | |
| Model | 7 | 5,089.509 | 727.073 | 211.621 | < 0.0001 |
| Error | 2,201 | 7,562.044 | 3.436 | | |
| <i>Effect tests</i> | | | | | |
| Season | 1 | 4,018.665 | 4,018.665 | 1,169.668 | < 0.0001 |
| Region | 1 | 854.56 | 854.560 | 248.727 | < 0.0001 |
| Season × region | 1 | 18.435 | 18.435 | 5.366 | 0.0210 |
| Site (region) | 4 | 90.488 | 22.622 | 6.584 | < 0.0001 |
| Seawater nutrients | | | | | |
| Model | 7 | 207.717 | 29.674 | 11.199 | < 0.0001 |
| Error | 299 | 792.265 | 2.650 | | |
| <i>Effect tests</i> | | | | | |
| Season | 1 | 132.23 | 132.230 | 49.903 | < 0.0001 |
| Region | 1 | 12.373 | 12.373 | 4.670 | 0.0310 |
| Season × region | 1 | 5.377 | 5.377 | 2.029 | 0.1550 |
| Site (region) | 4 | 51.189 | 12.797 | 4.830 | 0.0010 |
| Chl-<i>a</i> | | | | | |
| Model | 7 | 23.331 | 3.333 | 7.660 | < 0.0001 |
| Error | 508 | 221.045 | 0.435 | | |
| <i>Effect tests</i> | | | | | |
| Season | 1 | 0.249 | 0.249 | 0.572 | 0.4490 |
| Region | 1 | 0.001 | 0.001 | 0.002 | 0.9510 |
| Season × region | 1 | 1.525 | 1.525 | 3.505 | 0.0610 |
| Site (region) | 4 | 21.377 | 5.344 | 12.282 | < 0.0001 |

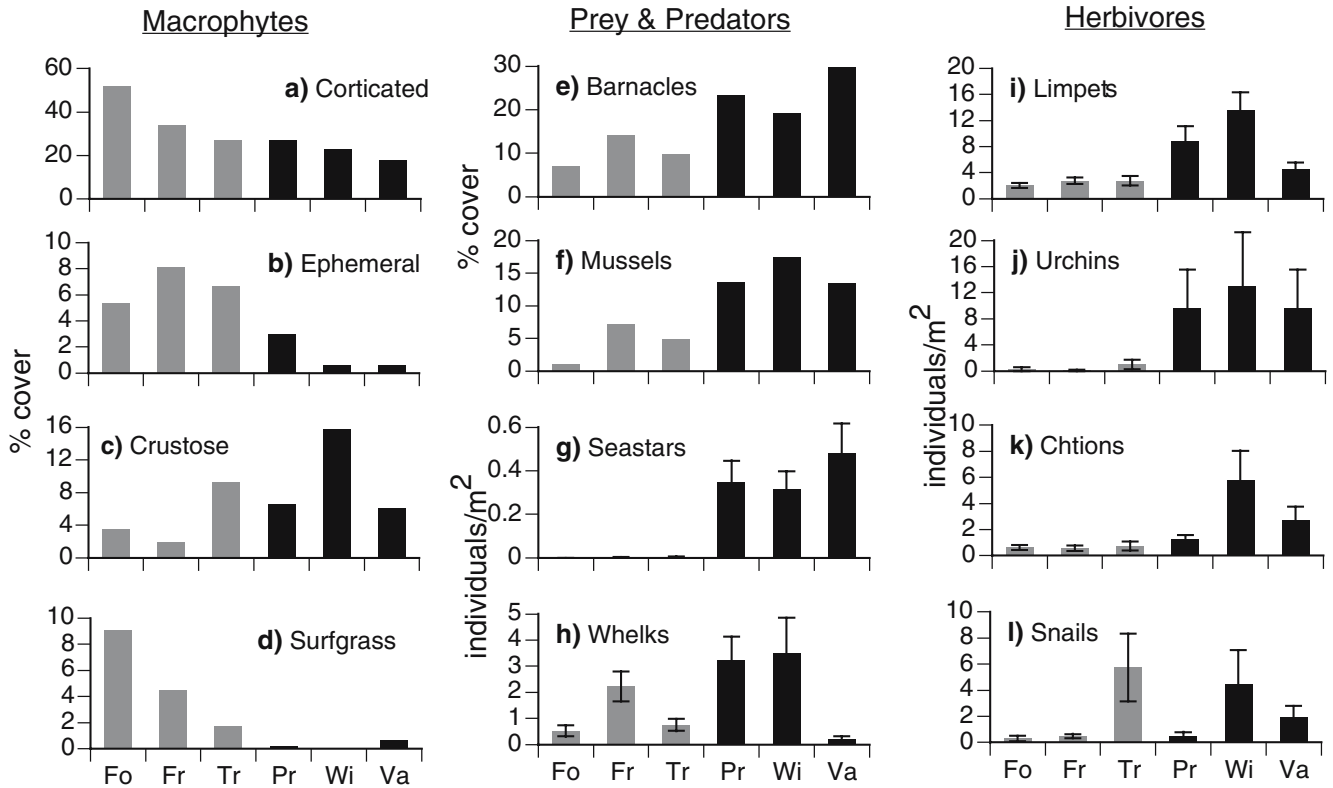


Fig. 4 Patterns of space occupancy and densities of mobile taxa for the dominant functional groups. Sites are arranged in order of increasing long-term SST from coldest to warmest. Bars for three western sites shaded gray; bars for three eastern sites black; Fo Forney, Fr Fraser, Tr Trailer, Pr Prisoners, Wi Willows, Va Valley. **a-d** Percent cover of macrophytes (corticated, ephemeral and crustose algae, and surfgrass); **e-f** percent cover of filter-

feeders [barnacles (*Chthamalus* spp. and *Balanus glandula*) and mussels (*Mytilus* spp.)]; **g** *Pisaster ochraceus* mean density (± 1 SE) per square meter based on seastar swath counts; **h** mean density (± 1 SE) of whelks per square meter (*Nucella* sp., *Acanthina* sp., and *Ocenebra* sp.); **i-l** mean densities (± 1 SE) of herbivores per square meter (limpets, urchins, chitons, snails)

region of SCI and macrophyte abundance was significantly inversely related to SST ($R^2=0.68$, $p<0.05$). Sessile filter-feeding invertebrates were more abundant on the warm, east side of the island and were significantly positively associated with SST ($R^2=0.79$, $p<0.05$; Fig. 5). Associations with long-term mean SST were observed in individual functional groups. Barnacles and mussels were positively correlated with SST, and macrophyte functional groups (with the exception of crustose algae) were strongly associated with lower water temperatures (Table 3). Herbivores and seastar predators were all positively correlated with SST, and whelk abundances were uncorrelated to SST (Table 3).

Recruitment patterns

Recruitment rates of barnacles and mussels were positively correlated with SST (Fig. 6). In general, warm-water sites with high invertebrate cover exhibited higher rates of recruitment. SST was significantly and positively correlated with total barnacle recruitment rate ($R^2=0.76$, $p<0.023$; Fig. 6). Total barnacle recruitment includes both *Chthamalus* spp. and *B. glandula*.

Recruitment rates for both species were positively correlated with SST [*Chthamalus* spp. ($R^2=0.62$, $p<0.062$) and *Balanus* ($R^2=0.90$, $p<0.004$)]. Mussel recruitment

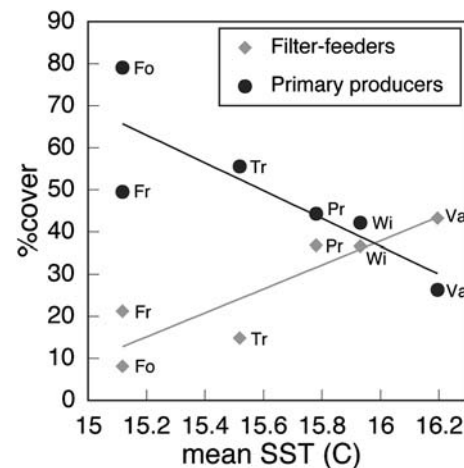


Fig. 5 Mean SST vs. percent cover of dominant space occupiers. Invertebrate filter-feeders [mussels and barnacles (gray diamonds)] are positively related to SST ($R^2=0.79$, $p<0.05$). Macrophytes [macroalgae and surfgrass (black circles)] display the opposite response ($R^2=0.68$, $p<0.05$). Site codes (as in Fig. 4) listed near each symbol

Table 3 Correlations (Spearman's rank correlation, r_s) between long-term mean SST and percent cover of different functional groups

| Group | r_s | P |
|-----------------------|---------|--------|
| <i>Filter-feeders</i> | | |
| Mussels | 0.7247 | 0.1032 |
| Barnacles | 0.8407 | 0.0361 |
| <i>Macrophytes</i> | | |
| Corticated algae | -0.9856 | 0.0003 |
| Crustose algae | 0.5798 | 0.2278 |
| Ephemeral algae | -0.8986 | 0.0149 |
| Surfgrass | -0.8721 | 0.0439 |
| <i>Herbivores</i> | | |
| Chitons | 0.9276 | 0.0077 |
| Urchins | 0.8117 | 0.0499 |
| Limpets | 0.7794 | 0.0576 |
| Snails | 0.4348 | 0.3889 |
| <i>Predators</i> | | |
| Seastars | 0.9959 | 0.0029 |
| Whelks | 0.0290 | 0.9565 |

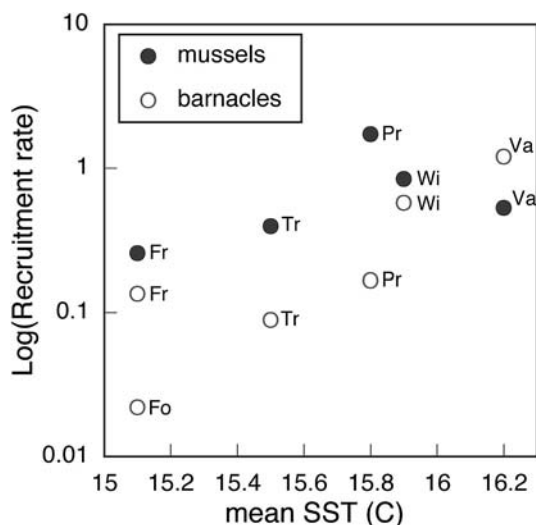


Fig. 6 Mean SST vs. log [mean recruitment rate (average number of recruits per collector per day)]. Barnacles (*Chthamalus* spp. and *Balanus glandula*) are open circles ($R^2=0.76$, $p<0.023$) and mussels (*Mytilus* spp.) are black circles ($R^2=0.31$, $p<0.320$). Site codes (as in Fig. 4) listed near each symbol

rates (*Mytilus* spp.) were positively, although not significantly correlated with SST ($R^2=0.31$, $p<0.320$). Recruitment rates of barnacles were positively correlated with adult abundance ($R^2=0.78$, $p<0.020$) and mussel recruitment rates were also positively correlated, although not significantly ($R^2=0.49$, $p<0.189$), with adult abundance (Fig. 7).

Invertebrate and algal performance

Spatial patterns in mussel growth and algal tissue C:N were correlated with the difference in mean annual SST. The ratio of C:N in the kelp, *E. menziesii*, was significantly

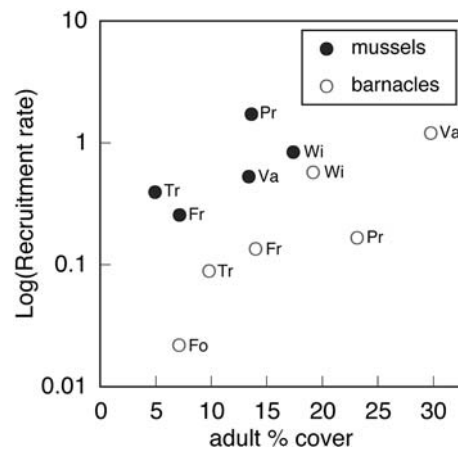


Fig. 7 Mean adult percent cover vs. log [mean recruitment rate (average number of recruits per collector per day)]. Barnacles (*Chthamalus* spp. and *Balanus glandula*) are open circles ($R^2=0.78$, $p<0.020$) and mussels (*Mytilus* spp.) are black circles ($R^2=0.49$, $p<0.189$). Site codes (as in Fig. 4) listed near each symbol

reduced at cold-water sites and in winter when seawater nutrient concentrations were highest (Fig. 8; Table 4). *E. menziesii* C:N ratios were positively associated with SST ($R^2=0.54$, $p<0.092$). Mussel growth rates were also significantly elevated at warm-water sites (Fig. 8; Table 5) and positively associated, although not significantly, with SST ($R^2=0.49$, $p<0.186$).

Discussion

Filter-feeding invertebrates and macrophytes are the two major groups of dominant space occupiers in rocky intertidal systems around the world, and with the recent focus on large-scale processes in ecology, many researchers have begun to address the question of what alters the balance between domination by filter-feeders and algae across shores. As Schiel (2004) points out, the relative importance of mechanisms (oceanographic forcing, competition, predation, facilitation, and differential physiological tolerances) underlying these large-scale spatial patterns have yet to be clearly defined in most large-scale studies. Our results represent the first quantitative description of intertidal community structure in relation to prevailing nearshore oceanographic regimes at the California Channel Islands. A sharp difference in mean annual SST occurs across SCI consistent with its location at the center of a major oceanographic transition region. Spatial patterns of abundance of the dominant sessile functional groups around SCI were highly correlated with SST. Macrophytes were most abundant at the cold sites in the western region of the island, where nutrients were also elevated relative to the eastern sites. Total filter-feeder abundance, mussel growth, and barnacle and mussel recruitment were positively correlated with SST and highest at the eastern sites, however there was no spatial pattern in chl-*a*

Fig. 8 Seasonal mean values for **a** *Egrecia menziesii* C:N ratios, and **b** *Mytilus californianus* size-specific growth rates (mm day⁻¹ × 10⁴) at six study sites around SCI. *Black bars* represent data from summer (April–September) and *gray bars* represent winter (October–March)

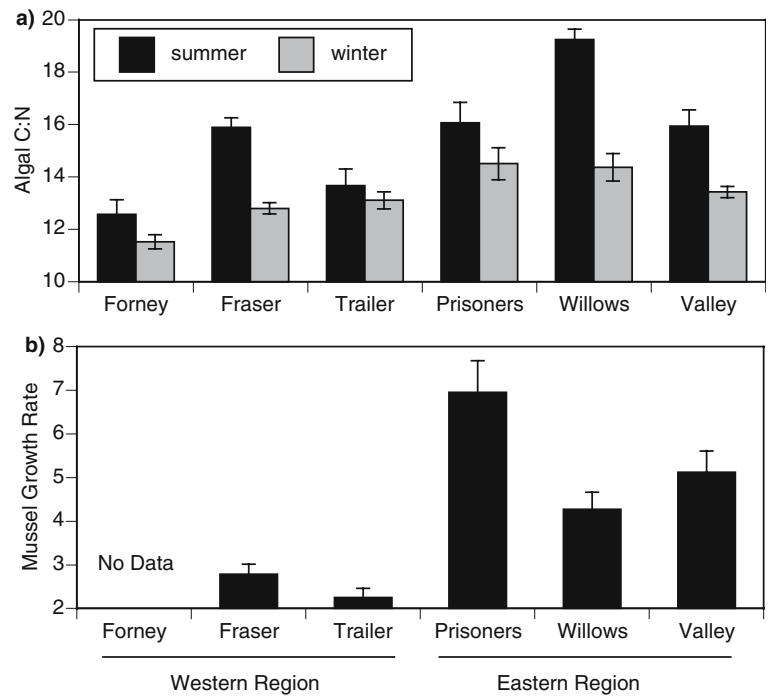


Table 4 *Egrecia menziesii*. Results of a nested ANOVA on tissue C:N ratios based on differences among seasons (summer, winter), regions (west, east) and sites nested within regions [Forney, Fraser, Trailer (west); Prisoners, Willows, Valley (east)]

| Source | df | SS | MS | F | P |
|---------------------|-----|---------|---------|--------|---------|
| Model | 7 | 322.311 | 46.044 | 11.673 | <0.0001 |
| Error | 123 | 485.194 | 3.945 | | |
| <i>Effect tests</i> | | | | | |
| Season | 1 | 147.209 | 147.209 | 37.318 | <0.0001 |
| Region | 1 | 125.821 | 125.821 | 31.896 | <0.0001 |
| Season × region | 1 | 9.966 | 9.966 | 2.526 | 0.1150 |
| Site (region) | 4 | 79.339 | 19.835 | 5.028 | 0.0009 |

Table 5 *Mytilus californianus*. Results of a nested ANOVA on size-specific mussel growth rates across SCI. Sites and regions as in Table 3

| Source | df | SS | MS | F | P |
|---------------------|-------|------------|-----------|---------|---------|
| Model | 4 | 4,181.542 | 1,045.386 | 98.513 | <0.0001 |
| Error | 1,315 | 13,954.364 | 10.612 | | |
| <i>Effect tests</i> | | | | | |
| Region | 1 | 2,608.107 | 2,608.107 | 245.777 | <0.0001 |
| Site (region) | 3 | 1,153.234 | 384.411 | 36.225 | <0.0001 |

concentration between the two major island regions. Although identification of the specific mechanisms driving these patterns is beyond the scope of this study, we discuss below the relative importance of some ecological and oceanographically based mechanisms contributing to variability in community structure.

Recent studies on the Oregon and central and northern California coast, propose a strong role of invertebrate recruitment rates in models of community

regulation (Connolly and Roughgarden 1998, 1999). The positive relationship between recruitment and adult abundance at the eastern warm-water SCI sites indicates that larval delivery may be an important structuring factor in these communities. Detailed analyses of spatial and temporal variability in recruitment of barnacles and mussels around SCI relative to oceanographic variability (Broitman et al. 2005) suggests that nearshore circulation is very important for larval delivery. Cold-water western sites experience temperature variability over short temporal scales associated with vertical mixing, while warm-water eastern sites experience longer temporal scale variability in temperature indicative of horizontal advection of surface waters. The increased recruitment of mussels and barnacles at warm-water sites may also reflect patterns of larval transport and delivery via wind-driven surface circulation (Garland et al. 2002; Noda 2004) associated with the Southern California Countercurrent (Dever et al. 1998; Winant et al. 2003). Although we have no information on recruitment patterns of herbivores and seastars around SCI, their abundances are also strongly correlated to SST. The abundance of whelks (the only invertebrate group in this study with non-planktonic larvae) at sites across SCI was not significantly correlated with SST. The consistently high correlations between SST and abundances of groups with planktonic larvae may reflect similar oceanographic forcing of larval delivery for many species at these warm-water sites.

The positive association between the abundance of filter-feeding invertebrates and SST may also result from increased growth/performance as well as enhanced larval recruitment. Numerous studies have shown positive relationships between filter-feeder growth and tempera-

ture (Dehnel 1956; Seed 1976; McDonald and Koehn 1988; Phillips 2005). The results of our mussel growth measurements suggest that warm-water conditions at SCI favor high mussel growth rates independent of chl-*a* concentrations in nearshore waters. The pattern of high mussel growth rates at warm-water sites and the lack of a relationship between mussel growth and chl-*a* concentration is similar to that at a range of sites around Point Conception (Phillips 2002, 2005). A similar pattern has been observed in Oregon, where barnacles tend to grow faster under warm-water conditions (Sanford and Menge 2001). The general lack of a relationship between chl-*a* concentration and sessile invertebrate growth, but the ubiquitous positive relationship with SST suggests that these intertidal invertebrates may be feeding on zooplankton or detritus associated with downwelling water masses (Shanks et al. 2003; Phillips 2005). Increased larval supply to southeastern sites is consistent with the patterns of invertebrate growth relative to temperature. It is possible that increased growth rates in warmer waters south of SCI may lead to higher larval production since reproductive output in mussels and barnacles scales with size.

Although spatial variation in recruitment and growth of competitively dominant invertebrates can strongly influence community patterns, factors influencing the dynamics of macroalgal populations tend to be underappreciated in models of community organization (Foster et al. 2003; Schiel 2004). Macroalgae are clearly the dominant space occupiers in many rocky intertidal communities along the US West coast (P. Raimondi and C.A. Blanchette, unpublished data) and factors influencing algal productivity may also strongly influence the structure of the entire community (Bustamante et al. 1995a; Wootton et al. 1996; Foster et al. 2003; Nielsen and Navarrete 2004). High relative macroalgal abundance at cold-water sites could result from reduced competition from invertebrate filter-feeders as an indirect effect of reduced invertebrate recruitment at cold-water sites. Additionally, the high abundance of herbivores at warm-water sites may control macrophyte abundance, particularly for corticated and ephemeral algae (Nielsen and Navarrete 2004). Crustose algae were the only algal group at SCI positively associated with both SST and herbivores. Several studies have documented positive interactions between herbivores and algal crusts, and grazing can either directly stimulate growth of crusts or indirectly benefit crusts by removing upright algal competitors (Lubchenco and Cubit 1980; Duggins and Dethier 1985; Steneck et al. 1991; Dethier 1994). Although methods to quantify recruitment rates of benthic invertebrates are reasonably well worked out, quantifying algal recruitment rates, particularly in intertidal systems, is difficult at best (Norton 1992; Bellgrove et al. 2004). Since many intertidal algal species have relatively limited dispersal capabilities (Santelices 1990; Kinlan and Gaines 2003) in comparison to invertebrates with planktonic larvae, we assume here that algal recruitment at a site scales in proportion to algal

abundance. Although the shape of this relationship is unknown and likely varies with algal growth rates and herbivory, our assumption is that factors influencing algal growth and productivity should generally reflect positively on algal recruitment at the local scale (Foster et al. 2003).

The inverse relationship between macrophyte abundance and temperature across SCI is likely to be directly affected by enhanced macrophyte growth in cold, nutrient-rich water. The strong relationship between temperature and nutrient availability is well-established (Jackson 1977; Wheeler 1980; Hanisak 1983; 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; Blanchette et al. 2002; Nielsen and Navarrete 2004). The nutrient status of seaweeds can be inferred from their C:N ratio (Anderson et al. 1999; Phillips and Hurd 2003) and based on the values reported here, *E. menziesii* showed a greater degree of nitrogen limitation at the warm-water eastern sites, and as expected, *E. menziesii* was most nitrogen limited in summer, consistent with patterns of nutrient availability. Although we only have this information for one species, these data support the general idea that algal productivity is enhanced at the cold-water western sites. The overall performance benefits of cold-water conditions for many macrophytes may account for their increased abundances at the west end of SCI. Reproduction is known to scale with size for most macrophytes, and increased algal growth is predicted to result in greater propagule supply, and hence high local abundance.

Conclusions

Characterizing local community patterns within a variable environmental framework is essential for interpreting results of studies conducted at single or few sites. Exploring linkages between community structure and physical forcing mechanisms through remote sensing holds the promise of predicting community patterns at locations which are either too remote or too numerous to directly instrument with oceanographic equipment and larval collectors. In examining associations among small-scale ecological patterns and large-scale oceanographic conditions we hope to provide a predictive framework in which local interspecific interactions and physical forcing mechanisms can be integrated to identify the main determinants of community structure across a variety of spatial scales. The overall community pattern observed here is similar to what is observed throughout the central and northern California coast, where spatial gradients in community structure largely follow physical forcing patterns (Connolly and Roughgarden 1998). These findings have important consequences for the conservation and management of marine resources. Marine

reserves are becoming an increasingly important tool for conservation, however, the design and ultimate effectiveness of reserves depends on understanding the nature of the benthic–pelagic linkages and connections among populations (Botsford et al. 2003; Gaines et al. 2003). A network of marine reserves has been recently created (April 2003) around the Channel Islands, California (Airame et al. 2003), including several small reserves at SCI. Although most intertidal species are un-harvested, understanding the linkages among oceanographic and community-level patterns for these relatively undisturbed communities on SCI will allow us to make predictions about how nearshore communities around the island may respond to the cessation of harvest pressure as reserves are established and enforced.

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