Ecological subsidies to rocky intertidal communities: Linear or non-linear changes along a consistent geographic upwelling transition?

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ABSTRACT

Through bottom–up inputs and larval transport, benthic–pelagic links can have an important effect on benthic community structure. Recent work on community structure of northeast Pacific rocky shores has focused on latitudinal differences in recruitment of intertidal invertebrates as a driver of variation in community structure. Recruitment differences are associated with a transition in upwelling near Cape Blanco in southern Oregon. Here we examine the transition in recruitment along an unstudied gap on the northern California and Oregon coasts, document a latitudinal gradient in bottom–up factors, and examine if major coastal promontories associated with upwelling plumes potentially separate benthic–pelagic coupling into regions. We monitored the recruitment of intertidal invertebrates, chlorophyll *a* concentrations in coastal waters, and the growth rates of mussels at numerous sites along the northern California and Oregon coasts. The transition in recruitment of intertidal invertebrates from north to south changed from very high levels north of Cape Blanco, to intermediate levels between Capes Blanco and Mendocino, to very low levels south of Cape Mendocino. The specific shape of the recruitment cline varied among species. Chlorophyll *a* concentrations and mussel growth rates were higher north of Cape Blanco than south of Cape Blanco, indicating that bottom–up factors may also drive regional differences in rocky shore community structure. Distinctive timing between regions of recruitment and plankton pulses suggests that benthic–pelagic coupling may be somewhat independent between these regions, which are separated by major coastal promontories. Our results highlight the large variability in spatially coupled ecosystems along the northern California and Oregon coasts that drive the latitudinal gradient in rocky shore community structure in the northeast Pacific.

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1. Introduction

Linkages between ecosystems can be important to population and community dynamics (e.g., Cederholm et al., 1999; Loreau et al., 2005; Polis and Hurd, 1996; Turner and Rabalais, 1994). In marine communities coupling between pelagic and benthic environments has often been found to be strong (Bustamante et al., 1995; Menge et al., 1997a, 2003, 2004; Navarrete et al., 2005; Witman et al., 2010). Benthic communities can be linked to inner shelf waters (sometimes termed benthic–pelagic coupling; e.g., Menge et al., 1997a) in two ways. First, oceanographic processes can affect the distribution and supply of propagules to benthic communities (Roughgarden et al., 1988; Wing et al., 1995b). Second, oceanographic processes can be key drivers of supplies of phytoplankton and detritus, which are primary food sources for filter-feeding

"basal" species in intertidal and other benthic communities. Flows from the shore to the inner shelf waters include the release of gametes or larvae and the production of macrophyte-derived detritus. Particulates and larvae inputs flowing across the boundaries of benthic communities are referred to as "ecological subsidies" (Polis and Hurd, 1996).

Studies along the U.S. west coast on rocky intertidal community-dynamics and oceanography provide a framework for understanding the effects of consistent ocean circulation patterns upon community structure through benthic–pelagic coupling. During April through September in the northern California Current system (hereafter NCCS), coastal upwelling dominates along northern California and Oregon (Fig. 1; Huyer, 1983). Upwelling is caused by the combination of equatorward winds and the Coriolis effect, which push warmer nutrient-poor surface waters offshore, generating circulation that leads to their replacement along the coast by cold nutrient-rich water from depth. The NCCS forms a southward-flowing coastal jet that is the frontal boundary between relatively cold coastal upwelled waters and warmer offshore waters. At Cape Blanco in southern Oregon, intensification of
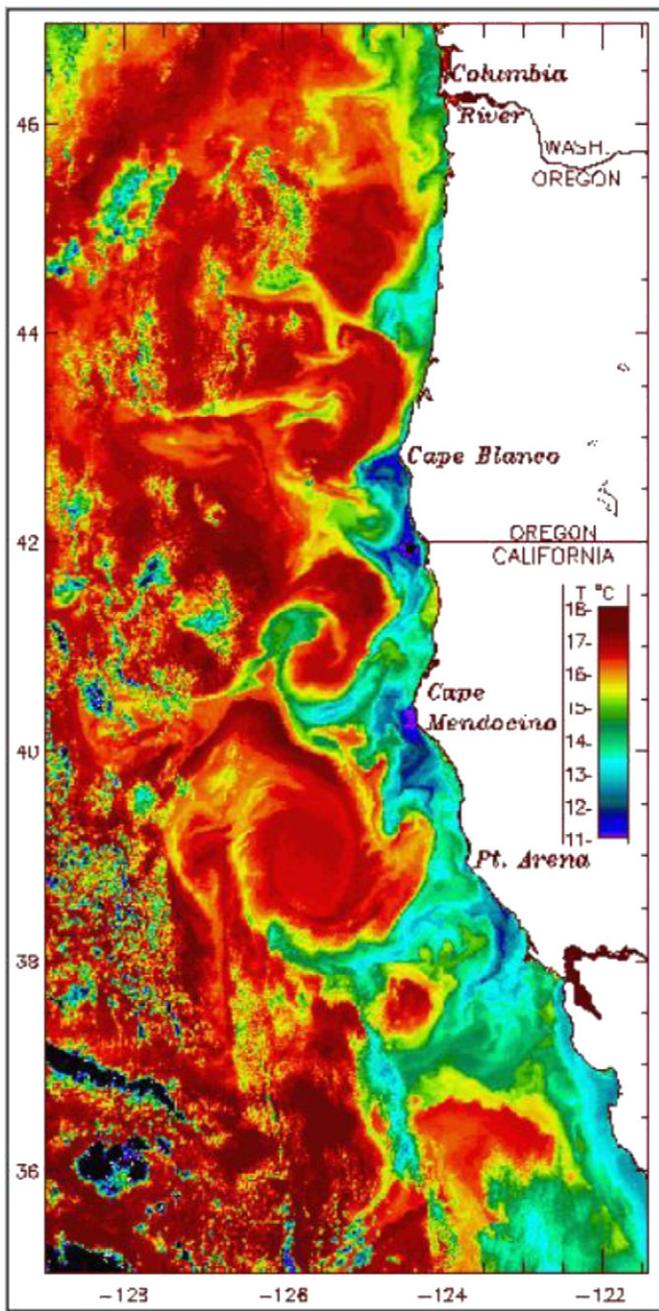
Fig. 1. Oregon and northern California sea surface temperature (AVHRR image) on 5 September 1994. Image courtesy of J. Barth and P. T. Strub, OSU College of Oceanic and Atmospheric Sciences.

Table 1

Nearshore oceanographic comparison of the region north of Cape Blanco and the region south of Cape Blanco (Barth et al., 2000; Batchelder et al., 2002a; Hickey 1998; Huyer, 1983; Largier et al., 1993).

	North of Cape Blanco	South of Cape Blanco
Upwelling	• Weaker • More intermittent • Occurs primarily during summer months	• Stronger • More consistent • Occurs throughout most of the year
Coastal jet	Follows the continental shelf bounding a relatively narrow zone of upwelled water.	Oceanic, meandering, and bounds a relatively large zone of upwelled water.
Important features	Straight coastline lacking areas of intensification of upwelling, and nearshore banks that result in gyres where productivity may be retained.	Large coastal promontories, such as Cape Mendocino, that promote intensified upwelling that can form upwelling plumes that stretch far offshore.
Potential for retention of plankton	Higher	Lower
Potential for delivery of subsidies	Higher	Lower

and Russell, 1988; Wing et al., 1998). Recruitment to coastal populations can occur when upwelling winds relax, bringing offshore waters with larvae back onshore (Farrell et al., 1991; Shanks et al., 2000; Wing et al., 1998). The intensification of upwelling at coastal promontories results in plumes of upwelled water, which may flush larvae offshore away from suitable adult habitat as they move generally southward in the California Current (Ebert and Russell, 1988) and potentially be prevented from reaching coastal waters south of the plume (Wing et al., 1998). Similarly, phytoplankton and other zooplankton (particulates) can be concentrated in gyres (Lamb and Peterson, 2005) or carried offshore by upwelling plumes and large meanders in the coastal jet (Abbott and Zion, 1985; Batchelder et al., 2002a; Peterson and Keister, 2002).

The role of cross-shelf transport associated with upwelling and relaxation events is controversial. Recent studies indicate that larval behavior can interact with currents to keep larvae close to shore, where mechanisms such as tidal bores, internal waves, and perhaps surf waves may transport larvae to the shore (e.g., Morgan et al., 2009a,b; Shanks and Brink, 2005; Shanks et al., 2010). Nonetheless, evidence also suggests that shoreward transport of larvae can also result from upwelling events, as described above. Mussel larvae, for example, appear to maintain a position near the bottom, and to be transported shoreward when upwelling occurs (Rilov et al., 2008). Studies in Oregon suggest that barnacle recruitment is often associated with upwelling relaxation (Dudas et al., 2009a,b; Shanks, 2009b) and analyses of long-term recruitment datasets suggest that with the inclusion of large-scale climatic patterns (e.g., North Pacific Gyre Oscillation, El Niño Southern Oscillation, Pacific Decadal Oscillation), upwelling explains 37–40% of the variance in recruitment of mussels and barnacles (Menge et al., 2011a).

The ecological structure of rocky shore communities varies along the U.S. west coast (Blanchette et al., 2009; Schoch et al., 2006). Competition, predation, and disturbance play a primary role in explaining the patterns of distribution and abundance of organisms at rocky intertidal sites along the coasts of Washington (Dayton, 1971; Paine, 1966) and Oregon (Menge et al., 1994, 1997a,b, 2004; Navarrete, 1996; Berlow, 1997). On the rocky shores of Washington and Oregon, which have ample recruitment, communities were thought to be structured by post-recruitment processes. In contrast, at rocky intertidal sites along the central California coast, fluctuations in the abundance of organisms were postulated to be the result of recruitment variability, because generally low recruitment prevented post-recruitment processes from coming into play (Gaines and Roughgarden, 1985; Roughgarden et al., 1988). The apparently different dynamics on the Washington and central California coasts led Roughgarden et al. (1988) to hypothesize that a

upwelling leads to the coastal jet separating from the continental shelf where it stretches, deepens and becomes oceanic as it moves well offshore (100+ km) to the south of the cape (Barth et al., 2000; Castelao and Barth, 2005; Keister et al., 2009). In general, Cape Blanco separates two ocean circulation regimes within the NCCS (Parrish et al., 1981, Fig. 1, Table 1).

Although the NCCS is very productive, ocean circulation mediates the supply of pelagic subsidies to rocky intertidal communities. Several factors underlie the transport of larvae to and from benthic habitats, including coastal upwelling, internal waves, tidal bores, and larval behavior (Farrell et al., 1991; Morgan et al., 2009a,b; Pineda, 2000; Shanks, 2009a,b; Shanks and Brink, 2005). With respect to upwelling, the offshore flow of water in coastally upwelled areas can carry benthic larvae offshore where they can be concentrated at the upwelling front (Roughgarden et al., 1988) or in gyres that may retain larvae (Ebert

latitudinal gradient in community structure exists along the U.S. west coast, which was postulated to be the result of a corresponding gradient in recruitment of invertebrates caused by the latitudinal gradient in coastal upwelling (e.g., Connolly and Roughgarden, 1999).

Several studies have examined Roughgarden et al.'s (1988) hypothesis with mixed results. A latitudinal gradient in both recruitment of intertidal invertebrates (Connolly et al., 2001; Broitman et al., 2008) and the abundance and distribution of dominant intertidal invertebrates (Connolly and Roughgarden, 1998) appeared to be consistent with the hypothesis, while predictions about top–down effects (Connolly and Roughgarden, 1999) were only partially supported (Menge et al., 2004). Rather than a gradual cline in recruitment with decreasing latitude, however, evidence suggested that an abrupt transition occurs at or around Cape Blanco, Oregon (Broitman et al., 2008; Connolly et al., 2001), where there is a concurrent abrupt transition in upwelling (Barth et al., 2000; Huyer, 1983; Parrish et al., 1981). Because the spatial resolution of the recruitment dataset was rather coarse, with an unsampled gap around Cape Blanco of ~350 km (3° latitude) between Cape Arago and Cape Mendocino, the nature of the transition in recruitment, whether linear or non-linear with distance alongshore, was unclear. Similarly, it was unknown if a parallel change in phytoplankton and particulate concentration, an important determinant of community structure as well (Menge et al., 1997a, 2004), was also correlated with ocean current patterns, as they are along the central Oregon coast. Determining the patterns of ecological subsidies within this region should help clarify how nearshore ocean circulation affects benthic–pelagic coupling.

In this study we quantified ecological subsidies over several years at sites from Point Arena, California, to Cape Meares, Oregon, a distance of ~850 km. We focused on two classes of ecological subsidies, inputs of larvae and of particulates, and how these varied across the previously unstudied gap in southern Oregon and northern California. We quantified recruitment rates of barnacles and mussels, phytoplankton concentrations, and growth rates of the dominant mussel species to determine the relationship between oceanic circulation and ecological subsidies. We predicted that bottom–up effects on phytoplankton and mussels were inversely related to the strength of upwelling. Areas of strong and persistent upwelling were predicted to have low recruitment and low bottom–up inputs to filter-feeding invertebrates because the concentration of larvae and particulate food for filter feeders would be diluted by advection away from the coastal zone. Areas with moderate and intermittent upwelling were predicted to have higher larval and food concentrations and thus inputs from ecological subsidies should be stronger.

We tested three alternative hypotheses concerning the unstudied gap. Changes in subsidies exhibit:

H1. a steady linear decrease from Cape Blanco southward,

H2. a single step function transition from high values north of Cape Blanco to low values south of Cape Blanco, and

**H3.** two step function transitions with one step at Cape Blanco and one step at Cape Mendocino.

Thus, while the coastal upwelling regime has a large transition at Cape Blanco, upwelling intensity increases from Cape Blanco to south of Cape Mendocino (Parrish et al., 1981), potentially leading to a linear decrease across the region (i.e., Hypothesis 1). Alternatively, the abrupt change in circulation at Cape Blanco could serve as a barrier between a region of high subsidies to the north and low subsidies to the south (i.e., Hypothesis 2). Another alternative is that the upwelling plume associated with Cape Mendocino (Largier et al., 1993) could serve as a second barrier to dispersal, generating successive nonlinear drops in subsidies around both Capes Blanco and Mendocino (i.e., Hypothesis 3).

2. Methods

Study sites (n = 24) were located on wave-exposed rocky shores along the U.S. West coast from Point Arena, California (38.94° N) to Cape Meares, Oregon (45.47° N) (Fig. 2). Recruitment and growth studies were conducted at the mid tidal-elevation of the mussel (*Mytilus californianus*) bed with haphazard placement of replicates. During each year of the study there were at least four study sites in the previously unstudied recruitment-transition region between Cape Mendocino (40.43° N) and Cape Arago (43.31° N) (Connolly et al., 2001).

2.1. Chlorophyll (a)

Chlorophyll-*a* abundance in inner shelf waters was measured at least monthly from May to August from 2000 to 2003 (minimum n = 4 sample dates per year). On each collection date five water samples were collected at each site from the edge of the reef during a low tide period (e.g., Menge et al., 1997b). Replicates were collected by dipping 250 ml opaque plastic (HDPE) brown bottles clamped to the end of a 2 m long pole to a depth approximately 50 cm below the water surface. Chlorophyll-*a* abundance was determined following established procedures (Menge et al., 1997b; Parsons et al., 1984). In the field, 50 ml of seawater was filtered through a 25 mm
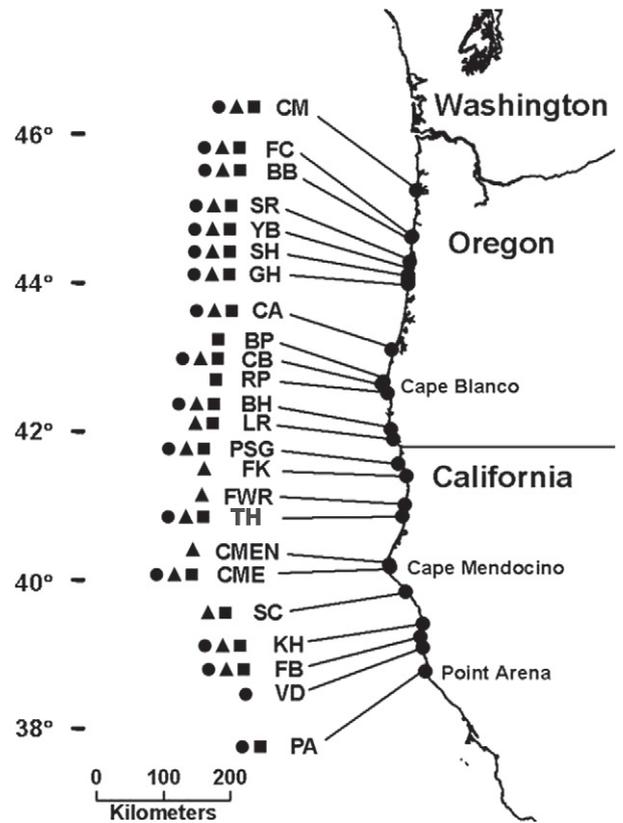
Fig. 2. Map of northern California and Oregon coasts showing locations of study sites and major headlands. The type of studies at each site is indicated by symbols as follows: ● = chlorophyll *a* concentrations; ▲ = mussel growth rates; ■ = mussel and barnacle recruitment. Sites are specified with a multi letter abbreviation as follows: CM = Cape Meares (45.47); FC = Fogarty Creek (44.84); BB = Boiler Bay (44.83); SR = Seal Rock (44.50); YB = Yachats Beach (44.32); SH = Strawberry Hill (44.25); GH = Gull Haven (44.20); CA = Cape Arago (43.31); BP = Blacklock Point (42.87); CB = Cape Blanco (42.84); RP = Rocky Point (42.72); BH = Burnt Hill (42.23); LR = Lone Ranch (42.10); PSG = Point St. George (41.78); FK = False Klamath Cove (41.50); FWR = Fresh Water Rocks (41.20); TH = Trinidad Head (41.07); CMEN = Cape Mendocino North (40.42); CME = Cape Mendocino (40.35); SC = Shelter Cove (40.03); KH = Kibessilah Hill (39.60); FB = Fort Bragg (39.43); VD = Van Damme (39.28); PA = Point Arena (38.94).

combusted Whatman glass fiber filter (GF/F) with a pore size of 0.7 μm using a low vacuum pressure (10 mm Hg), sealed in a centrifuge tube and placed on ice and transported to the laboratory where it was stored at −20 °C until processing. Chlorophyll-*a* abundance was determined using a Turner Designs Model TD 70 fluorometer after a 12-hour extraction in 90% HPLC acetone in the dark at −20 °C. The fluorometer had been previously calibrated using a pure chlorophyll-*a* standard. While point measures in the ocean can vary widely compared to temporally integrated measures (Gaines and Bertness, 1993), comparisons between data from our sampling program, more frequent bottle samples and continuous fluorometric sampling from field deployed fluorometers are all strongly correlated, and thus serve to identify clear regional patterns (K. Nielsen, F. Chan, and B. Menge, unpublished data).

2.2. Mussel growth

The most abundant mussel at all sites was *M. californianus*, and we thus focused on this species. To determine the growth rate of *M. californianus* at each site we followed established procedures (Menge et al., 1994, 2004). At each site mussels that were 35–50 mm in shell length were collected in situ and marked by filing a 2 mm notch in the growing (posterior) end of the mussel. As the mussel grows, the notch is repaired and leaves a distinct mark from which initial size and growth can be measured. Growth rates were calculated as proportional growth (final length − initial length/initial length) ∗ day^{-1} ∗ 1000. Mussels were placed in clumps of 30 or 50 into gaps in the mussel bed. Mussel clumps were held against the rock with plastic mesh cages (Vexar; NorPlex, Auburn, Washington) that were bolted to the rock using lag screws inserted into wall anchors placed into previously drilled holes. The mesh was loosened after one month to allow firmer attachment and removed after the second month. Approximately a year later, mussels were collected and measured for final length, and growth.

2.3. Recruitment

Mussel recruitment was measured using plastic mesh ovoids (SOS Tuffy pads, The Clorox Company, Oakland, California, USA; Broitman et al., 2008; Menge et al., 1994, 2004), hereafter termed "mussel collectors." Mussel collectors were placed haphazardly in gaps in the mid intertidal zone mussel bed. Five collectors per site were deployed and exchanged monthly from late March to December from 2000 to 2003. Mussel collectors were taken from the field to the lab and stored at −20 °C until processed. Mussels were counted by cutting open the mesh pad and spraying it down thoroughly with water into a lab tray. Tray contents were poured through a 250 μm sieve, and sieve contents were then cleaned off into Petri dishes with a small amount of water. Mussel collectors with exceptionally high recruitment (>4000 recruits per mussel collector) were sub-sampled by dividing the sample with a plankton splitter into either halves or quarters. Mussel recruits are defined as juvenile mussels that have metamorphosed into the adult form. They were counted in the lab and identified to genus (*Mytilus* spp.). Recent genetic analyses support earlier conclusions that ~10% of recruits are *M. californianus* and ~90% are the smaller mussel *M. trossulus* (P. Raimondi, unpublished data), a common mussel during early succession in mussel bed gaps (e.g., Paine and Levin, 1981; Wootton, 2002; Menge et al., 2011b).

Recruitment of barnacles was determined using 10×10×0.4 cm plexi-glass plates covered with safety walk tape (3M Company, Saint Paul, Minnesota, USA; Broitman et al., 2008; Menge, 2000), hereafter termed "recruitment plates." Recruitment plates were attached to the rock with a stainless steel lag bolt fastened with a plastic wall anchor in a drilled hole. Upon collection, recruitment plates were returned to the laboratory where recruits were counted under a dissecting scope. Recruitment plates were sub-sampled when total barnacle recruits were greater than 1000 by dividing the plate into four equal corner sections and randomly choosing a corner to count. Barnacle recruitment

is defined as the combination of barnacle cyprids (last planktonic larval stage), metamorphosed barnacles and empty barnacle tests (dead barnacles that were once recruits) found on a plate. Barnacle recruitment was monitored over the same time periods, exchanged on the same schedule as mussel collectors, and counted in the lab. We identified *Balanus glandula* and *Chthamalus dalli* cyprids and metamorphosed barnacles to species.

2.4. Analysis

Response variables were chlorophyll-*a* concentrations, growth rates of the mussel *M. californianus*, and recruitment of *Mytilus* spp., *B. glandula* and *C. dalli*. Annual site averages were used as the response. For chlorophyll-*a* abundance we used the average of the four collection dates per year at a site. In the mussel growth analysis average initial size of mussels at a site for each year was included as a covariate to account for small differences in initial mussel sizes used between sites and years. Recruitment was measured as the average number of recruits per day from April thru November. Assumptions of normality, homoscedasticity, linearity, and the influence of outliers were evaluated using diagnostic plots of residuals versus fitted values, and plots of normal probability versus residuals (normal QQ plot). Data were transformed as needed to meet ANOVA assumptions of normality (ln(*y*) for chlorophyll-*a* abundance, mussel and barnacle recruitment; square root of (*y*) for mussel growth). All models also included year and year by region or latitude interactions. Effect groups (Years and Regions) were compared and 95% confidence intervals of differences were constructed using Tukey–Kramer HSD.

Analysis of variance (ANOVAs) and analysis of covariance (ANCOVAs) were used to determine how the annual average for each biological parameter measured varied among sites. Based on a priori knowledge of the coastal oceanography in the study region, for each biological parameter, three models were compared for best fit: 1) a linear gradient based on latitude (hereafter "latitude model"), 2) a single step cline with the transition occurring at Cape Blanco (hereafter "two-region model"), and 3) a two step cline with transitions at Cape Blanco and Cape Mendocino (hereafter "three-region model"). When two regions were used, sites were grouped into a "North" (sites north of Cape Blanco) and "South" (sites south of Cape Blanco). When three regions were used, sites were grouped into "Northern" (north of Cape Blanco), "Central" (sites between Capes Mendocino and Blanco), and "Southern" (south of Cape Mendocino) regions. We included the CB (Cape Blanco proper) site with sites south of Cape Blanco because oceanographically CB is more similar to sites to the south than to the north (Barth et al., 2000; Broitman et al., 2008; Freidenburg, 2002). Cape Mendocino sites (actually a few km south of the cape) CMEN ("Cape Mendocino") and CMeN ("Cape Mendocino North") were grouped with sites further to the south of Cape Mendocino. Since the latitude model and two-region model had the same number of parameters, the fit of the models was compared using adjusted R^2 values for model fit. The higher parameter three-region model was compared to the other models using extra sum of squares *F*-tests.

We examined between-site correlations of mussel and barnacle recruitment, and chlorophyll-*a* concentration samples to determine if there was evidence for regional breakpoints in the timing of biological responses. Specifically, we examined if the timing of a biological response (e.g., *B. glandula* recruitment) was correlated among sites within a region but not between sites among regions. A NMS (non-metric multidimensional scaling; Kruskal, 1964; Mather, 1976) ordination was used to examine the correlations between multiple sites simultaneously using multiple types of data. The data for each response variable were transformed to standard deviates to eliminate differences in magnitude between sites and give equal weight to the different types of data. A subset of 14 sites was analyzed that maximized both the number of sites in each region and the number of months with concurrent recruitment and measures of chlorophyll-*a*. NMS ordination axes were

rotated to best show the regional correlation patterns in two dimensions, and we used a regions overlay to help visualize those differences.

We used nonparametric MRPP (multi-response permutation procedure; Mielke, 1984) procedures to test for regional groupings (i.e., two-region and three-region models) of sites in their timing of biological events. Tests were also done for pairwise differences between regions in the three region model. A Bonferroni-corrected significance level (p<0.0167) was used to protect for the multiple comparisons. MRPP was performed on rank distances between sites, as it is more analogous to the NMS procedure (McCune and Grace, 2002). Univariate analyses were run with JMP 4.0.4 (SAS Institute, 2001). Multivariate analyses were completed with PC-ORD (McCune and Mefford, 1999). Euclidean (Pythagorean) distance measures were used for MRPP and NMS ordination.

3. Results

We found a latitudinal gradient in chlorophyll-*a* abundance in coastal waters along the Oregon and northern California coasts (Fig. 3). The data were best fit by the latitude model (Table 2). From south to north, chlorophyll-*a* abundance was estimated to increase 1.34 times per degree of latitude (95% confidence interval from 1.23 to 1.46). Chlorophyll-*a* abundance differed among years (Tukey–Kramer HSD, p<0.05), with values approximately 50% lower in 2003 than in 2001 and 2002. The latitude model fit better than the two-region model ($R^2 = 0.531$ vs. $R^2 = 0.412$), and although the three-region model had a slightly better overall fit ($R^2 = 0.558$), the extra parameters in the three region model were not needed to explain the variation in chlorophyll-*a* (Extra Sum of Squares *F*-test, $F_{4, 56} = 0.832$, $P = 0.5105$). After accounting for year, chlorophyll-*a* in the Southern region was lower than both Central and Northern regions, but chlorophyll-*a* abundance in the Central and Northern regions was not different (Tukey–Kramer HSD, p>0.05).

M. californianus growth rates were higher at North sites than South sites (Fig. 4). After accounting for average initial mussel size, the two-region model (Table 2) explained more of the variation in mussel growth than did the latitude model ($R^2 = 0.620$ vs. $R^2 = 0.427$). The extra parameters in the full three region model did no better than the two region model in explaining mussel growth variation (Extra Sum of Squares *F*-test, $F_{3, 42} = 1.18$, $P = 0.33$). After accounting for year and initial mussel size, chlorophyll-*a* was not correlated with mussel growth (ANCOVA Effect Test, $F_{1, 26} = 2.85$, $P = 0.10$).
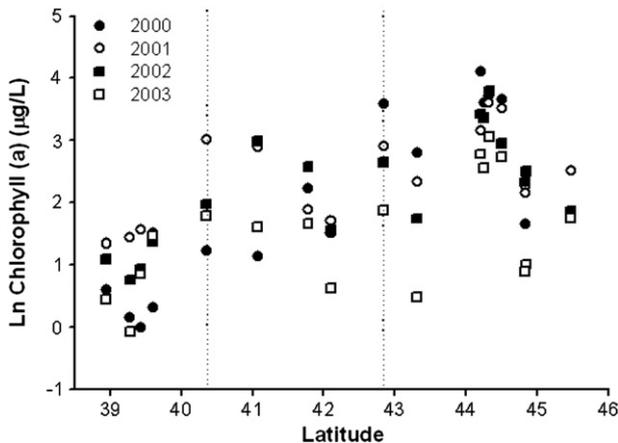
Mytilus spp. recruitment decreased with decreasing latitude (Fig. 5, top). The shape of the latitudinal change depended on whether or not Cape Arago (CA), a consistent outlier north of Cape Blanco, was included in the analysis. With CA included, the latitudinal model ($R^2 = 0.729$,

Table 2) fit better than either the two-region model ($R^2 = 0.680$) or the three-region model ($R^2 = 0.728$, with four more parameters). From north to south, *Mytilus* spp. recruitment decreased by 2.13 times per degree of latitude (95% confidence interval from 1.86 to 2.43). Without CA the transition in *Mytilus* spp. recruitment was best fit by the three-region model ($R^2 = 0.834$), improving on the two-region model (Extra Sum of Squares *F*-test, $F_{4, 47} = 3.51$, $P = 0.014$). Not including CA, the two-region model ($R^2 = 0.784$) had a slightly better fit than the latitude model ($R^2 = 0.771$). Northern sites had 40 times higher recruitment than Southern sites (95% confidence interval from 20 to 78.5, Tukey–Kramer HSD, p<0.05) and 14 times higher recruitment than Central sites (95% confidence interval from 7.6 to 25.5, Tukey–Kramer HSD, P<0.05), while Central sites had 2.8 times higher recruitment than

Table 2
Results of best fitting ANOVA or ANCOVA between the latitudinal model, two-region model and three-region model for Chlorophyll-*a* concentration, *M. californianus* growth, *Mytilus* spp. recruitment, *B. glandula* settlement and *C. dalli* settlement. CA = Cape Arago.

Analysis	Source	Df	MS	F	P
Chlorophyll (a) concentration	Year	3	2.633	4.549	**0.0061**
	Latitude	1	27.883	48.166	**<0.0001**
	Year X latitude	3	1.196	2.065	0.1143
	Residual	60	0.579		
M. californianus growth	Initial mussel size	1	0.028	0.731	0.3983
	Year	2	0.001	0.020	0.9799
	Two-region	1	1.859	49.209	**<0.0001**
	Year X two-region	2	0.033	0.873	0.4262
	Residual	36	0.038		
Mytilus spp. recruitment with CA	Year	3	1.745	1.794	0.1592
	Latitude	1	129.690	133.339	**<0.0001**
	Year X latitude	3	3.137	3.226	**0.0295**
	Residual	54	0.973		
Mytilus spp. recruitment without CA	Year	3	0.212	0.323	0.8088
	Three-region	2	69.930	106.327	**<0.0001**
	Year X three-region	6	1.779	2.705	**0.0244**
	Residual	47	0.658		
B. glandula settlement	Year	3	0.278	0.575	0.6339
	Latitude	1	55.240	114.0715	**<0.0001**
	Year X latitude	3	0.604	1.247	0.3016
	Residual	55	0.483		
C. dalli settlement	Year	3	1.242	1.279	0.2914
	Three-region	2	11.435	11.777	**<0.0001**
	Year X three-region	6	0.612	0.630	0.7054
	Residual	51	0.971		

Fig. 3. Yearly mean concentration of chlorophyll-*a* (μg/l) in coastal water samples as a function of latitude. Dotted lines indicate the location of Cape Mendocino (left) and Cape Blanco (right).
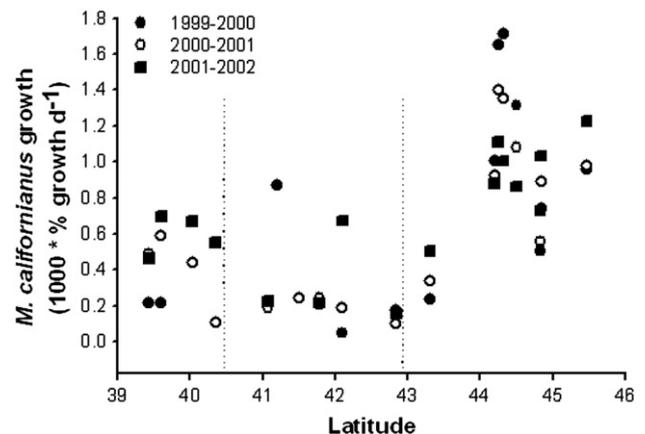
Fig. 4. Annual proportional growth per day of the mussel *M. californianus* as a function of latitude. Dotted lines indicate the location of Cape Mendocino (left) and Cape Blanco (right).
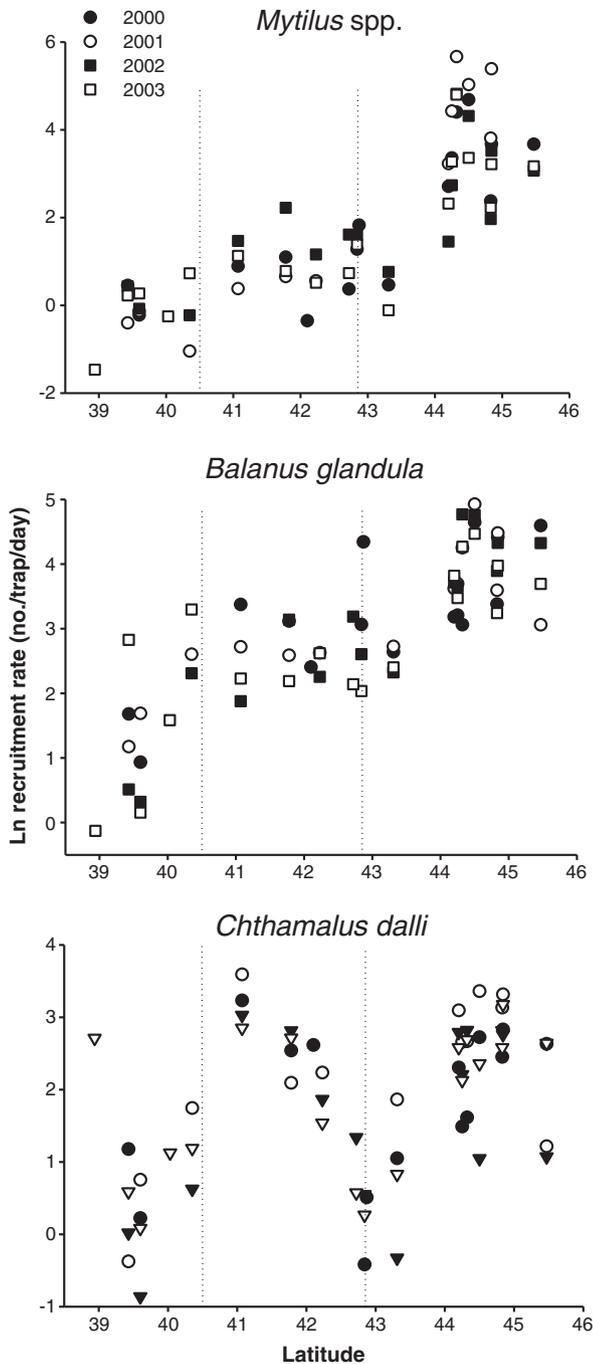
Fig. 5. Yearly mean *Mytilus* spp. (top) and *B. glandula* (middle) and *C. dalli* (bottom) recruitment rates from April through December expressed as numbers per collector per day as a function of latitude. Dotted lines indicate the location of Cape Mendocino (left) and Cape Blanco (right).

Southern sites (95% confidence interval from 1.4 to 6.0, Tukey–Kramer HSD, p<0.05).

Recruitment rate of the barnacle *B. glandula* decreased steadily with decreasing latitude (Fig. 5, middle). The latitude model best explained the transition in *B. glandula* recruitment ($R^2 = 0.696$, Table 2), with recruitment per day decreasing from north to south by 1.6 times with each degree latitude after accounting for year (95% confidence interval from 1.5 to 1.8). CA was a consistent outlier in the Northern region. Analysis without the CA site improved the fit of the three-region model (from $R^2 = 0.646$ to $R^2 = 0.729$) and the two-region model (from $R^2 = 0.526$ to $R^2 = 0.607$), but the latitude model still explained the variation in *B. glandula* recruitment better

for the given number of parameters ($R^2 = 0.720$, Extra Sum of Squares *F* Test, $F = 0.43$, $P = 0.79$). In the analysis without CA, Northern sites had 12.6 times higher recruitment than Southern sites (95% confidence interval from 7.0 to 22.8, Tukey–Kramer HSD, p<0.05) and 3.8 times higher recruitment than Central sites (95% confidence interval from 2.25 to 6.5, Tukey–Kramer HSD, p<0.05), while central sites had 3.3 times higher recruitment than Southern sites (95% confidence interval from 1.7 to 6.3, Tukey–Kramer HSD, p<0.05).

C. dalli recruitment rates were lowest at Southern sites (Fig. 5, bottom). None of the latitudinal change models explained the transition in *C. dalli* settlement well, but of the three models, the three-region model fit best (Table 2: three-region, $R^2 = 0.378$; latitude, $R^2 = 0.260$; two-region, $R^2 = 0.180$). The additional resolution provided by the extra parameters in the full three-region model from the full latitude model was weakly supported (Extra Sum of Squares *F* Test, $F_{4, 51} = 2.43$, $P = 0.0599$), but if (the non-significant) interaction terms were excluded, the extra parameters in the three-region model were strongly supported over the latitude model (Extra Sum of Squares *F* Test, $F_{1, 57} = 6.87$, $P = 0.01$). Further, deletion of the outlier site CA from the analysis even more strongly supported the need for the extra parameters in the three-region model with interactions (Extra Sum of Squares *F* Test, $F_{4, 47} = 3.79$, $P = 0.009$). Using the three-region model with interactions, Northern sites had 4.97 times higher recruitment than Southern sites (95% confidence interval from 2.2 to 11.2, Tukey–Kramer HSD, p<0.05) and 1.2 times higher recruitment than Central sites (95% confidence interval from 0.59 to 2.5, Tukey–Kramer HSD, p<0.05), while central sites had 4.1 times higher settlement than sites south of Cape Mendocino (95% confidence interval from 1.66 to 10.3, Tukey–Kramer HSD, p<0.05).
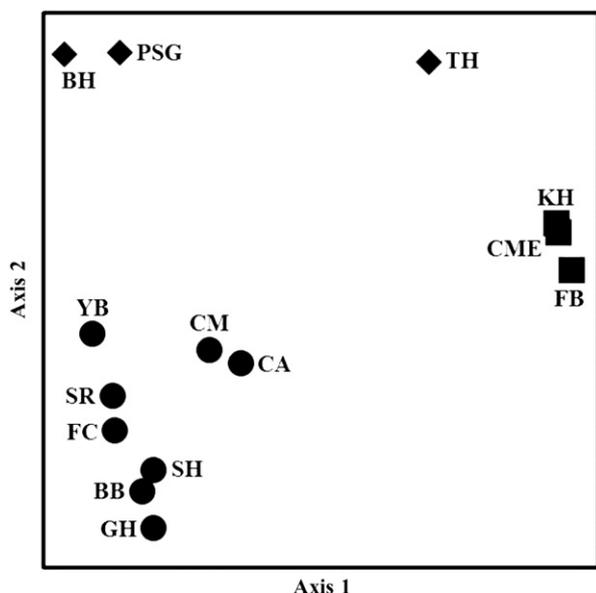
Fluctuations in chlorophyll-*a* concentration, *Mytilus* spp. and barnacle recruitment were more highly correlated between sites within regions than between sites among regions (Fig. 6, Table 3). A NMS ordination indicated a 3 dimensional solution was appropriate (Monte Carlo test, $P = 0.0196$, final stress = 6.190) in which sites visually form three clusters that correspond to the three geographic regions. Sites closer together in ordination space had more highly correlated temporal variation of biological responses than sites farther apart (e.g., FB versus KH: $R^2 = 0.648$ compared to TH versus YB: $R^2 = 0.003$). The three-region model fits the data better than the two-region model (Table 3; two-region model $A = 0.259$ versus three-region model $A = 0.468$). However, the TH site from the Central region was an outlier. In ordination space TH was located between the cluster of the other two sites in the Central region (BH and PSG) and the cluster of sites from the Southern region (Fig. 6). This resulted in marginal but nonsignificant evidence that chlorophyll-*a* abundance and settlement between the Central and Southern regions were more highly correlated between sites within each region than among sites between the two regions (Table 3).

4. Discussion

4.1. Latitudinal variation in bottom–up inputs

The increase from south to north in coastal chlorophyll-*a* abundance and *M. californianus* growth (Figs. 3 and 4, Table 2), indicates that variation in food supply subsidies may contribute to the latitudinal gradient in community structure (Connolly et al., 2001; Menge et al., 2004). The northward increase in chlorophyll-*a* abundance indicates that more phytoplankton is available to be consumed by filter-feeding invertebrates north than south of Cape Blanco (Fig. 3; note log scale).

The latitudinal change in coastal phytoplankton, like the latitudinal change in recruitment, is likely to be dependent in part on regional differences in upwelling (see below). Other potential factors that could have an influence include differences in nutrient availability, zooplankton grazing pressure, and onshore wave transport (e.g., McPhee-Shaw et al., 2011). The nutrient availability hypothesis is unlikely given that the latitudinal gradient in upwelling is negatively correlated with the

Fig. 6. NMS ordination of sites in *Mytilus* spp. recruitment, *B. glandula* and *C. dalli* settlement, and chlorophyll-*a* concentration standard deviate space. The ordination is based on standard deviates of sampling periods (monthly periods for recruitment and settlement, point samples for chlorophyll-*a*) from the site average of that parameter (e.g., *Mytilus* spp. recruitment). Sites are compared to each other using sampling periods. The closer the sites are to each other in ordination space the more highly correlated the standard deviates across sampling periods were between those sites and the better the timing of recruitment, settlement and chlorophyll-*a* concentration matched between those sites. The three dimensional ordination is rotated to show the regional structure of the ordination in two dimensions. Symbols code for region (solid circles = Northern, solid diamonds = Central, solid squares = Southern), and sites are specified with their multi-letter abbreviation (see Fig. 2 caption for code). The NMS ordination represented the structure of the original data well (90.5% of the variance represented). Axes 1 and 2 were correlated with multiple sampling periods from each parameter.

phytoplankton gradient. Recent analyses suggest that in fact, along the Oregon and northern California inner shelf, nutrient concentration is negatively, not positively associated with phytoplankton concentration (F. Chan et al., unpublished data).

The grazing pressure hypothesis is also unlikely. Zooplankton density in the inner shelf region is likely to be reduced by the offshore transport component of upwelling (e.g., Fig. 5, Roughgarden et al., 1988; Spitz et al., 2005; Wing et al., 1998), and with more intense upwelling to the south, this reduction would likely be greater in the south, so planktonic grazer abundance and phytoplankton abundance would be positively correlated. Since inverse correlations between grazers and phytoplankton are the typical signature of strong grazer effects, this positive correlation would be opposite to the pattern needed to drive the phytoplankton gradient. A recent analysis (McPhee-Shaw et al., 2011) has shown that along northern California, spring phytoplankton blooms are most strongly associated with increases in significant wave height (SWH). Since SWH increases with increasing latitude along the US west coast

(Schoch et al., 2006), at least some of the northward increase in coastal phytoplankton blooms could also be associated with SWH.

4.2. Mussel growth

While phytoplankton is just one potential food source for filter feeding invertebrates in the rocky intertidal zone (others include detritus, bacteria, and zooplankton; Morris et al., 1980), mussel growth is faster when phytoplankton is the primary component of the particulate resources available to filter feeders (Bracken, 2003; Bracken et al., in prep.). In our analysis, chlorophyll-*a* abundance was not correlated with *M. californianus* growth. In a longer time series (1990–2006) analysis, however, mussel growth was explained by a combination of temperature and food (chlorophyll-a) abundance (Menge et al., 2008). Menge et al. (2008) also showed that site-linked differences in mussel growth that had existed in the 1990s disappeared in the 2000s, a difference that was largely associated with a large increase in food abundance in the years 2000–2001. In this context, although mussel growth rates and chlorophyll-*a* abundance were both higher in the North than in the South, it is not surprising that we did not find a correlation between the two. The data reported here were taken over a shorter (3 year) period that occurred during the years of peak coastal chlorophyll-*a* abundance (2000–2003), when among-site and among-region differences were likely reduced.

As noted, temperature has been shown to be strongly associated with mussel growth (Blanchette et al., 2006; Menge et al., 2008). However, over the latitudinal range (~39° N to 46° N) of this study, air and water temperatures vary little (Schoch et al., 2006), so temperature seems an unlikely explanation of the differences in mussel growth reported here. Time of emersion could explain the North–south difference, and tide range does decline southward, but does so clinally, not abruptly as does mussel growth (Fig. 4, Schoch et al., 2006). Thus, the primary environmental factors that vary abruptly across Cape Blanco and are most strongly associated with the abrupt change in mussel growth around this cape are upwelling and phytoplankton abundance.

The higher growth rates of *M. californianus* north of Cape Blanco than south of Cape Blanco are further evidence of regional differences in bottom–up inputs to the northern California and Oregon coasts. Since mussels are the dominant competitor for space in this region (Paine, 1966), regional differences in *M. californianus* growth rates are likely to affect community structure. North of Cape Blanco the higher growth rate of *M. californianus* is likely to intensify competition for space and therefore also increase the importance of predation and disturbance of *M. californianus* as factors opening up space for other species (Menge and Sutherland, 1987; Paine, 1966). In contrast, the slower growth rate of *M. californianus* south of Cape Blanco is likely to decrease the intensity of competition for space while increasing the importance of recruitment events to fluctuations in cover of different species (Gaines and Roughgarden, 1985).

4.3. Latitudinal recruitment transition

The associated transition in recruitment does not appear to happen specifically at Cape Blanco as previously thought (Connolly et al., 2001). Rather, the intermediate levels of recruitment found in the Central region between Cape Blanco and Cape Mendocino appear to signify a transition zone between the very high levels of barnacle and mussel recruitment north of Cape Blanco and the very low levels of recruitment south of Cape Mendocino (Fig. 5, Table 2). For all species, CA was a consistent outlier in the Northern region, which may be explained by strong highly localized upwelling at Cape Arago (B. Menge, personal observation). The outlier status of this site is emphasized by the high recruitment seen at the next site south, Blacklock Point, located just north of Cape Blanco. Our data, and three additional years of data by Freidenburg (2002) reveal levels of recruitment at this site that are

Table 3
Results of MRPP (multi-response permutation procedure; Mielke, 1984) tests for two-region and three-region models, and tests for all pairwise comparisons between regions. The chance-corrected within-group agreement (A) is a measure of the effect size. A = 0 when the heterogeneity within groups equals what is expected by chance, and A = 1 when all items within groups are equal.

Regions	A	P
Three region model	0.4676	<**0.0001**
Two region model	0.2592	**0.0013**
Multiple comparisons (significance when P<0.0167)		
Northern vs Central	0.2546	**0.0012**
Northern vs Southern	0.3782	**0.0005**
Central vs Southern	0.3175	0.0249

much higher than at CA, more comparable to sites north of CA and intermediate between these and CB.

The groupings of variation in correlations of recruitment and chlorophyll-*a* abundance between sites in the NMS ordination also matched well to the three-region model. The exception was TH, which did not group out in a tight cluster with the other sites in the Central region (Fig. 6). A comparison of the MRPP results for the two-region and three-region models indicates strong evidence for three regions, but the MRPP results for the comparison between the Central to the Southern region gave suggestive but inconclusive evidence for a difference between those two regions (Table 3). The physical or biological processes that cause variation in recruitment and coastal chlorophyll-*a* abundance are evidently decoupled between the Northern and Central regions and at least partially decoupled between Central and Southern regions.

Several nearshore current patterns could help explain potential causes of the Central transition region. While upwelling is stronger and the upwelling front is typically farther offshore in the Central than in the Northern region, upwelling is typically even more intense and the upwelling front tends to be located even further offshore in the Southern region (Huyer, 1983). Cold water filaments, which can be tens of meters deep and extend more than 200 km offshore, are associated with an intensification of upwelling at headlands in the California Current (Davis, 1985; Kelly, 1985), including Cape Blanco (Barth et al., 2000) and Cape Mendocino (Largier et al., 1993). The areas immediately south of coastal headlands are often associated with an anticyclonic eddy (Barth et al., 2000; Largier et al., 1993) that can result in the retention of and higher recruitment of benthic larvae (Ebert and Russell, 1988; Wing et al., 1995a). In contrast, north of coastal headlands nearshore waters move southward in the general flow of the California Current, and hence larvae and other plankton may get swept offshore with the recently upwelled cold water in the filaments (Barth et al., 2000; Barth, 2003; Largier et al., 1993; Wing et al., 1995a). The interaction between gradual upwelling intensification and the proposed strong offshore flushing of larvae at Capes Blanco and Mendocino could result in the non-linear changes in larval concentration observed in the transition from the Northern to Central to Southern regions as well as the decoupling of processes that cause variation in recruitment and coastal chlorophyll-*a* abundance between regions.

As has also been documented previously (Broitman et al., 2008; Navarrete et al., 2008), the nature of the change in recruitment of sessile invertebrates north and south of Cape Blanco differed for each species studied (Fig. 5, Table 2), indicating that each species interacts differently with the physical and biological environment. While the transition at Cape Blanco was species-specific, there were no consistent differences between species in the sharp decline in recruitment between the Central and Southern regions for all species measured (Fig. 5, 95% confidence intervals for differences between regions largely overlapped).

Of the different species, *Mytilus* spp. had by far the largest change in recruitment at Cape Blanco (Fig. 5, 95% confidence intervals for difference in *Mytilus* spp. recruitment between Northern and Central regions did not overlap with intervals for *B. glandula* and *C. dalli*). In contrast, *C. dalli* varied relatively little across the transition region compared to the patterns for *Mytilus* spp. and *B. glandula* recruitment (for best fitting model: *C. dalli*, $R^2 = 0.378$; *Mytilus* spp., $R^2 = 0.834$; *B. glandula*, $R^2 = 0.720$), with greater differences occurring between sites within a region than between regions (Fig. 5).

The different patterns of recruitment between species may be the result of differences in the life history and larval behavior of the different species studied. Zooplankton species composition and abundance changes from the north to the south of Cape Blanco, which likely results from both the separation of the coastal jet at Cape Blanco from the continental shelf to offshore waters and the stronger more persistent upwelling that occurs south of Cape Blanco (Batchelder et al., 2002a;

Peterson and Keister, 2002). Zooplankton get transported into offshore oceanic waters by jets and filaments south of Cape Blanco (including at Cape Blanco), whereas north of Cape Blanco losses of zooplankton from shelf waters appear to be smaller (Batchelder et al., 2002a; Peterson and Keister, 2002; Lamb and Peterson, 2005). Behavior, such as vertical migration, may enable zooplankton to avoid being advected offshore (Batchelder et al., 2002b; Marta-Almeida et al., 2006; Shanks, 2009a,b; Shanks and Shearman, 2009). With the very different circulation regimes in the Northern and Southern regions, mechanisms and behaviors that enable a zooplankter to be retained in one region may not be effective in the other region (Batchelder et al., 2002a; Peterson and Keister, 2002). Thus, *B. glandula*, *C. dalli* and *Mytilus* spp. larvae likely have different behaviors, planktonic durations, and occur in the plankton at different times resulting in differential retention in nearshore waters (see also discussion in Menge et al., 2011a, 2011b).

Connolly et al. (2001) argued that the latitudinal transition in recruitment was predominantly caused by regional differences in the offshore advection of larvae by upwelling, but it is appropriate to revisit this hypothesis in light of the data presented here documenting a broader latitudinal transition of ecological subsidies that includes particulates (Figs. 3 and 4). A latitudinal difference of particulate inputs may contribute importantly to the latitudinal transition in mussel and barnacle recruitment along the coasts of northern California and Oregon by affecting the reproductive output of mussels and barnacles. Along the central Oregon coast the reproductive output of *B. glandula* is positively associated with nearshore productivity as measured by chlorophyll-*a* (Leslie et al., 2005). Sites within a high productivity region had 5x greater larval production than sites within a lower productivity region. While reproductive output of *B. glandula* was not correlated with subsequent recruitment at this scale (65 km separating regions), at larger spatial scales approaching or exceeding larval dispersal distances, a relationship between overall larval production and recruitment within a region may occur (Grosberg and Levitan, 1992), as has been found for brooding corals on the Great Barrier Reef (Hughes et al., 2000).

The rocky coast along northern California and Oregon is punctuated by a transition in pelagic subsidies. Bottom–up inputs (phytoplankton) to rocky intertidal filter feeders were lower south than north of Cape Blanco. The associated transition in recruitment does not appear to happen specifically at Cape Blanco as previously thought (Connolly et al., 2001). Rather, the region between Capes Blanco and Mendocino appears to be a transition zone between the very high levels of barnacle and mussel recruitment north of Cape Blanco and the very low levels of recruitment south of Cape Mendocino. Nonetheless, the latitudinal difference in community structure (Connolly and Roughgarden, 1998; Roughgarden et al., 1988) in the northeast Pacific is likely influenced by latitudinal differences in subsidies (recruitment and phytoplankton inputs). The transition in phytoplankton as a bottom–up effect is likely to affect both competition for space (Sanford and Menge, 2001) and the reproductive output of mussels and barnacles (Leslie et al., 2005). The potential for the reproductive output of mussels and barnacles to be affecting the latitudinal change in recruitment suggests that while the offshore advection of larvae can be important (Farrell et al., 1991; Roughgarden et al., 1988) it may not be the only factor affecting recruitment.

4.4. Generality

The non-linear transitions in key ecological processes observed in this study have parallels in other upwelling-dominated regions of the world. In Chile, researchers have found that a major oceanographic discontinuity occurs at about 32° S latitude, and that recruitment rates and abundances of mussels and change sharply at this non-linearity (Navarrete et al., 2005). A similar oceanographic discontinuity and related ecological changes were also detected in the Benguela Current ecosystem off the west coast of South Africa (Wieters et al., 2009). Finally large differences in community structure and oceanographic conditions

were observed on east vs. west coasts of the South Island of New Zealand (Menge et al., 2003). Thus, such changes appear to characterize a number of coastal ecosystems, if not all.

4.5. Conclusions

Our study shows that the ecological transition between Cape Blanco in southern Oregon, and Cape Mendocino (and southward) in California, a distance of about 330 km, primarily occurs as a series of non-linear decreases in mussel recruitment, mussel growth, and *C. dalli* recruitment. Although phytoplankton abundance seemed to decline more gradually with latitude, the limitation of the analysis to 1999–2003 coincided with a period of dramatic increases in phytoplankton abundance along the central Oregon coast (Menge et al., 2008, 2009), a change that was associated with climatic variation (Menge et al., 2009). Temporally and spatially more extensive sampling (Barth et al., 2007; Menge et al., 2004) indicates that most of the time the change across this region is more likely to be non-linear as well. This leaves the decline in *B. glandula* as the only component whose latitudinal change was consistent with a gradual decline interpretation. This complexity in change with latitude, and the existence of "outlier" sites (e.g., CA, TH) that are interpretable as being dependent on local-scale environmental features, indicates that understanding of variation among communities along a lengthy coastline will require integrating biophysical variation across multiple scales, from local to regional to geographic.

Acknowledgments

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