

## Fifteen degrees of separation: Latitudinal gradients of rocky intertidal biota along the California Current

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### *Abstract*

The region of the eastern North Pacific coastline dominated by the California Current was surveyed annually from 2001–2003 to examine (1) benthic macro-invertebrate and algal populations, (2) the magnitude and patterns of key environmental variables, and (3) how dynamic populations and communities of macroalgae and invertebrates respond to spatial differences in nearshore geomorphology, wave dynamics, and oceanography of the coastal shelf. We used a highly replicated spatially nested sampling design consisting of 144 shore segments (bedrock platforms longer than 50 m) with three replicate segments per site (~1 km), three sites per area (~10 km), and sixteen areas (>10 km) grouped into six domains (hundreds of kilometers). Results suggest that (1) low zone diversity was higher at northern latitudes when measured at segment, site, and area scales, but at domain scales there were more species at southern latitudes; (2) community structure showed high fidelity to geographic location with community similarity inversely related to separation distance, and the only regional scale biological discontinuity in community structure was centered near Pt. Conception; and (3) wave runup was the most significant physical parameter affecting overall community structure, however, tidal range, precipitation, air and water temperature, upwelling, salinity, and sand were significant mechanisms forcing differences in community structure within the region.

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Understanding the underlying causes of gradients of diversity has been a long-standing focus of the ecological community. The problem is complex and has been beset by controversy, yet great strides have been made (Huston 1995; Rosenzweig 1995; Hubbell 2001). A recent focus has been on the relative contributions of local factors, dispersal, and scale-dependent regional factors that influence regional species pools (Ricklefs 2004; Witman et al. 2004; Russell et al. 2006). The increased focus on large-scale dynamics, however, has exposed a major shortcoming in many of the datasets that have been used to evaluate diversity hypotheses: the level of detail and resolution is

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often coarse and does not enable the evaluation of ideas relating to local-scale processes and patterns of diversity. In contrast, local-scale datasets that do include high detail and resolution and understanding of interactions have historically had their own limitations, the major one being that they are largely useless for gaining insights into large-scale patterns of diversity and community structure. Thus, the generation of datasets that include high resolution on a local scale and occur across large spatial and, ideally, long temporal scales would be an important step forward in our attempts to understand geographic patterns of diversity and community structure (e.g., Witman et al. 2004; Russell et al. 2006).

This need for high-resolution, large-scale studies of community structure has become dramatically more urgent as evidence grows of the massive effects of humans on global ecosystems (e.g., Harley et al. 2006). Accurately predicting the consequences of climate change on marine biodiversity is a major unresolved issue in ecology and will remain elusive until we have better estimates of biodiversity and an understanding of the forces that affect large- and small-scale variability. For example, recent research in marine systems provides evidence that variations in marine benthic communities are strongly driven by changes in ocean temperature (Sanford 1999), larval recruitment (Gaines and Roughgarden 1985; Menge et al. 2003; Navarrete et al. 2005), nearshore wave dynamics (Denny 1988), and such bottom-up oceanic influences as nutrient concentration and phytoplankton productivity (Menge et al. 1997a; Menge et al. 1997b; Menge et al. 2003). All of these have been shown to vary with physical oceanographic processes (Gaines et al. 1985; Menge et al. 1997a; Connolly et al. 2001). But a rigorous assessment of the spatial scales of correlation between biota and key forcing mechanisms of atmospheric, oceanic, and benthic boundaries has not been attempted.

Many of our most pressing conservation issues are concerned with processes operating on scales of the landscape, but our conventional knowledge base is comparatively fine-scale (Dayton 1994). For example, climate change broaches issues of very large-scale importance, but our best empirical understanding of the mechanisms of ecological response to climate change may be at the level of the individual organism (e.g., Sanford 1999; Harley et al. 2006). Historically, researchers have examined local processes such as competition, predation, or disturbance at one or a few sites (e.g., Connell 1961; Paine 1966). The linkages between physical processes and biological responses have been studied in the rocky intertidal (e.g., Denny 1988; Menge et al. 1997a; Menge et al. 2003) and in the nearshore subtidal (e.g., Smith and Witman 1999; Duggins et al. 2001). Species interactions, disturbance mechanisms, and productivity can be related to environmental heterogeneity on small (m) to regional (km) scales in general (Menge and Sutherland 1987; Menge and Olson 1990; reviewed by Huston 1999) and specifically in the marine realm (e.g., Paine 1966; Dayton 1971; Menge 1976). Studies have focused on various physical forcings directly influencing marine plants and animals by controlling habitat structure and exerting (or ameliorating) direct stresses. Water quality and flow conditions of the

nearshore, such as temperature, salinity, nutrient concentration, and current velocities, affect the feeding and growth rates for a variety of suspension-feeding organisms (Lesser et al. 1994; Sanford et al. 1994). Wind, wave, and tide-generated currents affect nearshore populations directly by physical disturbance (Denny et al. 2003) or indirectly by alongshore propagule transport (Gaylord et al. 2002; Kinlan and Gaines 2003). Other physical attributes such as substrate composition (Raimondi 1988; Snelgrove and Butman 1994) and desiccation (Menge 1978; Haring et al. 2002) have been linked to the mortality, abundance, and diversity of sessile and mobile populations. But if we are interested in large-scale patterns or long-term change, we cannot necessarily extrapolate from the numerous studies done locally (Underwood and Petraitis 1993). Consequently, in recent years it has become clear that our understanding of benthic marine communities is more limited than we had hoped.

In this article, we present the results of community surveys of rocky intertidal community structure using a nested sampling scheme across a latitudinal range of 15°. We believe that the spatial and temporal scope of the sampling combined with the detail level of the surveys is unprecedented. Our surveys provide a necessary resource for the rigorous assessment of the actual latitudinal patterns of rocky intertidal community structure, patterns which previously were only qualitatively and unevenly known. Our overall goal was to provide a carefully designed and executed assessment of patterns of community structure, determine how these vary across a range of spatial scales, and analyze their relationship to physical conditions and processes at a system-appropriate scale, that of the California Current Large Marine Ecosystem. Our approach was to combine intensive small-scale sampling with a high degree of spatial replication to characterize rocky shore areas along the West Coast of North America from 33°N to 48°N. We used this database to evaluate how community structure (abundance, distribution, diversity) varied across local to regional to coastal scales. We address the following questions: (1) What are the latitudinal patterns of diversity? (2) What are the significant spatial scales of variation for population abundances? (3) What are the geographical patterns of community structure? (4) Are there key taxa that underlie the emergent community patterns? (5) What are the patterns of key environmental variables likely to influence populations and community structure? and (6) Can the relative effects of environmental variables on patterns of community structure be ascertained?

## Materials and methods

*Site selection*—We developed a nested sampling design to quantitatively assess patterns of benthic nearshore populations and communities at spatial scales ranging from meters to thousands of kilometers within the California Current region (Table 1). Our multisite field surveys were designed to provide an unprecedented look at the large-scale patterns of population and community variability and of their associations with corresponding

Table 1. The biological and physical spatial units for this study.

Biological		
Quadrat	0.25 m <sup>2</sup>	A macrobiota sample unit consisting of a 0.25 m <sup>2</sup> area.
Transect	50 m	A macrobiota sample consisting of 10 quadrats positioned at randomly spaced intervals along a 50-m horizontal line within each zone in a shore segment ( <i>see</i> Zone below).
Physical		
Zone		The low, mid, and high zones within the intertidal shoreline.
Low	MLLW	Mean lower low water datum.
Mid	MSL	Mean sea level datum.
High	MHHW	Mean higher high water datum.
Segment	50–100 m	A section of shoreline with all three zones that is physically uniform for a horizontal distance greater than 50 m.
Site	~1 km	Three replicate shore segments within a distance of 1 km.
Area	10 s km	Three sites within a distance of 15 km.
Domain	100 s km	Two or more areas within potential biogeographic boundaries.
Region	1,000 s km	The portion of the eastern North Pacific coast affected by the California Current and containing all smaller spatial units.

variation in the physical environment. The study region spans two major biogeographic boundaries in the North Pacific: Pt. Conception and Cape Mendocino (Morgan et al. 2005). Other potential boundaries of ecological importance were also considered, including Pt. Reyes, Cape Blanco, the Columbia River, and Strait of Juan de Fuca. At the largest scale, we divided the coast into six domains to capture both major and minor biogeographic boundaries. At the smallest scale, our design relied on locating rocky shore segments that were physically similar (Fig. 1). Segment selection was initially based on a region-wide assessment using 1 : 63,360 scale, low-altitude vertical aerial color photography. Stereo photointerpretation was used to identify all possible low-angle platforms (relatively flat bedrock outcrops) longer than 50 m. Final segment selection was based on field visits to quantify the physical features, including topographic complexity, and wave energy in addition to access and safety. Topographic complexity included slope angle, surface roughness, and aspect of each zone. On each rocky segment selected for sampling, the slope angle of each zone was measured with a digital inclinometer. The aspect was determined with a compass, and the roughness was estimated in the field using the difference between a taut 50-m tape and the added distance when the tape was allowed to conform to the surface texture. We made every attempt to locate three segments within a distance of 1 km to provide spatial replicates, but to accommodate this criterion, the degree of physical similarity was occasionally compromised by the high topographic variability at the 1-km scale. No explicit dissimilarity cutoff values were defined a priori, but the quantified physical characteristics of each segment enabled statistical comparisons. Similarly, we attempted to locate three sites within a 15-km area, but exceptions occurred at Tillamook (17 km) and Trinidad (164 km), where the favorable spacing of three suitable segments within a 1-km site and combining three sites within a 15-km area either did not exist or the sites were inaccessible. Distances among areas varied considerably as this was dictated by

regional geology and the locations of suitably large bedrock outcrops (Table 2). The resulting levels of nesting were segments within sites within areas, for a balanced 144 × 48 × 16 design. There were six domains of unequal size and containing different numbers of areas.

*Biological characterization*—Three vertical zones in each of the 144 segments were sampled annually from 2001 to 2003. The zones were identified by surveyed elevations based on the local tidal datum to ensure that samples were collected at elevations with the same mean annual submersion times. This design potentially allows for detection of oceanic versus atmospheric effects over small and large scales, because the marine signal is presumably stronger at lower elevations than at higher intertidal levels, which are subject to longer atmospheric exposure times (Helmuth et al. 2002). The low zone was sampled at mean lower low water (MLLW), which corresponds to an elevation of 0 m everywhere along the eastern North Pacific coast and where organisms are submerged approximately 90% of the time. The mid zone was sampled at mean sea level (MSL: 50% submergence time), and the high zone at mean higher high water (MHHW: 10% submergence time). These submersion times do not take into account the effect of wave runup. The elevation of MSL and MHHW changes relative to the distance and direction of the nearest amphidromic node. For each sampled segment, we determined the local MSL and MHHW elevations from tide tables and used a surveying level and stadia rod to locate the appropriate transect elevation for each zone relative to the predicted tide at the time of the measurement (National Oceanic and Atmospheric Administration, <http://co-ops.nos.noaa.gov>). These measurements were subsequently compared to the actual tide and were typically within ±0.25 m of the target elevation.

The low zone of any segment could only be sampled during extreme low tides, which, along the eastern North Pacific, occur for approximately six days per fortnightly tidal cycle, except in March and September when there are

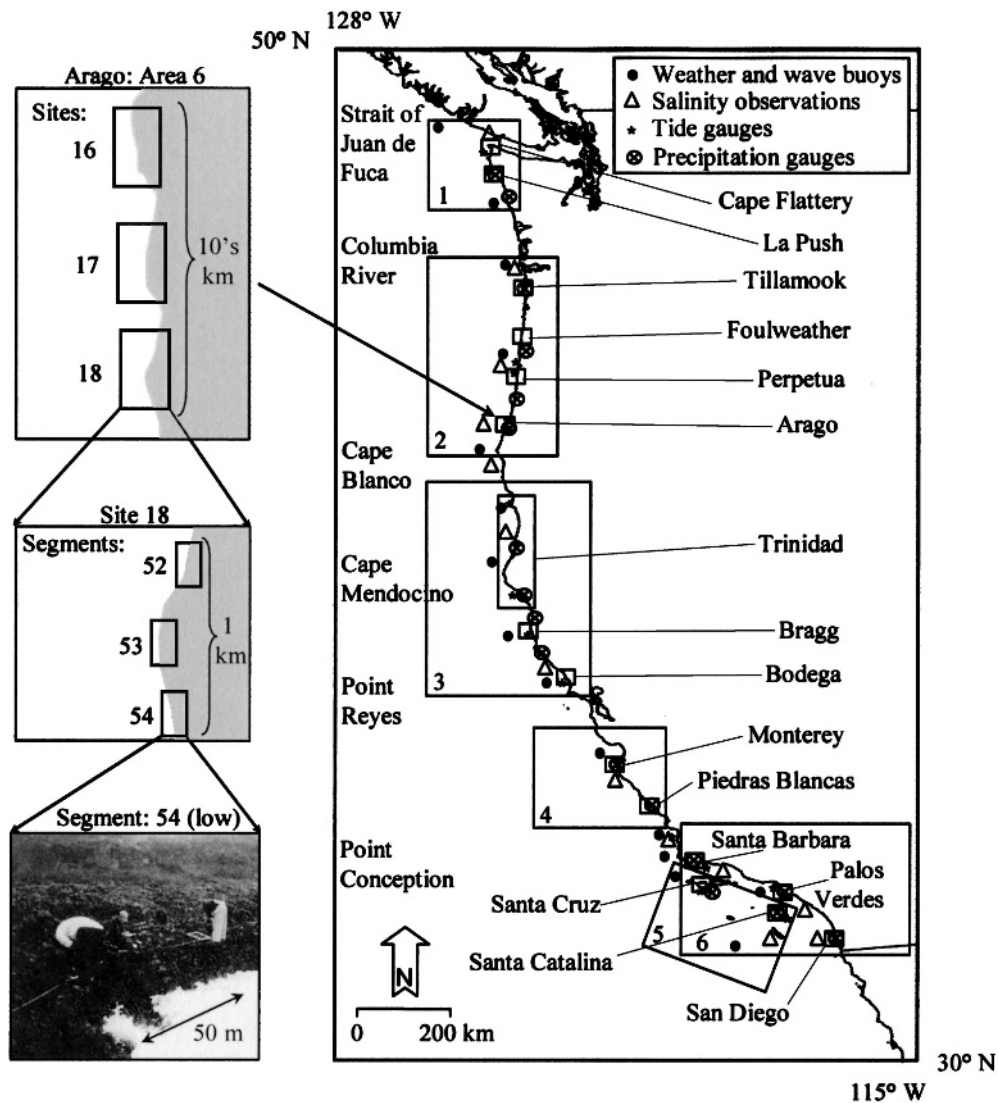


Fig. 1. Locations of project domains and areas are outlined. Areas are labeled and domains are numbered. The domains, areas, and sites are listed in Table 2. Insets show an example of the nested design for Area 6 at Cape Arago with three sites (16–18), and three segments (52–54) in site 18. Three elevations were sampled within each segment. Horizontal transects were positioned at mean lower low water, mean sea level, and mean higher high water. Locations of tide gauges are shown as stars, salinity observation stations are shown as triangles, National Oceanic and Atmospheric Administration weather and wave buoys are shown as dots, precipitation stations are shown as circled crosses, and all locations are listed in Table 3. Some symbols have been offset for clarity.

no extreme low tides. Our six-person team could sample one site per day (three replicate segments), and thus six sites (two areas) per fortnightly tide. The exposed rocky shores along the northern coast of Washington and Oregon are generally not safe to sample until late spring because of extreme fall and winter wave conditions. Therefore, we sampled in Southern California during the winter (November–February), Central and Northern California in the spring (April–May), and Oregon and Washington in the summer (June–August). This sampling schedule, driven entirely by logistical requirements, potentially introduces a temporal bias in the data since some biota might be expected to show significant variation attributable to seasonal variations in recruitment, light levels, nutrient

delivery, and disturbance from storms. To evaluate the effect of this potential bias we conducted seasonal sampling at two areas in Oregon from 2003 to 2004.

Mean species abundance was quantified using the transect-quadrat method (Lubchenco and Menge 1978), in which percent cover of sessile taxa, sand, and bare rock were estimated, and the density of mobile macrofauna were counted in a (0.5 × 0.5 m) quadrat placed at 10 randomly spaced intervals along a horizontal 50-m transect tape. Species were identified in the field using Smith and Carlson (1989), Morris et al. (1980), and Kozloff (1996) as references for invertebrates and Abbott and Hollenberg (1976), Gabrielson et al. (2000), and Hansen (1997) as references for macroalgae. This project focused on high

Table 2. Spatially explicit locations for each level of the nested sampling design. Locations are listed from north to south with cumulative distances. Rock type are listed by area. Not shown are replicate segments sampled at each site.

Region	No.	Domain	Area (with major rock type)	No.	Site	Distance (km)	Position				
							Lat.	Long.			
California Current	1	Washington (WA)	Strait of Juan de Fuca to Columbia River Mouth	1	Cape Flattery	0	48.39	-124.66			
				2	Waatch Point	6	48.34	-124.69			
				3	Makah Reef	8	48.32	-124.67			
				4	Chilean Memorial	50	47.94	-124.66			
				5	Teahwhit Head	57	47.87	-124.60			
				6	Giants Graveyard	59	47.87	-124.57			
	2	Oregon (OR)	Columbia River Mouth to Cape Blanco	7	Ecola Point	280	45.92	-123.98			
				8	Cape Falcon	296	45.77	-123.98			
				9	Smugglers Cove	297	45.76	-123.97			
				10	Boiler Bay	399	44.83	-124.06			
				11	Depoe Bay	401	44.81	-124.07			
				12	Otter Crest	408	44.75	-124.07			
				13	Strawberry Hill	463	44.25	-124.11			
				14	Stonefield Beach	466	44.22	-124.11			
				15	Gull Haven	468	44.20	-124.12			
				16	Squaw Island	563	43.33	-124.38			
				17	North Cove	565	43.31	-124.40			
				18	Arago Proper	566	43.31	-124.40			
				3	Northern (NC) California	Cape Blanco to Pt. Reyes	19	Trinidad Head	816	41.07	-124.16
							20	Point Delgada	932	40.03	-124.08
							21	Kibesillah Hill	980	39.60	-123.79
							22	Todd Point	1,001	39.42	-123.82
							23	Point Cabrillo Lighthouse	1,009	39.35	-123.83
							24	Van Damme State Park	1,015	39.29	-123.79
	25	Duncans Landing	1,120				38.39	-123.09			
	26	Mussel Point	1,128				38.32	-123.08			
	27	Horseshoe Cove	1,129				38.32	-123.07			
	4	Central (CC) California	Pt. Reyes to Pt. Conception				28	Point Lobos	1,340	36.52	-121.96
							29	Malpaso Creek	1,344	36.48	-121.94
							30	Soberanes Point	1,348	36.45	-121.93
				31	Piedras Blancas Point	1,444	35.66	-121.29			
				32	San Simeon Point	1,448	35.63	-121.20			
				33	Pico Creek	1,451	35.62	-121.15			
	5	Channel (CI) Islands	Pt. Conception to Tiajuana River	35	Frasier Point	1,641	34.06	-120.00			
				34	Blue Gum	1,642	34.05	-120.00			
				36	University Trailer	1,643	34.04	-120.00			
				37	Howlands Landing	1,738	33.46	-118.52			
				38	Bird Rock	1,741	33.45	-118.49			
				39	Blue Cavern Point	1,742	33.45	-118.48			
	6	Southern (SC) California (Mainland)	Pt. Conception to Tiajuana River	40	North Alegria	1,592	34.47	-120.28			
				41	South Alegria	1,592	34.47	-120.27			
				42	Arroyo Hondo	1,596	34.46	-120.07			
				43	Resort Point	1,709	33.76	-118.42			
				44	Whites Point	1,718	33.71	-118.26			
				45	Point Fermin	1,718	33.71	-118.29			
				46	LaJolla	1,838	32.84	-117.28			
				47	False Point	1,840	32.82	-117.28			
	48	Sunset Cliffs	1,851	32.72	-117.26						

spatial replication of samples within an area, and to some extent, this constrained our ability to identify every organism to the species level. However, taxonomic identification at the genus, and even family or complex, level can be sufficient for distinguishing natural spatial patterns (Dethier and Schoch 2006).

Our samples (transects) consisted of the mean values from 10 sample units (quadrats). A pilot study in 2000 showed that 10 sample units accounted for 95% of the diversity (measured as taxon richness) per sample with approximately 80% of the taxa accounted for by the first six sample units. Therefore, additional sample units would not appreciably increase the estimates of segment diversity. Similarly, the pilot survey showed that the first site (of three sites per area) contributed a mean of 81% to the area taxon richness, the second site accounted for an additional 12%, and the third site contributed the remaining 7%. Provided that replicate segments are carefully matched for physical similarity, this pilot determined that adding additional sites to an area would not appreciably increase area-scale taxon richness.

*Environmental characterization*—Atmosphere and ocean: At the domain scale, the monthly upwelling index from 2001–2003 was obtained from the Pacific Fisheries Environmental Laboratories (National Marine Fisheries Service, <http://www.pfeg.noaa.gov>). For each area, monthly water temperatures, wind velocity, and direction from 2001–2003 were obtained from buoys operated by the National Data Buoy Center (National Oceanic and Atmospheric Administration), and salinities were acquired from archived shore station data at Scripps (Scripps Institution of Oceanography). Because there is considerable variation in distance from these observation platforms to individual areas, data from closer platforms are potentially more relevant than from platforms farther away. Monthly air temperatures and precipitation from 2001–2003 were obtained for each area from coastal observation stations in or near each area (Western Regional Climate Center, <http://www.wrcc.dri.edu>). The tidal range and times of low tides were obtained from primary or secondary tide gauge stations (National Oceanic and Atmospheric Administration).

*Waves*: Until recently, wave exposure comparisons among intertidal study sites were limited to categorical assessments, but recent work by Denny et al. (2003), Helmuth and Denny (2003), and Lindgarth and Gamfeldt (2005) have shown this to be inadequate. We calculated the offshore wave power for each area using

$$P = \left( \frac{1}{8} \rho g H_s^2 \right) \frac{gT}{4\pi} \quad (1)$$

where  $\rho$  is water density ( $1,020 \text{ kg m}^{-3}$ ),  $g$  is the acceleration caused by gravity ( $9.8 \text{ m s}^{-2}$ ),  $H_s$  is the significant wave height, and  $T$  is the wave period (Komar 1998). Values for  $H_s$  and  $T$  were obtained for 2001–2003 from the nearest weather buoy to each area (National Oceanic and Atmospheric Administration).

The Iribarren number  $\zeta_s$  can be used to compare the effect of wave dynamics as a function of local bathymetry

(Battjes 1974):

$$\zeta_s = \frac{S}{\sqrt{\left( \frac{H_s}{L_\infty} \right)}} \quad (2)$$

where  $S$  is the shore slope (e.g.,  $\tan \alpha$ ), and  $L_\infty$  is the deep water wave length in meters:

$$L_\infty = \frac{gT^2}{2\pi} \quad (3)$$

Dissipative or low-angle shorelines correspond to Iribarren numbers  $<0.4$ , and reflective or high angle shorelines yield values  $>2$ . Values in between generally represent shores subjected to the greatest wave forces.

Wave runup is a measure of the swash excursion across the intertidal zone. Runup directly affects intertidal organisms by providing water to elevations above the still-water level, thus continuing the supply of food or nutrients and preventing desiccation during low tides. This may affect the growth rates and abundance of many intertidal organisms (Menge et al. 1996). In areas of high runup many species can extend their vertical range, thus considerably raising the community above normal elevations (Kozloff 1996). We used mean runup  $R_m$  as a first order approximation for swash height and estimated it for impermeable substrates as

$$R_m = H_s C \zeta_s^{0.34} \quad (4)$$

(Holman 1986; Shih et al. 1994), where  $C$  is a constant. Holman (1986) found that for combinations of runup and the rise in sea level caused by radiation stress (the build-up of water along the coast from incoming waves), the  $C$  coefficient equals 0.90 across a smooth surface. Based on our estimates of shore segment roughness, we used 0.60, the value for  $C$  empirically found by Van der Meer and Stam (1992), to best account for turbulence across a rough impermeable surface. The theory behind these methods is explained in Komar (1998), and an application is fully described in Schoch and Dethier (1996).

*Data analysis*—The Moran test for spatial autocorrelation was used to evaluate whether spatial modeling was appropriate for analyzing relationships between population abundances among neighboring segments for the zone in which the taxon was most abundant. The covariance structure used to analyze overall spatial autocorrelation among samples was calculated using the nearest neighbor algorithm and the Euclidean distance between all segment locations based on the geographical coordinates (Legendre 1993).

Spatial statistics were also used to test the hypothesis that diversity was related to latitude and longitude. We log-transformed the species abundances to improve normality, then modeled the data using a local regression fit (LOESS) at the segment, site, and area levels for each zone and for all zones, with longitude and latitude as predictors to examine the spatial trends in two directions (Sokal and Rohlf 1995). Spatial statistics were used so that geographic relationships

were retained (i.e., correlations were weighted relative to distances among neighbors) (Kaluzny and Vega 1997). Spatial statistical tests were performed using S-Plus (Mathsoft Inc.).

The frequency, or the proportion of segments in which each taxon was observed, was evaluated to determine which organisms showed a spatial preference or dominance with respect to tidal elevation and geography. Taxa similarity was analyzed to determine the number of organisms that were common among domains for each zone and for all zones combined.

The population abundance and environmental parameter data were also tested for significant spatial scales of variation among sites, areas, and domains with fully nested analysis of variance (ANOVA) (Sokal and Rohlf 1995). There were not enough degrees of freedom for four-level nesting because only three segments were sampled per site, therefore, segment and year covariates were not included in this analysis. Trinidad area samples were omitted from this analysis because these sites were spaced in excess of 15 km, thus potentially distorting the area scale analyses. Interannual differences were analyzed using one-way ANOVA with a Bonferroni adjustment for multiple comparisons. Considering that any signal of change among our annual samples may be strongly aliased by unquantified variability at seasonal and fortnightly frequencies, we tested for seasonal differences in the context of spatial variability at two Oregon areas using nested ANOVA balanced across segments, sites, and seasons. For environmental variables measured only at the area scale, one-way ANOVA was used to evaluate for differences among areas, and one-way ANOVA with a Bonferroni adjustment for multiple comparisons was used to evaluate differences among domains. Nested ANOVA and one-way ANOVA were performed using S-Plus (Mathsoft Inc.).

The multivariate analyses methods of Clarke and Warwick (1994) and PRIMER software (Clarke and Gorley 2001) were used to test for spatial patterns in community structure. The data matrix of taxon abundances at the segment level was square-root transformed, and a Bray-Curtis similarity matrix was calculated. We then used non-metric multidimensional scaling (MDS) to group communities. Two-way nested analyses of similarity (ANOSIM) (Clarke and Green 1988) were used to test for differences within and among sample groups (sites nested within areas). One-way ANOSIM was used to test for differences among domains.

Pearson's correlations were used to examine relationships between individual environmental variables and the two-dimensional structure represented by the ordination plots of community similarity, and joint plots were produced in PC-ORD to visualize these relationships (McCune et al. 2002). This technique was also used to examine the relationship between the ordination scores and the taxa that best explained the observed pattern of community similarity. Spearman's rank correlations were used to determine the best overall environmental predictor of the observed multidimensional pattern in community similarity using the BIOENV module in PRIMER (Clarke and Ainsworth 1993).

## Results

*Environmental characteristics*—The spatial patterns of key environmental variables along the eastern North Pacific coast between 33°N and 48°N from 2001–2003 are summarized in Figure 2. Table 3 lists the results for spatial regressions and hypothesis tests of significant variability at different spatial scales and among years. We observed significant variation in all area scale parameters at both area and domain scales, whereas of the factors measured at the segment scale, wave runup, and sand exhibited significant variation only at the area scale. Upwelling, tides, and salinity (measured only at the domain scale) exhibited significant variation among domains. There was no significant temporal variation, relative to the spatial differences, observed among years in any of the measured environmental variables.

At segment scales (tens of meters), slope (Fig. 2a) and roughness (Fig. 2b) were not different among sites, areas, or domains but were positively correlated with latitude and longitude. Wave runup was also correlated with latitude and longitude and was variable only at the area scale (Fig. 2c). Wave runup increased slightly from south to north with the highest wave runup in the vicinity of Cape Mendocino and the lowest in the Southern California Bight. Sand abundance (Fig. 2d) was different only at the area scale. The Northern and Central California areas also had the least sand observed per segment relative to the Washington, Oregon, and Southern California areas. The areas at Cape Perpetua and Santa Barbara had the most sand, particularly in 2001 and 2003.

At area scales (tens of kilometers), air temperature, water temperature, and wind velocity decreased from south to north (Fig. 2e–g). Wind direction south of latitude 40°N was more westerly, with the exception of the Southern California Bight where, like north of latitude 40°N, the winds were more southwesterly (Fig. 2h). Temperatures and wind parameters were different at the area and domain scales but not among years. Precipitation substantially increased (Fig. 2i) and wave period decreased (Fig. 2j) from south to north in all years. Wave height decreased slightly from south to north in 2001 but increased slightly in 2002 and 2003 (Fig. 2k). Wave power also decreased slightly from south to north in 2001 but not in 2002 or 2003 (Fig. 2l). Precipitation, wave period, wave height, and wave power were all different at the area and domain scales but not among years.

At domain scales (hundreds of kilometers), the tidal range increases from south to north with a mean range of about 1.5 m south of latitude 37°N to a mean range of about 2.3 m north of latitude 45°N (Fig. 2m). The tide range was different among domains. The mean salinity for the period of record decreased from about 33 south of latitude 40°N to about 31 at Cape Flattery, Washington, near 48°N (Fig. 2n). The difference in salinity among domains was not statistically significant. The lowest salinity values and greatest variability were from observation stations in the vicinity of the Columbia River plume. The mean upwelling index decreased from south to north (Fig. 2o), ranging from 100–150 m<sup>3</sup> s<sup>-1</sup> of offshore transport south of latitude 40°N to 20–40 m<sup>3</sup> s<sup>-1</sup> of net onshore

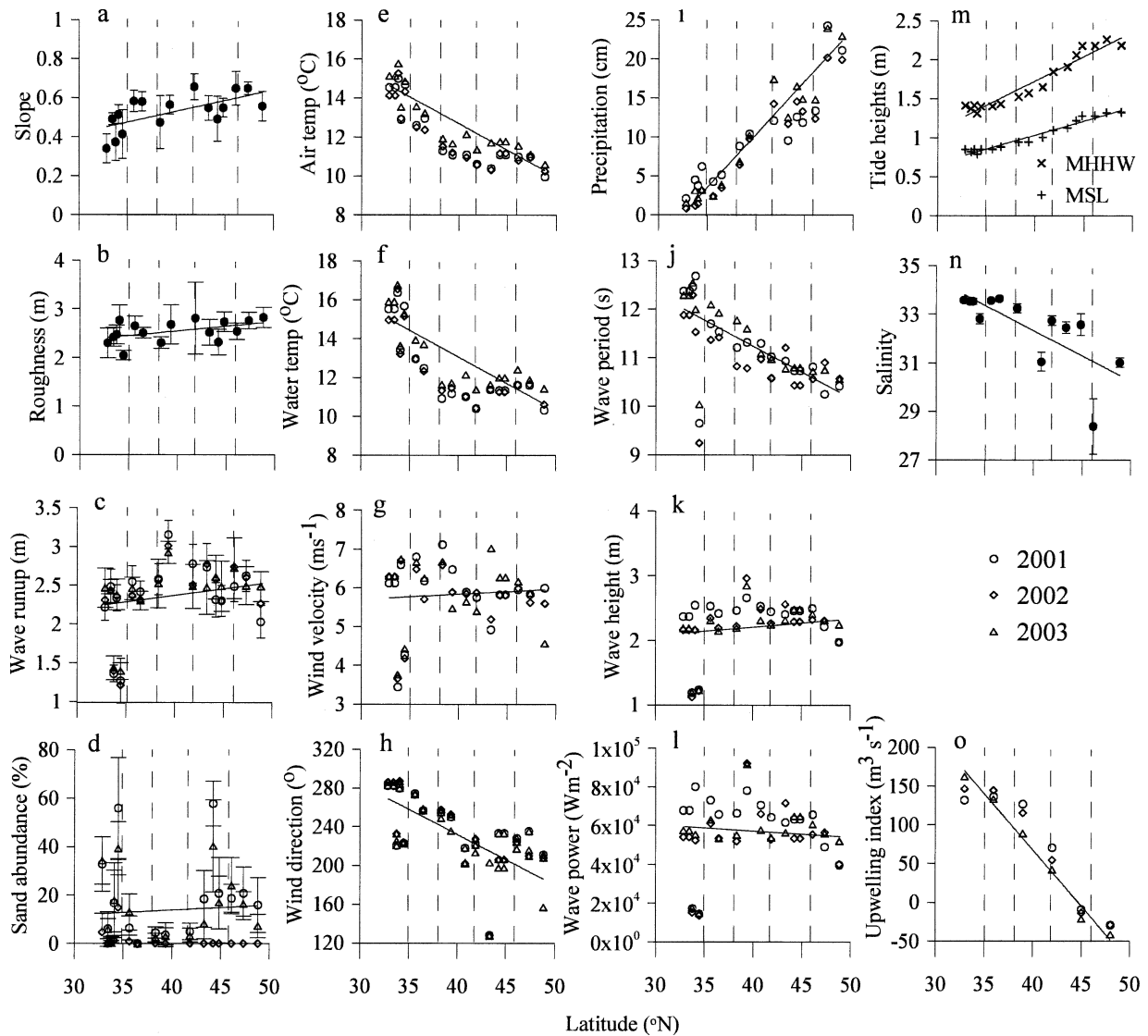


Fig. 2. Site scale mean (a) slope angle and (b) roughness are from field measurements in 2000 at each segment. (c) Mean annual wave runup was calculated for each segment from 2001–2003, and (d) mean sand abundances are percent cover from 2001–2003. Error bars in a–d are  $\pm$  one standard deviation of the site mean. Area scale (e) air temperature, (f) water temperature, (g) wind velocity, (h) wind direction, (i) precipitation, (j) wave period, and (k) wave height for 2001–2003 at 15 buoys and 16 shore stations. (l) The wave power was calculated for each area based on wave height and period. Domain scale (m) mean (19-yr) tidal ranges at 17 primary and secondary tide gauges. (n) Mean salinities for the period of record (*see* Table 3) from 13 coastal stations. (o) Upwelling index from 2001–2003 from six coastal stations. Observations are from stations listed in Table 3 and shown on Fig. 1. All averages are based on mean monthly values. Symbol legend is shown above panel o. Solid lines plotted on each graph represent the best linear fit. Regression results are listed in Table 3. Dashed vertical lines mark latitudes of domain boundaries.

transport north of latitude  $45^{\circ}\text{N}$ . The upwelling index was different among domains but not among years.

**Biological characteristics**—We observed higher species richness to the north rather than to the south but this pattern depended on the spatial sampling scale so that the diversity increase with latitude was evident at smaller scales (meters to kilometers) but shifted to a decrease with latitude at larger scales (tens to hundreds of kilometers). Our surveys from 2001–2003 cumulatively observed 268 taxa in 144 segments. The low zone had a total of 237 taxa, the mid zone

had 229, and the high zone had 163, with considerable overlap of taxa distributions among zones. Taxon richness among areas ranged from 176 at Cape Flattery, Washington, to 140 at Santa Barbara, California. We identified 161 taxa to the species level and 45 to the genus level (when species were indistinguishable), and 62 were grouped into complexes (when genera were indistinguishable). There were 126 primary producers, 139 invertebrates, and 3 vertebrates (fishes). For a comprehensive list of observed taxa and their distributions, *see* Web Appendix 1: [http://www.aslo.org/lo/toc/vol\\_51/issue\\_6/2564a1.pdf](http://www.aslo.org/lo/toc/vol_51/issue_6/2564a1.pdf).

Table 3. Results of spatial and temporal analyses for environmental variables of the eastern North Pacific coast. All data are from 2001–2003 with the exception of tidal range and salinity (as noted below). See text for more information. Significant differences are in bold.

Variables	ANOVA				Spatial regression		One-way ANOVA			
	Site		Area		Domain		Region		Year	
Domain scale					$F_{5,12}$	$p$ value	$R^2$	$p$ value	$F_{2,15}$	$p$ value
Upwelling index	–	–	–	–	117.00	< <b>0.001</b>	0.92	< <b>0.001</b>	0.06	0.813
Tidal range*	–	–	–	–	34.27	< <b>0.001</b>	0.98	< <b>0.001</b>	–	–
Salinity†	–	–	–	–	1.32	0.357	0.66	<b>0.004</b>	–	–
Area scale			$F_{16,34}$	$p$ value	$F_{5,45}$	$p$ value	$R^2$	$p$ value	$F_{2,48}$	$p$ value
Air temperature‡	–	–	39.92	< <b>0.001</b>	3.02	<b>0.006</b>	0.85	< <b>0.001</b>	1.34	0.252
Water temperature‡	–	–	47.45	< <b>0.001</b>	77.75	< <b>0.001</b>	0.86	< <b>0.001</b>	0.86	0.356
Wind velocity‡	–	–	12.53	< <b>0.001</b>	7.31	< <b>0.001</b>	0.01	0.778	0.02	0.901
Wind direction‡	–	–	16.39	< <b>0.001</b>	12.02	< <b>0.001</b>	0.48	< <b>0.001</b>	0.27	0.603
Precipitation§	–	–	2.91	<b>0.007</b>	79.33	< <b>0.001</b>	0.90	< <b>0.001</b>	0.26	0.871
Wave period‡	–	–	17.65	< <b>0.001</b>	5.89	< <b>0.001</b>	0.41	< <b>0.001</b>	0.11	0.746
Wave height‡	–	–	34.13	< <b>0.001</b>	14.52	< <b>0.001</b>	0.15	<b>0.011</b>	0.38	0.538
Wave power	–	–	17.68	< <b>0.001</b>	9.77	< <b>0.001</b>	0.13	0.192	0.54	0.468
Segment scale	$F_{384,32}$	$p$ value	$F_{32,10}$	$p$ value	$F_{10,5}$	$p$ value	$R^2$	$p$ value	$F_{2,429}$	$p$ value
Slope angle	0.86	0.675	1.48	0.191	3.28	0.052	0.34	<b>0.004</b>	0.19	0.794
Roughness	1.06	0.403	0.81	0.624	0.85	0.544	0.21	<b>0.042</b>	0.11	0.844
Runup	0.80	0.776	54.17	< <b>0.001</b>	0.11	0.988	0.31	< <b>0.001</b>	0.21	0.649
Sand abundance	0.66	0.926	13.00	< <b>0.001</b>	0.79	0.578	0.07	0.702	1.82	0.178

\* Primary and secondary tidal stations included in this analysis are from Tatoosh Island, WA; La Push, WA; Tillamook, OR; South Beach, OR; Waldport, OR; Charleston, OR; Crescent City, CA; Shelter Cove, CA; Fort Bragg, CA; Bodega, CA; Monterey, CA; San Luis, CA; Santa Barbara, CA; Santa Monica, CA; La Jolla, CA; Prisoners Harbor, CA; and Avalon, CA.

† Salinity observations are from Neah Bay: 1955–1994; Columbia River: 1966–1974; Newport: 1965–1969; Charleston: 1966–1999; Port Orford: 1964–1974; Trinidad: 1977–2000; Bodega: 1975–2000; Pacific Grove: 1941–1975; San Luis: 1956–1961; Santa Monica: 1956–2004; San Clemente: 1965–2000; Newport Beach: 1924–2000; and La Jolla: 1916–2000.

‡ Coastal buoys are 46206, 46041, 46029, 46050, 46015, 46027, 46022, 46014, 46013, 46042, 46028, 46054, 46025, 46069, and 46047.

§ Precipitation observation are from Quillayute, WA; Clearwater, WA; Tillamook, OR; Newport, OR; Honeyman State Park, OR; North Bend, OR; Arcata, CA; Shelter Cove, CA; Fort Bragg, CA; Fort Ross, CA; Monterey, CA; Piedras Blanca, CA; Santa Barbara, CA; San Pedro, CA; Cabrillo NM, CA; Santa Cruz, CA; and Avalon, CA.

*Patterns of relative diversity*—This survey does not qualify as an assessment of biodiversity per se because many organisms were not identified to the species level. However, multiple scale comparisons of taxon richness were made to assess distributional patterns of relative diversity (Fig. 3). Table 4 lists the results of nested ANOVAs that report the variability in taxon richness that is attributable to different spatial scales. Table 4 also lists results of spatial regressions that tested the relationship between latitude and longitude and relative diversity among segments, sites, areas, and domains for each shore zone.

A significant segment level diversity gradient from south to north, driven primarily by the regional end points, was evident in the cumulative richness for all zones (Fig. 3a). The low zone (Fig. 3b) in particular showed a linear trend in relative richness from south to north with 25% of the variability in richness explained by latitude and longitude. Central California segments in the mid and high zones were generally more diverse (Fig. 3c,d). The nested ANOVAs showed that segments were not a significant source of variability in any zone or in all zones combined relative to the variability contributed at other scales (Table 4).

Cumulative richness at the site scale also increased from south to north for all zones (Fig. 3e), with a particularly linear trend in the low zone (Fig. 3f) where 38% of the variability was explained by latitude and longitude. An apparent unimodal relationship between richness and latitude in the mid (Fig. 3g) and high (Fig. 3h) zones was

not statistically significant. The nested ANOVAs indicated that the only significant source of variability in the mid zone was at the site scale (Table 4).

In contrast to the segment and site scale results, at the area scale regional trends were less evident for mid and high zones (Fig. 3k,l, respectively), and all zones (Fig. 3i) combined. But low zone richness (Fig. 3j) increased slightly from south to north, a trend that was driven primarily by the regional end points.

In strong contrast to the patterns at the two smallest sampling scales, at the domain scale for all zones combined, cumulative richness decreased rather than increased from south to north (Fig. 3m). This trend was driven primarily by the mid (Fig. 3o) and high zones (Fig. 3p) in which the richness trend appeared strongly unimodal. No trend with latitude was apparent in the low zone (Fig. 3n).

The results from our analysis of taxon distribution based on frequency of observation are plotted on Figure 4. Out of a total of 268 taxa observed, 168 were most frequently observed in the low zone, 73 in the mid zone, and only 27 in the high zone. Interestingly, even though the cumulative domain richness (all zones and all years) decreases slightly from south to north (described above), the number of taxa observed most frequently was considerably higher in Washington than in any other domain further south. For example, 78 taxa occurred most frequently in Washington, and 47 of these occurred most frequently in the low zone (Fig. 4a). Primary

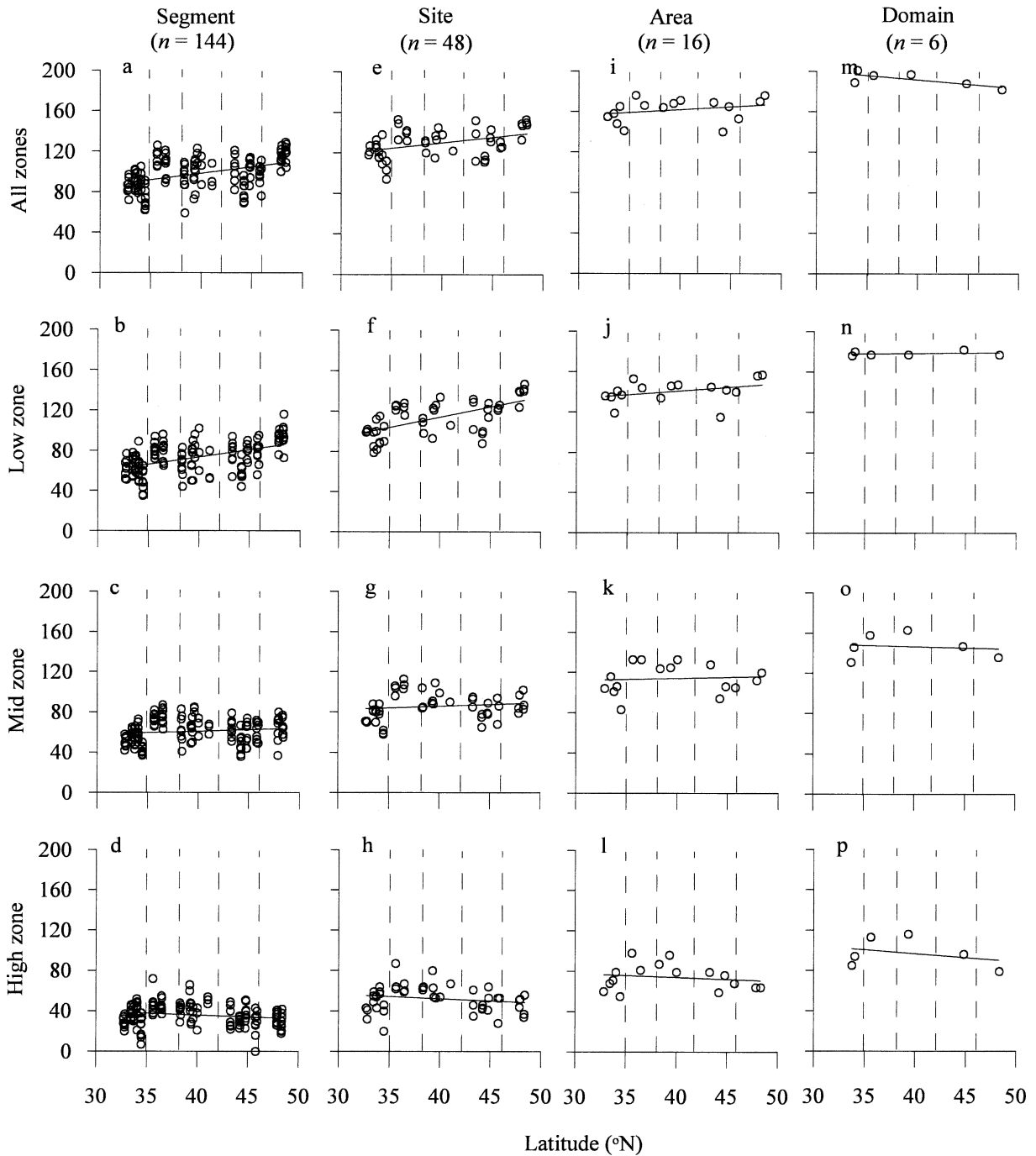


Fig. 3. Relative diversity observed from 2001–2003 for (a–d) segment-, (e–h) site-, (i–l) area-, and (m–p) domain-level aggregations for (a, e, i, m) all zones combined, and at each zone: (b, f, j, n) low, (c, g, k, o) mid, and (d, h, l, p) high. The numbers of taxa observed are plotted against latitude. Solid lines plotted on each graph represent the best linear fit. Regression results are listed in Table 4. Dashed vertical lines mark latitudes of domain boundaries.

producers occurred less frequently in Southern California and Oregon, and carnivores and omnivores occurred more frequently in Washington. The mid (Fig. 4b) and high (Fig. 4c) zones were consistent with this pattern with more taxa in the Washington domain. Web Appendix 1 lists frequencies of observation for each taxon by zone and domain.

Matrices showing domain-level taxon similarities are shown in Table 5 for each zone (and for all zones combined). These matrices show the numbers of taxa that occurred in adjacent domains and provide an index for comparing the degree of similarity of both adjacent and distant domains. Domains correspond approximately to Washington (WA), Oregon (OR), Northern California

Table 4. Results of nested ANOVA analyses to test for differences in relative diversity among segments (within sites), among sites (within areas), and among areas. One-way ANOVA was used to test for differences among domains (adjusted for multiple comparisons). Spatial regressions of cumulative taxon richness (2001–2003) at segment, site, area, and domain scales are shown for all zones and individually for each zone. Significant differences are in bold.

Zone	Nested ANOVA						One-way ANOVA		
	Segment		Site		Area		Domain		
	$F_{108,18}$	$p$ value	$F_{18,6}$	$p$ value	$F_{6,2}$	$p$ value	$F_{5,138}$	$p$ value	
All	0.36	0.993	1.06	0.421	15.86	<b>0.004</b>	24.92	< <b>0.001</b>	
Low	0.37	0.991	0.98	0.468	15.79	<b>0.004</b>	21.21	< <b>0.001</b>	
Mid	0.28	0.998	4.93	<b>0.004</b>	2.81	0.137	16.09	< <b>0.001</b>	
High	0.43	0.978	2.42	0.068	1.59	0.280	10.85	< <b>0.001</b>	
				Spatial regression					
	$R^2$	$p$ value	$R^2$	$p$ value	$R^2$	$p$ value	$R^2$	$p$ value	
All	0.19	< <b>0.001</b>	0.16	<b>0.005</b>	0.07	0.315	0.55	0.093	
Low	0.25	< <b>0.001</b>	0.39	< <b>0.001</b>	0.12	<b>0.018</b>	0.06	0.640	
Mid	0.02	0.109	0.02	0.354	0.01	0.786	0.01	0.819	
High	0.03	<b>0.034</b>	0.03	0.207	0.02	0.556	0.10	0.535	

(NC), Central California (CC), Channel Islands (CI), and Southern California (SC) as listed in Table 2. For example, of the 182 taxa observed in Washington across all zones, 170 (95%) of the same taxa were observed across all zones in Oregon, but only 116 (63%) were also observed across all zones in Southern California. In the low zone, 56% of the taxa observed in Washington were also observed in Southern California, and only 50% and 53% of the taxa observed in Washington in the mid and high zones, respectively, were also observed in Southern California.

The results of our seasonal comparison among Cape Foulweather and Cape Perpetua are shown on Fig. 5 with richness for each season, area, and zone grouped by trophic level. The results of statistical tests are listed in Table 6. In the low zone (Fig. 5a), taxon richness varied among sites and seasons at Cape Perpetua and among sites at Cape Foulweather. Differences were found only among Cape Perpetua segments in the mid zone (Fig. 5b) and among high zone segments and sites at Cape Foulweather (Fig. 5c). Thus, within these two capes, richness evidently varies little among spring, summer, and fall seasons.

*Patterns of population abundances*—The results of spatial autocorrelations and regressions are listed in Web Appendix 1 and summarized in Table 7. Smaller  $p$  values indicate stronger autocorrelation. Therefore, abundances of 169 taxa (63%) were highly autocorrelated, an additional 6 were significantly autocorrelated, and 93 taxa (35%) were spatially independent. Spatial correlation was evident to some degree in 83 taxa (31%), but most taxa abundances (185) were weakly related to latitudinal and longitudinal coordinates. Hence, abundances of more than half of the taxa tended to covary, but these trends seem generally weakly related to location along the coast.

Spatial patterns were further evaluated by plotting segment mean abundances for each taxon by the zone in which each taxon was most frequent. Taxon distributions were qualitatively binned into one of five general regional-scale patterns: (1) high in the north and low in the south (83

taxa), (2) high in the south and low in the north (82 taxa), (3) high in the center and low in the north and south (82 taxa), (4) high in the north and south and low in the center (10 taxa), and (5) no pattern (11 taxa). Figure 6 shows selected examples (four invertebrates and one alga) for each distribution category, and Web Appendix 1 lists the category for each taxon.

The results of nested ANOVA tests on taxon abundance from the zone in which each taxon was most frequent and by levels of aggregation (sites within areas, areas within domains, and among domains) were binned into the five regional distribution categories listed above and summarized in Table 8. We did not analyze within-site variability (i.e., among replicate samples or segments) with our nested model because of insufficient degrees of freedom with only three segments per site. For 53 taxa, abundances varied only at the site level. Fewer taxa (48) varied only at the area level, and only 11 taxa varied just at the domain level. Many taxa (65) were not variable at any level, although these were uncommon organisms (observed in <1% of all samples). Some taxa were variable at more than one level, for example, site and area (42 taxa), area and domain (12 taxa), site and domain (23 taxa), and all three levels (14 taxa). This suggests that the site and area levels and the combined site and area level are the spatial scales where variability in population abundance is significant for 53% of the taxa, and this increases to 70% if we do not consider the uncommon taxa. Taxa more frequently observed in the northern and central range of the region were more variable at the site level, whereas taxa more frequently observed in the southern range of the region were more variable at the area level.

One-way ANOVAs (corrected for multiple comparisons) were tested for among-year differences in sample means at zones of most frequent occurrence for each taxon (Table 8), but these results should be viewed with caution because of potential aliasing of higher frequency signals. For example, our annual samples do not take into account seasonal variability, therefore seasonal differences can be aliased

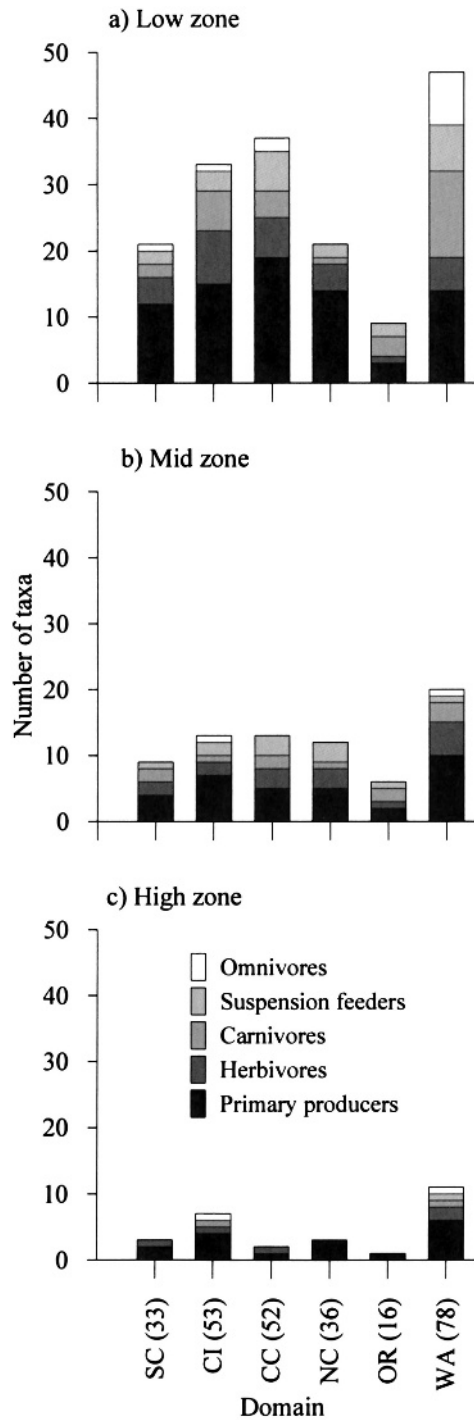


Fig. 4. Number of taxa occurring most frequently in each domain plotted by zone (a–c). Bar height indicates the total number of taxa, and each bar is divided into the major trophic levels. The symbol legend for different trophic levels is shown in panel c. Numbers in parentheses indicate the taxa totals across all zones for each domain. Taxa totals by zone and trophic level are discussed in the text.

into observed annual differences, thus potentially masking actual annual changes. Interestingly, as with the spatial tests, among-year differences occurred mostly at the site (7 taxa) and area (15 taxa) levels. These analyses clearly point

Table 5. Matrix of taxa similarity among domains. Matrix values are the number of taxa observed in both (x and y) domains during the 2001–2003 surveys. Domains are described in the text and in Table 2.

		All zones						
		Domain						
Domain		WA	OR	NC	CC	CI	SC	
Domain	WA	179	170	162	152	125	116	
	OR		186	173	161	131	121	
	NC			194	174	144	131	
	CC				193	155	139	
	CI					197	167	
	SC						189	

		Low zone						
		Domain						
Domain		WA	OR	NC	CC	CI	SC	
Domain	WA	160	154	144	134	108	100	
	OR		165	156	145	115	108	
	NC			166	159	127	116	
	CC				170	136	122	
	CI					168	152	
	SC						158	

		Mid zone						
		Domain						
Domain		WA	OR	NC	CC	CI	SC	
Domain	WA	140	119	117	106	75	68	
	OR		148	135	116	81	72	
	NC			156	133	93	82	
	CC				151	102	87	
	CI					147	110	
	SC						139	

		High zone						
		Domain						
Domain		WA	OR	NC	CC	CI	SC	
Domain	WA	95	76	70	62	47	42	
	OR		102	81	70	49	44	
	NC			106	89	62	55	
	CC				104	79	64	
	CI					96	71	
	SC						94	

to significant variability in population abundances at the smaller spatial scales (also see Fig. 3a–d). See Web Appendix 1 for test results of each taxon.

*Patterns of community structure*—The characteristic high variability in abundances of individual populations makes discerning spatial patterns difficult. Using multivariate analyses, however, we compared entire communities for patterns across multiple spatial scales. Comparisons of community similarity were made with the combined 2001–2003 data at the segment level for the low zone (420 samples × 237 taxa), the mid (427 samples × 229 taxa), and the high zone (419 samples × 163 taxa) to determine: (1) whether groups of communities can be explained by geographic location; (2) which taxa were statistically forcing the community distributions; and (3) which environmental parameters were correlated with community patterns.

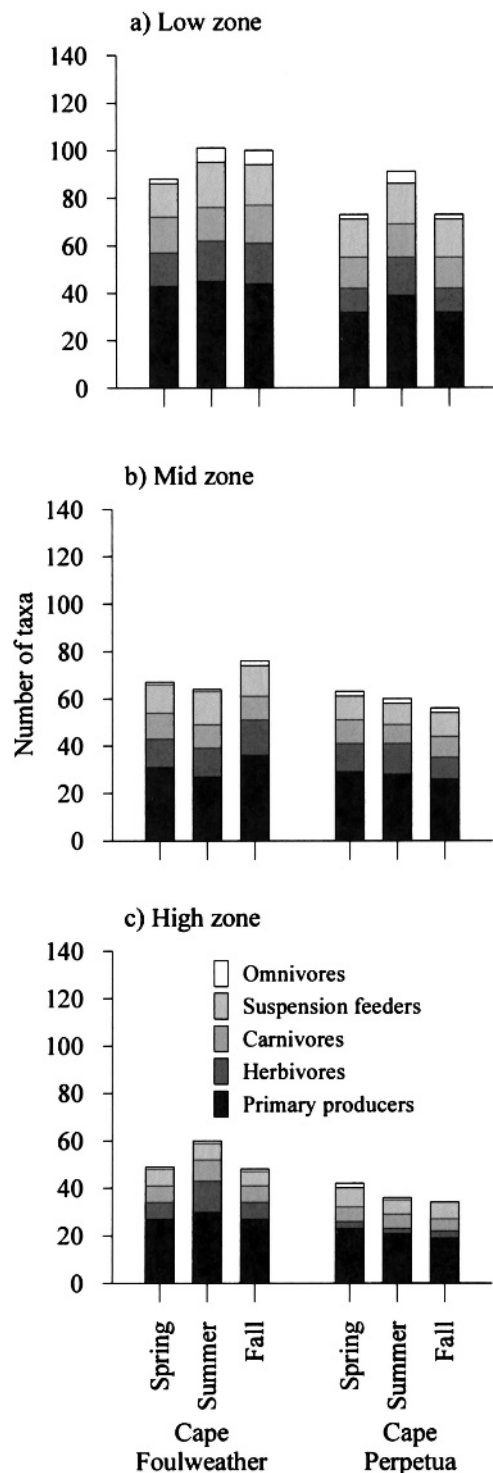


Fig. 5. Relative distribution of taxa over two consecutive years at Cape Foulweather and Cape Perpetua in Oregon by season (spring, summer, fall), zone (a–c), and by trophic level. The symbol legend for the different trophic levels is shown in panel c.

The two-dimensional solutions of the MDS ordinations for each zone generally sort into distinct clusters at the area and sometimes domain scale (Fig. 7). There are varying degrees of sample heterogeneity within each polygon, and in some cases among-area heterogeneity was low enough to

Table 6. Nested ANOVA results for testing differences in relative diversity among seasons in the context of among segments and among sites variation at the Cape Foulweather and Cape Perpetua areas in Oregon. Significant differences are in bold.

		Nested ANOVA					
		Segment (n=54)		Site (n=18)		Season (n=6)	
Area	Zone	$F_{27,18}$	p value	$F_{18,6}$	p value	$F_{6,2}$	p value
Foulweather	All	1.88	0.173	4.78	<b>0.004</b>	1.00	0.421
	Low	0.62	0.851	2.90	<b>0.037</b>	4.30	0.069
	Mid	1.15	0.360	2.11	0.102	1.74	0.254
	High	2.96	<b>0.005</b>	3.92	<b>0.011</b>	0.28	0.768
Perpetua	All	1.96	0.331	1.70	0.177	0.91	0.451
	Low	2.48	0.098	3.83	<b>0.015</b>	5.13	<b>0.035</b>
	Mid	2.70	<b>0.010</b>	0.38	0.882	0.46	0.652
	High	0.58	0.882	1.98	0.122	0.23	0.804

warrant combining more than one area into a single polygon. Since all the areas have the same number of samples, smaller polygons are interpreted to have communities that were more similar than area-level communities represented by larger polygons. Also, polygons farther apart are interpreted to be less similar than polygons closer together.

Low zone communities (Fig. 7a) in Southern California (domain 6: polygons 14–16) and the Channel Islands (domain 5: polygons 12 and 13) were clearly distinguished from domains further north (Global  $R = 0.902$ , with maximal separation when  $R = 1$ ,  $p = 0.001$ ), and from each other ( $R = 0.684$ ,  $p = 0.001$ ). Washington (1, areas 1 and 2) and Oregon (2, areas 3–6) domains showed some similarity but were statistically different ( $R = 0.101$ ,  $p = 0.003$ ). In all other pairwise comparisons, domain communities differed ( $p < 0.001$ ), but qualitative comparisons show differences among domains increasing with separation distance (e.g.,  $R$  values increased from north to south, WA–OR = 0.101, WA–NC = 0.385, WA–CC = 0.567, WA–CI = 0.875, WA–SC = 0.879). All communities at the area level were different, although the most similar were Cape Foulweather and Cape Arago ( $R = 0.103$ ,  $p = 0.004$ ), Cape Arago and Trinidad ( $R = 0.059$ ,  $p = 0.050$ ), Trinidad and Fort Bragg ( $R = 0.093$ ,  $p = 0.006$ ), and Trinidad and Bodega ( $R = 0.265$ ,  $p = 0.002$ ). North of Pt. Conception, the areas that were the least similar to any other area were

Table 7. Hypothesis tests for spatial auto-correlation of taxon abundances are summarized by the number of taxa at different levels of significance. Spatial regressions are summarized by number of taxa and strength of correlation to latitude and longitude. See Web Appendix 1 for individual values.

Autocorrelation		Regression	
p value	No. of taxa	Mult. $R^2$	No. of taxa
<0.001	169	<0.1	185
<0.01	6	<0.2	63
<.1	10	<0.3	17
<1	83	<0.4	3

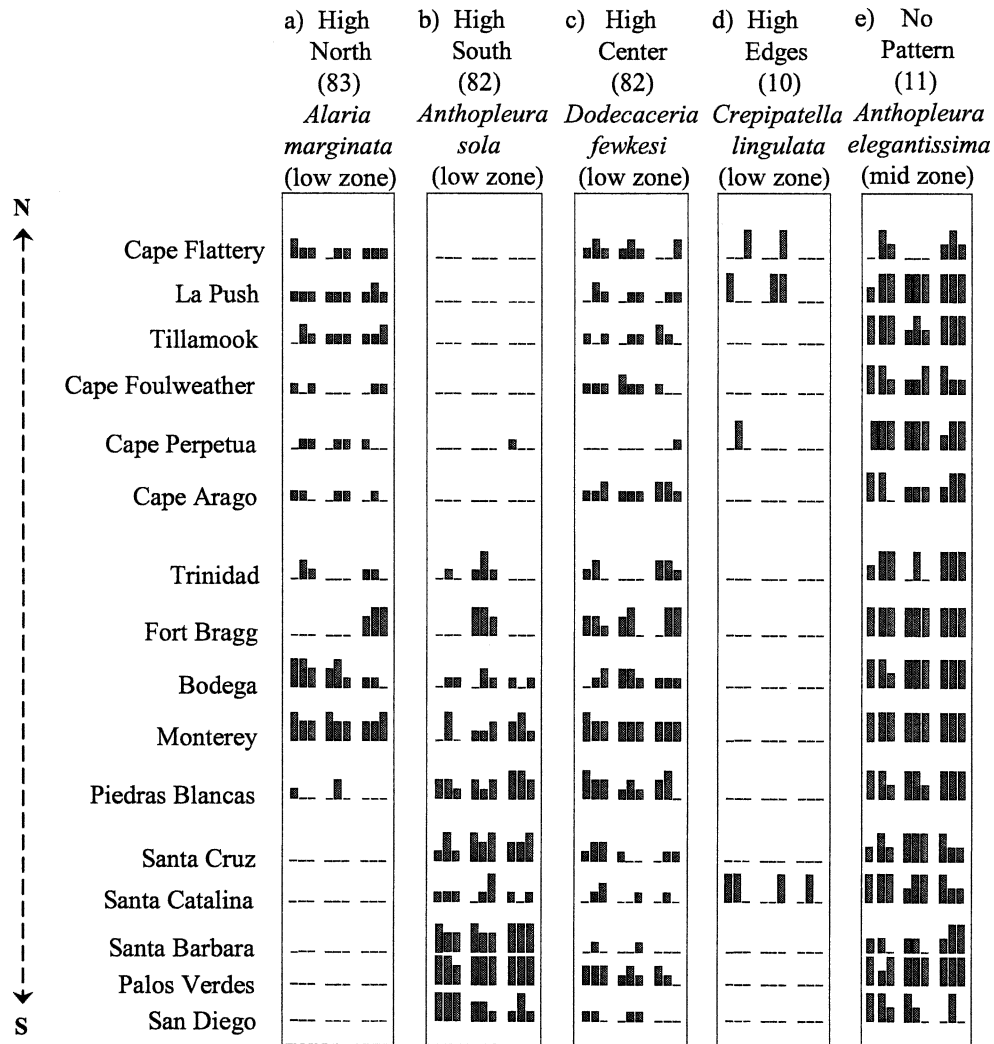


Fig. 6. Relative population abundances are shown for taxa that represent the predominant spatial distribution patterns (a–e). Each panel represents a different species. Each bar indicates the species abundance (percent cover or counts) per segment, for the zone in which each species was most abundant, relativized by the highest observed value for each species. Clusters of three bars represent a site, and each row of clusters within each panel represents an area. Areas are labeled along the left margin. See text for additional explanations and Web Appendix 1 for a complete listing of all taxa distribution patterns.

Cape Perpetua (all  $R > 0.8$ ), Monterey (all  $R > 0.8$ ), and Piedras Blancas (all  $R > 0.8$ ).

In the mid zone (Fig. 7b), the Channel Island and Southern California domains (areas 12 and 13, and 14–16) were different from each other ( $R = 0.316$ ,  $p = 0.001$ ), and together these domains south of Pt. Conception were different from all domains north of Pt. Conception ( $R = 0.472$ ,  $p = 0.001$ ). All domain-level mid zone communities north of Pt. Conception differed from one another ( $p < 0.001$ ), but qualitatively, Washington and Oregon domains (areas 1 and 2, and 3–6) were most similar. Differences among domains increased with separation distance (e.g.,  $R$  values increased from north to south, WA–OR = 0.279, WA–NC = 0.391, WA–CC = 0.644, WA–CI = 0.767, WA–SC = 0.772). At the area level, all mid zone communities differed except Trinidad and Fort Bragg ( $R$

= 0.070,  $p = 0.140$ ). Cape Arago and Trinidad were relatively similar ( $R = 0.127$ ,  $p = 0.04$ ), as were Tillamook and Cape Perpetua ( $R = 0.146$ ,  $p = 0.020$ ). North of Pt. Conception, and as in the low zone, the areas that were the least similar to any other area were Cape Perpetua (all  $R > 0.6$ ), Monterey (all  $R > 0.6$ ), and Piedras Blancas (all  $R > 0.6$ ).

The two-dimensional ordination plot of high zone community similarity (Fig. 7c) shows a less distinct separation between domains north and south of Pt. Conception, but community structure nevertheless differed among domains ( $R = 0.263$ ,  $p = 0.001$ ). Despite the similarity between the Channel Islands (areas 12 and 13) and other Southern California communities (areas 14–16) ( $R = 0.103$ ), these were also statistically different ( $p = 0.001$ ). Washington and Oregon high zone communities

Table 8. Summary of nested ANOVA analyses for individual populations, from the zone in which it was most frequently observed, at the among site (S), area (A), and domain (D) scales. Values are the numbers of taxa with significantly different abundances at each level (and combinations) and in each category. The null ( $\emptyset$ ) row indicates the number of taxa not significantly different at any level. Column 7 are numbers of organisms at each level with significantly different abundances among years (2001–2003). See Web Appendix 1 for a complete listing of results.

Levels	Category*					Nested ANOVA total	One-way ANOVA year
	1	2	3	4	5		
	High north	High south	High center	High edges	No pattern		
S	19	8	22	2	2	53	7
A	12	18	12	2	4	48	15
D	1	5	2	2	1	11	1
S&A	11	10	20	0	1	42	3
A&D	3	7	1	0	1	12	0
S&D	5	9	8	0	1	23	5
S&A&D	4	7	3	0	0	14	1
$\emptyset$	28	18	14	4	1	65	236
Totals	83	82	82	10	11	268	268

\* Categories for organism distributions are: higher frequency (1) towards the north, (2) towards the south, (3) near the center, (4) near the north and south and low in the middle, and (5) no pattern.

(areas 1–6) were similar ( $R = 0.048$ ,  $p = 0.050$ ), but in all other pairwise comparisons, domain level high zone communities north of Pt. Conception differed ( $p < 0.001$ ). In contrast to low and mid zones, in the high zone the greatest qualitative differences were observed between Central California (areas 10 and 11) and all other domains (e.g.,  $R$  values for CC–WA = 0.672, CC–OR = 0.655, CC–NC = 0.598, CC–CI = 0.545, CC–SC = 0.693). At the area level, all communities differed except Tillamook and Cape Foulweather ( $R = 0.106$ ,  $p = 0.18$ ), Tillamook and Cape Perpetua ( $R = 0.098$ ,  $p = 0.200$ ), Trinidad and Fort Bragg ( $R = 0.140$ ,  $p = 0.062$ ), and Trinidad and Bodega ( $R = 0.113$ ,  $p = 0.051$ ). Other areas that were similar but statistically different were Cape Flattery and Tillamook ( $R = 0.215$ ), Cape Flattery and Cape Arago ( $R = 0.131$ ), La Push and Tillamook ( $R = 0.183$ ), La Push and Cape Perpetua ( $R = 0.181$ ), and Tillamook and Cape Arago ( $R = 0.191$ ) (all  $p < 0.05$ ). North of Pt. Conception, the areas that were the least similar to any other area were Monterey (all  $R > 0.6$ ) and Piedras Blancas (all  $R > 0.5$ ).

*Effects of populations on community structure*—Pearson's correlation coefficients were used to explore the taxa that best explain ( $\rho > 0.20$ ) the ordination patterns shown on Fig. 7 as species vectors. Pearson's correlation coefficients express the linear relationship between individual variables (taxa) and all the samples used to construct the ordinations. A coefficient was calculated for each taxon along the axes that explain most of the variability. The resulting x and y coordinate was plotted, and a line was drawn connecting this plotted point to the ordination centroid. The length of the radiating line was calculated as the hypotenuse of the triangle created by the x and y distances from the ordination centroid (McCune et al. 2002). Therefore, the species vectors, the angle and length of the radiating dashed lines in each plot on Fig. 7, relate to the direction and relative magnitude of the Pearson's correlation (in two-dimensional community ordination space).

In the low zone, 13 taxa accounted for most of the variation ( $\rho = 0.87$ ), with the greatest contributions ( $\rho > 0.20$ ) from *Phyllospadix* (surf grass) and encrusting corallines (red algae) (Fig. 7a and Table 9). In the mid zone, 18 combined taxa best explained ( $\rho = 0.84$ ) the community distribution patterns (Fig. 7b). The greatest contributions were, in rank order: erect corallines (red algae), bare space (no organisms), *Lottia* spp. (limpets), Littorines (snails), encrusting corallines (red algae), *Tetraclita rubescens* (barnacle), and *Chondracanthus canaliculatus* (red alga) (Table 9). In the high zone, seven taxa best explained the ordination pattern (Fig. 7c). The greatest contributions were, in rank order: bare space, *Mytilus californianus* (mussels), *Pollicipes polymerus* (barnacles), *Lottia* spp. (limpets), Littorines (snails), *Balanus glandula* (barnacle), and encrusting algae (non-coralline crusts) (Table 9).

*Effects of environmental parameters on community structure*—We explored the physical variables that best explained the observed patterns of community separation (Fig. 7) by using Pearson's correlation coefficients as explained above. The environmental vectors are shown on Fig. 7 as solid lines. The relative magnitudes for each environmental variable are listed in Table 9. For the low zone communities, the 10 environmental variables accounted for a combined correlation of  $\rho = 0.92$ , with the most important (in rank order for  $\rho > 0.20$ ) being air temperature, water temperature, upwelling, precipitation, sand, tide range, and salinity (Fig. 7a). For mid zone and high zone taxa, the 10 environmental variables in each case accounted for a combined correlation of  $\rho = 0.86$ . The most important in rank order for the mid zone were tide range, upwelling, air temperature, water temperature, precipitation, salinity, and wave period (Fig. 7b). In the high zone the key predictors were, in rank order, upwelling, precipitation, water and air temperature, tide range, and salinity (Fig. 7c).

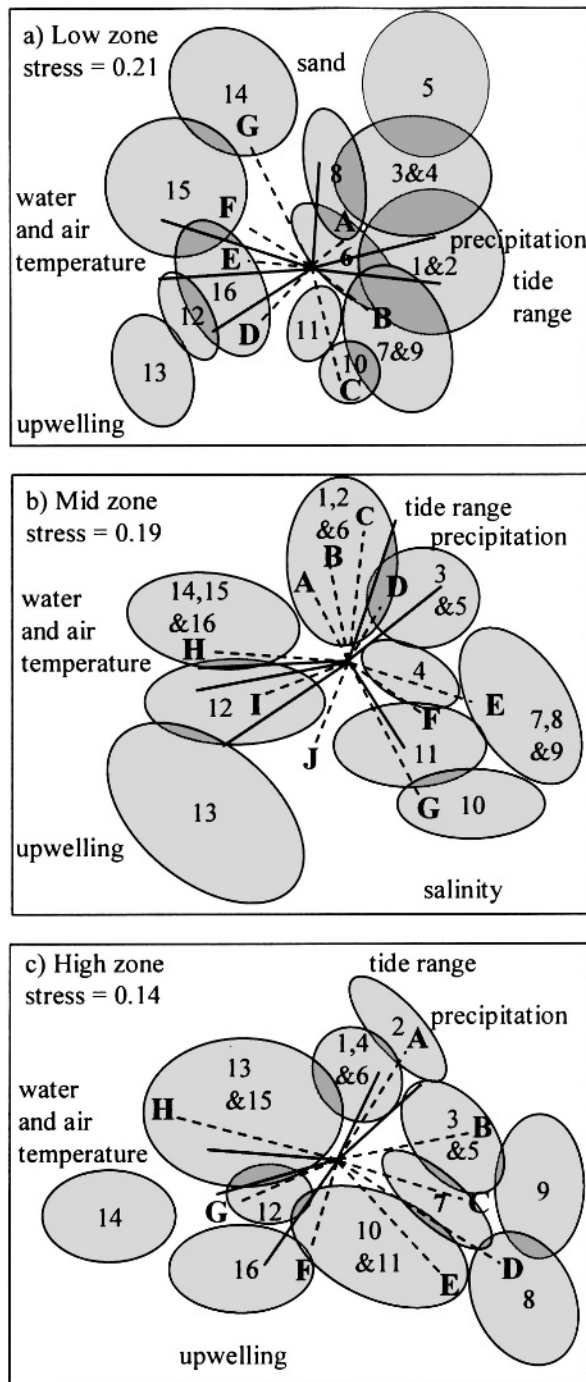


Fig. 7. Two-dimensional solutions are shown for non-metric multidimensional scaling ordinations of Bray-Curtis community similarity matrices for the (a) low zone, (b) mid zone, and (c) high zone communities. Stress values indicate goodness-of-fit with lower values indicating a better fit. There are approximately 433 data points on each plot representing communities sampled from 2001–2003. These have been grouped by area for clarity, and each group is shown with a labeled polygon. Polygon labels correspond to the area numbers shown in Table 2. Solid lines (environmental vectors) radiating from the ordination centroid show the correlation vectors for physical variables (labeled) that best explain the observed pattern. Pearson's correlation coefficients for each environmental vector are listed in Table 9. Dashed lines

Interestingly, whereas the Pearson's correlation analysis of environmental vectors across the entire region helped explain the observed two-dimensional pattern of community structure as shown on the plots, these linear correlations cannot explain the actual multidimensional structure of the community data. We used Spearman's rank correlations calculated by the BIOENV module in PRIMER (Clarke and Ainsworth 1993) to gain a better understanding of the multidimensional relationship between the environmental variables and the observed community structure. This analysis indicated that the best overall environmental predictor of the observed community pattern was wave runoff in the low zone ( $\rho = 0.484$ ), mid zone ( $\rho = 0.337$ ), and high zone ( $\rho = 0.206$ ).

## Discussion

**Diversity patterns**—The most striking discovery of this study is the unusual diversity (taxon richness) patterns (Fig. 3). In particular, in contrast to the usual increase in diversity with decreasing latitude (the most commonly observed “latitudinal gradient” in biodiversity: Gaines and Lubchenco 1982; Gray 2001; Koleff and Gaston 2001), diversity in the low intertidal zone decreases with decreasing latitude, both at the segment scale (local transect or meters) and site scale (clusters of local transects or kilometers). At larger scales (area, tens of kilometers, and domain, hundreds of km) the pattern weakens (area) and even shows a trend toward the usual increasing with decreasing latitude pattern (domain) (Fig. 3b,f,j,n). Patterns in the mid and high zones show little change with latitude (Fig. 3) and weaken the trends seen across all zones combined, although the low zone influence still dominates at the segment and site scales (Fig. 3a,e,i,m).

Our analysis contrasts strongly with those of Gaines and Lubchenco (1982). Using compilations of algal distributions along the coasts of North and Central America (Pielou 1977, 1978), they showed a sharp increase in algal species richness along the North American west coast between the 50°N to 45°N range, a slight decrease at 40°N, and then another sharp increase to 35°N. Recall that our surveys occurred between 48°N and 33°N.

What might be the basis for the differences between the Gaines and Lubchenco (1982) and the present analyses? One obvious difference is that our surveys included both macrophytes and invertebrates, whereas the Gaines and Lubchenco (1982) analysis focused on macrophytes only. Analysis at the domain scale indicates that low zone macrophyte richness in our surveys was slightly higher in Central California, lowest in Oregon, and of comparable richness in Washington, Northern California, and the Channel Islands, but highest in Washington in the mid and high zones (Fig. 4). If invertebrate species are added (i.e.,

←

(species vectors) terminating at letter designations indicate the groups of taxa best explaining the observed pattern. These taxa groups are listed by letter designation in Table 9 with Pearson's correlation coefficients for each vector.

Table 9. Pearson's correlation coefficients for environmental variables and taxa with the highest correlations ( $\rho > 0.20$ ) to the ordination patterns as shown in Fig. 9.

Vector	Variable	Pearson's $\rho$ by zone		
		Low	Mid	High
Solid lines				
	Air temperature	0.846	0.801	0.627
	Water temperature	0.838	0.796	0.628
	Upwelling index	0.762	0.816	0.652
	Precipitation	0.738	0.763	0.642
	Sand abundance	0.720	0.417	0.233
	Tide range	0.708	0.819	0.633
	Salinity	0.558	0.641	0.529
	Wave period	0.479	0.514	0.438
	Wave height	0.471	0.463	0.429
	Runup	0.453	0.445	0.414
Dashed lines				
A group	<i>Balanus glandula</i>	0.224	0.429	0.604
B group	Lepidochiton complex	0.426		
	Littorina complex		0.608	0.605
	<i>Tonicella lineata</i>	0.484		
	<i>Mazzaella splendens</i>	0.450		
C group	Crustose corallines	0.717		
	Lottia complex		0.709	0.612
D group	<i>Halidrys dioica</i>	0.488		
	<i>Eisenia arborea</i>	0.435		
	<i>Ceratostoma nuttalli</i>	0.372		
	<i>Mazzaella affinis</i>	0.415		
	<i>Mytilus californianus</i>			0.898
	<i>Nucella emarginatalostrina</i>		0.440	
	<i>Semibalanus cariosus</i>		0.421	
	<i>Tetraclita rubescens</i>	0.422		
E group	<i>Corynactis californica</i>	0.350		
	<i>Katharina tunicata</i>		0.430	
	<i>Leptasterias hexactis</i>		0.434	
	<i>Microcladia coulteri</i>		0.467	
	<i>Pollicipes polymerus</i>			0.719
	<i>Tonicella lineata</i>		0.466	
F group	<i>Chondracanthus canaliculatus</i>	0.459		
	<i>Strongylocentrotus purpuratus</i>		0.505	
	Erect corallines		0.513	
G group	Erect corallines		0.793	
	Crustose corallines		0.607	
	Fleshy crust			0.490
	<i>Phyllospadix</i> sp.	0.817		
H group	Bare space		0.749	0.936
	<i>Fissurella volcano</i>		0.466	
I group	<i>Chondracanthus canaliculatus</i>		0.507	
	<i>Laurencia pacifica</i>		0.475	
J group	<i>Tetraclita rubescens</i>		0.567	

herbivores, carnivores, suspension feeders, and omnivores), the overall increase from south to north emerges, but with some interesting variation among domains (e.g., the occurrence of the highest and lowest overall richness patterns in adjacent northern domains, Washington and Oregon).

A second factor contributing to the differences between the present analysis and that of Gaines and Lubchenco (1982) is differences in scale and resolution. The pioneering analysis of Gaines and Lubchenco was necessarily constrained by a dataset that included just biogeographic

distributional ranges of algae, based on the end points (north and south) with no information on abundances. Our surveys were done at a much finer resolution and thus were much more sensitive to gaps in distributions where species present to the north or south were locally absent at some segments, sites, or areas (e.g., the low richness values seen in Oregon compared to Washington or Northern California; Fig. 4).

A third factor contributing to the between-analysis differences is a difference in the range of habitats surveyed. The Gaines and Lubchenco (1982) survey was based on a literature survey, which essentially constitutes a spatially and temporally integrated collection of the observations of many workers across all benthic habitats. In contrast, our survey was constrained to emergent rocky surfaces on sloping intertidal benches and thus did not sample tide-pools, narrow channels and crevices, undersides of boulders and ledges, cobblefields, caves, and subtidal habitats. These differences doubtless account for the smaller number of taxa we recorded ( $\sim 180$  at  $48^\circ\text{N}$ ,  $\sim 200$  at  $33^\circ\text{N}$ ) compared to the Gaines and Lubchenco (1982) analysis ( $\sim 220$  at  $50^\circ\text{N}$ ,  $\sim 550$  at  $35^\circ\text{N}$ ).

A further implication of these comparisons is that habitat heterogeneity both directly (through the provision of microhabitat diversity) and indirectly (through effects on interactions) contributes strongly to total diversity patterns. In our surveys, richness at the domain level increased by only  $\sim 20$  taxa from north to south whereas in the Gaines and Lubchenco (1982) analysis, richness increased by  $\sim 330$  species. Clearly, within-habitat (open rocky surfaces on benches) processes have only a modest effect on large-scale richness patterns. However, the gradual shift in the slope of the richness line from negative at the largest (domain) scale to positive at the smallest (segment) scale (Fig. 5m,i,e,a) suggests that organisms are patchier to the south than to the north, indicating that even within this single habitat type, habitat heterogeneity has an influence on richness patterns.

*Biogeographic patterns of community structure*—Connolly and Roughgarden (1999a); (see also Roughgarden et al. 1988) proposed that community patterns in the rocky intertidal subweb dominated by sessile invertebrates and their predators were driven by the gradient of increasing upwelling from the northern to southern ends of the California Current Large Marine Ecosystem (CCLME). The proposed underlying mechanism was the rate of offshore advection of larvae. With weaker upwelling to the north, advection rates should be low and settlement and recruitment therefore should be higher, leading to strong competition for space, high prey and predator abundances, and, thus, strong predation. With strong upwelling to the south, advection rates should be high and settlement and recruitment should be lower, generating weak competition for space, low prey and predator abundances, and weak predation.

Investigation of rates of recruitment, abundance of mussels and barnacles, predator abundance and effect, and other factors are only partially consistent with these predictions (Connolly and Roughgarden 1998; Menge et al.

2004), suggesting other factors have an important influence on community structure. Further, Connolly and Roughgarden's (1999b) model was focused on the mussel–barnacle–whelk–sea star component of the community. Thus, answering the question of the factors that drive both the dynamics of this invertebrate component and the broader community, including macrophytes and their consumers, remains an open question.

Determination of the factors underlying the structure of the entire rocky intertidal community across 15° of latitude is a daunting task. As we argued in the introduction of this article, achievement of this goal can only result after a number of studies have been completed, a major one of which is the assessment of what patterns of community structure actually exist across the entire range of the CCLME. In addition to contributing to this goal, our surveys, including both the biotic and physical measurements, provide insights into the complex factors that underlie community structure in this system. Below we highlight some of the major associations.

*Upwelling*—Our analyses suggest that upwelling was a stronger driver of community structure in the south even in those years when upwelling was strong in the north (Fig. 7). As discussed above, other studies have suggested that upwelling may structure benthic communities by the selective alongshore and offshore advection of larval propagules of some animal populations but not of others (Connolly and Roughgarden 1998; Connolly et al. 2001; Menge et al. 2004). But additional effects of upwelling include fostering growth and abundance of macrophytes and phytoplankton, with likely impacts on their respective consumers (Menge 2000; Menge et al. 2003). Evidence suggests that phytoplankton concentration can be an important factor underlying growth of sessile invertebrates and thus the intensity of competition (Sanford and Menge 2001; Menge et al. 2004; Leslie 2005), but the larger-scale consequences of these effects need further investigation.

*Temperature*—Our multivariate analyses suggest that high air and water temperatures were important mechanisms forcing low zone southern communities and were strongly associated with bare space in the mid and high zones (Fig. 7). Helmuth et al. (2002) also found evidence that interactions between latitude, seasonal changes in tidal dynamics, and air temperature may be important forcing agents of community structure. During the period of our survey, the greatest latitudinal gradient in both mean annual air and water temperatures was 0.71°C per degree of latitude between 33°N and 40°N and only a 0.12°C per degree of latitude between 40°N and 48°N. Therefore, the steep southern temperature gradients may limit organisms with narrow temperature tolerances to a smaller latitudinal range, and conversely the lower northern temperature gradient may enable populations in the north to become more broadly distributed, thus possibly explaining the dominance of northern populations in this region.

*Salinity*—Our analyses show that higher salinities in warm water appear to affect the Southern California

communities, whereas higher salinities in cold water affected the communities in Central and Northern California and relatively lower salinities in cold water affected the communities along the Washington and Oregon Coasts. The low salinities of the northern domains can be explained by the dominance of the Columbia River plume in surface waters and by high precipitation. Witman and Grange (1998) showed that high precipitation rates may affect local salinity and subsequently subtidal community structure by altering the spatial distributions of key predators. The high salinity and warm water of Southern California results from low input of fresh water and high rates of evaporation. The higher salinities and cold water in Northern and Central California can be explained by the upwelling of bottom water along the portion of the coast most strongly influenced by the temporally consistent offshore advection of surface water.

*Sand*—Changes in low zone community structure largely corresponded to latitudinal gradients in salinity, precipitation, tide range, magnitude of upwelling, and water and air temperature. Deviations from this linear shift corresponded to high sand abundances. The same pattern was evident in mid zone communities, with the exception that sand abundance did not contribute to the linear deviation as strongly as salinity. Most of the subtidal shelf off the U.S. West Coast is sandy, particularly where the shelf is wide and relatively shallow. Intertidal shores adjacent to these reservoirs of sand, such as the areas at Cape Perpetua and Santa Barbara, may be strongly affected by seasonal sand scour and burial. These sand-affected segments showed lower numbers of taxa than neighboring segments with no sand.

*Waves*—Deep water waves are dispersive with longer wavelengths traveling faster than shorter wavelengths, therefore the period of deep-water waves increases as they propagate from a storm system. Thus, from 2001–2003, the long period swells of Southern California are likely to have originated from a distant source and the shorter period waves of Washington from a local source. Wave power is a function of both wave period and wave height. During our study, wave heights were slightly higher in the north, but, importantly, wave period was much longer in the south. This explains why wave power was not significantly correlated to latitude and longitude. Wave runup, however, a function of wave height, length, bottom slope, and roughness, was strongly correlated to latitude and longitude, possibly owing to the lower-angle segment slopes in the south that cause wave energy to dissipate as spilling breakers as opposed to plunging breakers further north. Our multidimensional analysis of relationships between environmental variables and community structure showed that wave runup was the single most important physical parameter affecting overall community structure, suggesting that wave perfusion may favor desiccation-prone organisms.

*Population abundances*—Our results suggest that there is significant connectedness among shore segments, presum-

ably because of environmental similarities, covariation of environmental variables, and mechanisms favoring the dispersal and recruitment of pelagic larvae and spores. The spatial autocorrelation analyses showed that the abundances of 65% of the taxa were not independent of those at neighboring beach segments. This high number of autocorrelated abundances cautions against parametric statistical analyses but does not necessarily lead to a statistical bias (Diniz-Filho et al. 2003). Thus, for many or perhaps most benthic taxa in this system, the populations at one segment may be part of a metapopulation that responds similarly to environmental shifts.

Our nested ANOVA analyses examined the spatial scales where population abundances were most variable. Interestingly, taxa more frequent in the northern and central portion of the region were more variable at the smaller site scale (kilometers), whereas taxa more frequent in the south were more variable at the larger area scale (tens of kilometers). Along with the finding that diversity in the north is slightly higher at the site scale and in the south increases substantially at the area scale, this suggests that an important spatial scale of interest for studies of diversity and change may be the area level (tens of kilometers) in the south, whereas in the northern and central portion of the region the important scale may be at the site level (<1 km). Interannual variability was also greatest at the site and area scales although most taxon abundances (236 out of 268) exhibited no significant interannual differences among the three years.

If the sampled rock platforms were exact physical replicates then we would expect lower within-site and within-area variability in addition to highly autocorrelated population abundances. However, in apparent contradiction to this hypothesis, we found high variance in population abundances among our replicate sites. Even though we considered our segments to be replicate samples, this is a statistical construct and not realistic in a natural environment because exact replicates along a latitudinal oceanic gradient are unlikely to exist. The biological variance we observed is most likely a function of slight differences in the physical structure of each rock platform, compounded by species interactions as well as more remote oceanic and atmospheric forcings. Because interactions are local, interactions between species are also more likely to affect local taxon richness at the smaller (segment and site) scales in comparison to the larger (area and domain) scales, where dispersal and oceanographic effects are more likely to predominate (Russell et al. 2006).

Given these considerations, our analyses of population abundances are consistent with a broader version of the upwelling-based hypothesis proposed by Roughgarden et al. (1988) and Connolly and Roughgarden (1999b). That is, interactions, the effects of which are expected to dominate variation among populations and communities on the local scale, may have a stronger influence to the north (where greater population variation was observed at smaller scales). In contrast, propagules, particulates, and nutrients, factors in which variation is oceanographically-driven, may have a relatively stronger influence to the south (where greater population variation was observed at larger scales).

*Community structure*—At the domain scale, where smaller scale site and area effects on taxa are spatially integrated, we found that community structure changes gradually with latitude even though overall diversity is not considerably different among domains. Many of the taxa found in Washington were also found in more southern domains but fewer southern taxa were found in Washington, suggesting that along the California Current during our period of observation northern taxa exerted a more dominant presence. This is logical considering the north to south flow direction of the California Current. Of the 268 taxa found, most occurred frequently in the low zone (168), and most taxa were observed most frequently in Washington (82), Central California (56), and the outer coast of the Channel Islands (58). Fewer taxa were most frequently observed in Southern California (39), Northern California (41), and Oregon (17) even though most of the taxa observed in Washington were also found in Oregon (93%) and Northern California (89%). This suggests that most taxa associated with the California Current were found (at some point) in all domains, but that some taxa were more frequently observed and subsequently were more strongly associated with geographically local observations (i.e., sites). The Channel Islands are notable in that they are perfused by water from both the California Current (the outer coast) and the Southern California Bight (the inner coast), and thus have unusually high diversity for that domain when all island shores are considered (Blanchette et al. 2006).

Our analyses showed two contrasting types of taxa driving the differences between communities (Table 9, Fig. 7). Some taxa occurred everywhere and dominated certain segment scale communities by sheer abundance (e.g., *Balanus glandula*, crustose and erect corallines, *Semibalanus cariosus*, *Mytilus californianus*), and some taxa changed communities by high frequency but relatively low abundances (e.g., *Mazzaella splendens*, *Tetraclita rubescens*, *Chondracanthus canaliculatus*). Many taxa were unique to a geographic location but were either infrequently observed or were in very low abundances (or both), and thus were not statistically influential given the large number of taxa (268) being considered in the analysis. For example, in the low zone, 27% of the taxa were found in fewer than 5% of the sampled segments, and this increases to 38% and 41% in the mid and high zones, respectively. These taxa were not important drivers of statistical community structure but they may still have significant ecological effects on the community (see Berlow 1999).

*Community distribution*—Surprisingly, our analysis of community distribution patterns did not reveal biogeographic boundary locations other than the well known boundary at Point Conception. Some populations exhibited spatial distribution patterns supporting biogeographic boundaries at Monterey, Pt. Reyes, Cape Mendocino, Cape Arago, but few taxa were consistently bounded by the same geographic feature. This suggests that bathymetric or oceanic features may present boundaries to the dispersal of some taxa but not to others, and therefore, are not boundaries in a general sense but rather temporally or

spatially “leaky” barriers to certain taxa with life histories sensitive to the magnitude of the barrier. Apparently, the strongest barriers like Pt. Conception result in distinctly different communities, but weak barriers such as those around Capes Arago, Blanco, and Mendocino cause more gradual shifts in community structure.

There was a clear distinction between the low and mid zone area-scale communities on the Southern California mainland and those on the Channel Islands outer coast (Fig. 7a,b). This pattern is present but less evident in the high zone (Fig. 7c). The Channel Island high zone communities shifted in a direction consistent with the area samples further north, indicating that these communities may be part of the northern oceanic and biological continuity (Blanchette et al. 2006). The mainland area communities, however, are not only clearly distinct from all other communities but also deviate from the gradual north to south shift in community structure and may, therefore, be forced by other physical and biological mechanisms associated with the Southern California Bight. This distinction is also supported by evidence of genetic divergences found within some kelp species occupying both the outer coast of the Channel Islands and the Southern California Bight (Miller et al. 2000).

Our surveys have filled a major gap in our understanding of patterns of community structure in rocky intertidal communities along the CCLME. In addition, as has already been demonstrated (Russell et al. 2006), the resulting database can be a highly valuable resource for synthetic analyses of patterns of diversity and abundance across biogeographic scales. Our most surprising result was the documentation of an inverse pattern of diversity: species richness was greater to the north rather than to the south. Further, this pattern depended on spatial sampling scale; the inverse pattern was evident at smaller scales (meters to kilometers) but shifted to the more normal increase with decreasing latitude at larger scales (tens to hundreds of kilometers).

Analyses examining the contribution of environmental parameters to variation in community structure and population abundance indicated that broad patterns of community structure varied with a subset of the possible factors that could influence the biota, with strong associations with gradients in temperature (air and sea), upwelling, precipitation and tidal range, and, in the low zone, sand. Community responses were complex, varying by zone and latitude in which factors had the greatest association with structure and abundance. Not surprisingly, wave runup had the overall most important effect in structuring these communities. Population densities varied differentially with the scale of sampling and in a manner consistent with the hypothesis that oceanographic variability can drive patterns of community structure and dynamics. Population variation was greatest on local scales to the north, where recruitment and phytoplankton inputs are known to be greater, possibly leading to stronger influences of species interactions, whereas population variation was greatest on large scales to the south, where recruitment and phytoplankton inputs are known to be low, possibly leading to stronger influences of processes dependent on oceanography.

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