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Benthic community structure and spatiotemporal thermal regimes in two upwelling ecosystems: Comparisons between South Africa and Chile

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Abstract

On the basis of 16-yr satellite time series (1987–2003) of sea surface temperature (SST) and using univariate and multivariate statistical techniques, we quantified patterns of fluctuation in oceanographic conditions, as well as their spatial structure along the coasts of South Africa and Chile between 29.0° and 34.5°S. Since variations in environmental conditions over multiple timescales are driven by oceanographic–atmospheric processes modulated by coastal morphology, all of which affect in different ways coastal organisms, we hypothesized that dynamic properties of the environment contribute to characteristic patterns on rocky intertidal biomass structure across upwelling ecosystems. Although long-term mean temperatures were similar between coasts, the relative importance of annual, semiannual, intraseasonal, and high-frequency SST fluctuations differed; South Africa is more strongly pulsed over shorter timescales. Similar spatial discontinuities in thermal regimes were observed, with changes at about 32°S. Multivariate summaries of benthic community structure derived from functional group biomasses revealed striking differences between South Africa and Chile, as well as between regions north and south of 32°S within each ecosystem. Between-continent and regional-scale differences in community structure were largely unrelated to mean SST, but correlated with the different measures of temporal variance in SST. For all functional groups, as well as aggregate measures of benthic community composition, the weekly to annual SST fluctuations explained large fractions (>35%) of biological variability. Results highlight the importance of quantifying the temporal variance of regimes of hydrographic conditions since multispecies assemblages are expected to respond in different ways to the driving oceanographic processes behind these fluctuations.

Since the mid- to late 1980s marine ecologists started to accept the idea that the structure, diversity, and dynamics of benthic communities is not only controlled by processes occurring at local scales (i.e., chiefly species interactions), but also by the interplay between these and processes occurring over much larger scales, such as dispersal, the arrival of nutrients and propagules, or even speciation and regional extinction (Ricklefs 1987; Roughgarden 2006). A large number of studies at the interface between benthic ecology and oceanography have since identified some of the main physical processes in the coastal ocean that can control or modulate the organization of benthic communities (Menge et al. 1997; Connolly and Roughgarden 1998; Navarrete et al. 2005). These processes are involved in three main benthic–pelagic pathways. First, delivery of nutrients for benthic micro- and macroalgae, as well as plankton and particulate matter for filter feeders, critically depends upon coastal processes and initiates strong bottom-up influences in benthic communities (Menge et al. 1997; Nielsen 2003; Wieters 2005). Second, dispersal and subsequent recruitment of species with pelagic larval stages to benthic populations are largely driven by the interaction between larval behavior and physical transport processes (Siegel et al. 2008). Third, variability in environmental conditions, chiefly sea surface temperature (SST), can have direct consequences on physiology, behavior, foraging, and general ecology of benthic organisms through its effects on vital rates (Sanford 2002; Fernández et al. 2007). Benthic communities conformed by multiple species at the same and different trophic levels and with essentially different niches defined by their requirements and resource uses (Leibold 1995) are therefore influenced to varying degrees by all these processes over a wide range of spatial and temporal scales. Although disparate individual responses could be expected in such diverse species assemblages, we hypothesized that the "stationary" (long-term mean) and "dynamic" (temporal variability) properties of the environment leave characteristic and measurable patterns on structure of species within functional or trophic groups.

The diverse physical processes influencing benthic organisms produce complex spatiotemporal fluctuation regimes in nearshore SST. In the coastal ocean, SST fluctuations are enhanced, buffered, or modified by large-scale circulation and local topographic features that change patterns of water column structure, wind stress, or currents (Hormazabal et al. 2001; Picket and Paduan 2003; F. Tapia, S. Navarrete, M. Castillo, B. Broitman, and E. Wieters unpubl.). Consequently, numerous studies have

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examined the relationship between SST and biological variables at the individual, population, or community level (Lagos et al. 2005; Navarrete et al. 2005). The basic tenets of this study are that local species abundance in multispecies benthic communities represents a time-integrated measure of biological and ecological (species interactions) responses to fluctuating oceanographic conditions and that quantitative patterns of SST can capture variation in critical processes affecting the dynamics of component species.

The four major eastern boundary current ecosystems (EBCEs; Benguela, Canary, Humboldt, and California current systems) are characterized by comparatively narrow continental shelves, equatorward surface flow over a poleward undercurrent, prevalent equatorward wind stress, and coastal wind-driven upwelling. Upwelled water is generally cold, salty, nutrient rich and oxygen poor inshore (*see* Hill et al. 1998 for review). On a global scale, these similar physical characteristics appear to drive similar biological processes, and one of the consequences is that EBCEs account for a disproportionate amount of primary and secondary production in the world (Chavez and Toggweiler 1995; Pauly and Christensen 1995) and support similar assemblages of zooplankton and pelagic fish (Parrish et al. 1983). Likewise, similarities have been observed in seasonal succession of phytoplankton, from diatoms to dinoflagellates (Smith et al. 1983) and interdecadal shifts in dominance of fish species, anchovy or anchoveta alternating with sardine (Lluch-Belda et al. 1989; Cury et al. 2000). Relative to nonupwelling regions, rocky intertidal communities of EBCEs appear to have higher primary productivity and greater biomass and abundance, but lower diversity (Bustamante et al. 1995; Bustamante and Branch 1996; Menge et al. 2003). Since these studies have shown that the consequences of upwelling-driven environmental conditions on pelagic and benthic ecosystems are related to both main field average conditions as well as their temporal and spatial fluctuations, sensible among-system comparisons hinge critically on quantifying the regimes of hydrographic variability. However, beyond broad generalizations from local sites and large-scale low-frequency analyses documenting interannual variation, we still lack quantitative information about variability in environmental conditions across most EBCEs.

The two Southern-Hemisphere EBCEs, the Benguela and Humboldt on the west coasts of southern Africa and Chile, respectively, are the most productive of the coastal wind-driven upwelling systems of the world (Thomas et al. 2001; Carr and Kearns 2003). In conjunction with the environmental variability described above, a regional break in mesoscale features appears to occur at ~32°S in both these systems (Shannon 1985; Navarrete et al. 2005). Persistent, year-round upwelling-favorable conditions and geographically broad upwelling centers characterize the regions to the north. In contrast, the regions poleward of 32°S are distinguished by marked seasonality in wind forcing, with distinct upwelling events that last about a week and are concentrated in spring and summer (*see* reviews by Shannon 1985; Strub et al. 1998; Field and Shillington 2006). Here we use a combination of univariate and multivariate quantitative approaches to directly compare patterns of environmental variability across space within and between EBCEs. On the basis of these analyses we determined, for example, whether the relative strength of seasonality is similar between these EBCEs or whether spatial (latitudinal) gradients and discontinuities are more pronounced in one region than the other. We then explore whether benthic organisms within functional and trophic groups inhabiting these ecosystems respond in similar ways and magnitudes to oceanographically driven environmental variability. To this end we quantified patterns of biomass distribution of key intertidal functional groups along mid-latitudes (29.0–34.5°S) and their spatial association with coastal SST dynamics.

Methods

The systems—Despite the broad similarities in oceanographic conditions along central Chile and the west coast of South Africa, intrinsic differences also emerge. The continental shelf is narrow and steep along Chile, with both the inner and outer shelf breaks occurring within 50 km, whereas the outer shelf in South Africa is broad and extends 100–200+ km beyond the inner shelf, causing a much smoother slope. The Benguela also differs from the Humboldt in that it is bound at both the equatorward and poleward ends by warm water masses, with the Angola–Benguela front to the north and the Agulhas retroflection to the south. Water for upwelling appears to come from greater depth (>100–200 m) along South Africa and is primarily South Atlantic Central Water (Shannon 1985). In central Chile, a mix of Equatorial Subsurface Water and sub-Antarctic Water is upwelled from less than 50 m and appears to be more nutrient rich (Blanco et al. 2001; Carr and Kearns 2003).

Community structure—To obtain comparable data for rocky intertidal community structure along the west coasts of South Africa and central Chile, identical field surveys were conducted at respectively 27 and 16 study sites, spaced tens to hundreds of kilometers apart and spread between 29.0°S and 34.5°S (Fig. 1). Surveys were conducted during austral spring and summer months between 2001 and 2004, with most sites surveyed in several years. Details of sampling methods are described in Broitman et al. (2001) and Wieters (2006). Briefly, percentage cover and density of sessile and mobile species respectively were quantified in a minimum of eight 0.25-m^2 quadrats haphazardly placed along transects stretched parallel to the shoreline across the mid- and low intertidal zones of one to three rocky benches at each study site. Surveys were restricted to open-coast, wave-exposed shores to avoid the confounding effects of wave action, and because the majority of the rocky shores in both countries are subject to intense wave action. Density estimates of larger predators (e.g., *Concholepas*, *Heliaster*, *Stichaster*) and herbivores (e.g., *Fissurella*, *Acanthopleura*, *Scutellastra argenvillei*) were obtained by counts within defined areas (i.e., 1- × 7-m strips). Biomass (wet weight) per species was calculated for each quadrat using site-specific conversions of cover to mass for sessile

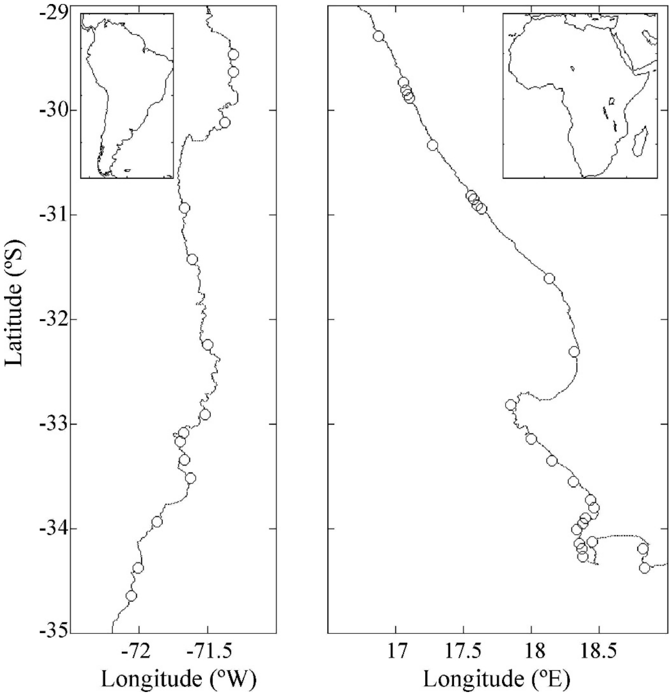

Fig. 1. Location of study sites (circles) on wave-exposed, rocky intertidal shores spread across mid-latitude regions of central Chile (left) and South Africa (right).

species and length : mass regressions for mobile species (Wieters 2006). Species abundances were pooled into functional groups to allow direct comparisons between Chile and South Africa, as the two systems have different species but comparable functional groups. The functional groups were defined according to morphological and anatomical characteristics associated with productivity potential and susceptibility or resistance to herbivory (algae) or trophic position and foraging strategy (invertebrates) (*see* table 1.1 in Wieters [2006] and table 2 in Broitman et al. [2001] for functional group composition). For the mean biomass (g m^{-2}) estimates presented here, replicate benches and years are pooled for each site. To obtain a more robust, multivariate characterization of community variability across and within each EBCE, we used principal component analyses (PCA) with biomasses of functional groups as the variables (*see* below).

Variability in SST—We relied on a remotely sensed SST time series to summarize temporal and spatial variation in oceanographic processes across each study region. SST is an important proxy for the physical structure of the nearshore ecosystem and is tightly linked to other critical environmental variables (e.g., onshore nutrient availability). Specifically, we used a 16-yr time series (1987–2003) of SST derived from 4-km-resolution advanced very-high-resolution radiometer thermal imagery. The data represent nearshore temperatures approximately 5–10 km off shore, on the basis of averages of the first two cross-shelf pixels closest to the coastline. Comparisons of satellite-derived SST with that recorded in situ by onshore loggers placed at subsets of these same study sites in each system showed similar spatial and temporal patterns of variation and were strongly and positively correlated across the study regions (Lagos et al. 2005; Wieters 2006).

Long-term (16-yr) mean, minima, and maxima of SST were calculated from monthly averages for each alongshore pixel (4 km). Minima and maxima were represented as the lower and upper 5% quantiles, respectively. To examine temporal variability in SST at different temporal scales at each site (weekly, monthly, intraseasonal, semiannual, annual, and long-term), time series of 7-d composite images were subjected to two different techniques. First, to estimate the percentage of total temporal variability that is explained by annual, semiannual, and intraseasonal variability, we performed a least-squares harmonic regression analysis. The predicted harmonic means for the different timescales were then removed from the time series and the variance over the residuals was calculated. Comparison of these variances against the total variance in the original time series allowed us to estimate the percentage of variation explained by each cycle. Second, to examine variation in weekly to monthly timescales, we performed autocorrelation analyses of site-specific time series after removing the annual and semiannual trends. Autocorrelation functions for the entire regions of Chile and South Africa were obtained by aggregating autocorrelation estimates at each lag for all time series within each region. Autocorrelation functions represent dissimilarity between observations at increasing time lags and the lag-1 estimate (in this case, 7 d) is an indicator of linear dependence between successive observations in a time series, and was used to test for differences in biweekly SST dynamics (Buishand and Beersma 1993). We chose these approaches because consistent and recurring environmental fluctuations offer reliability for biological responses and are thus those most expected to have important long-term structural consequences for abundance patterns, species coexistence, and stability of aggregate community properties (reviewed by Holt 2008).

The variables (scales) of temporal variation in SST act simultaneously and are correlated to varying degrees across regions and systems. We used PCA with the six estimates of temporal SST variability at all sites (mean, long-term variance, percentage annual, percentage semiannual, percentage intraseasonal, and lag-1 autocorrelation) to reduce the complexity of the ensemble and characterize the spatial structure of temporal variability. Reducing the data through PCA also allowed us to aggregate sites with similar environmental conditions. The distribution of weights (eigenvectors) represents the relative contribution of each variable to each principal component (PC1, PC2, etc.) and was examined to interpret the environmental implications of the different principle components. As a first step to describe and compare the dynamics of these two coastal upwelling systems, analyses were carried out on pooled data for South Africa and Chile.

Biophysical coupling—To discern whether the biomass of functional groups responded to the differences in temporal SST dynamics between South Africa and Chile,

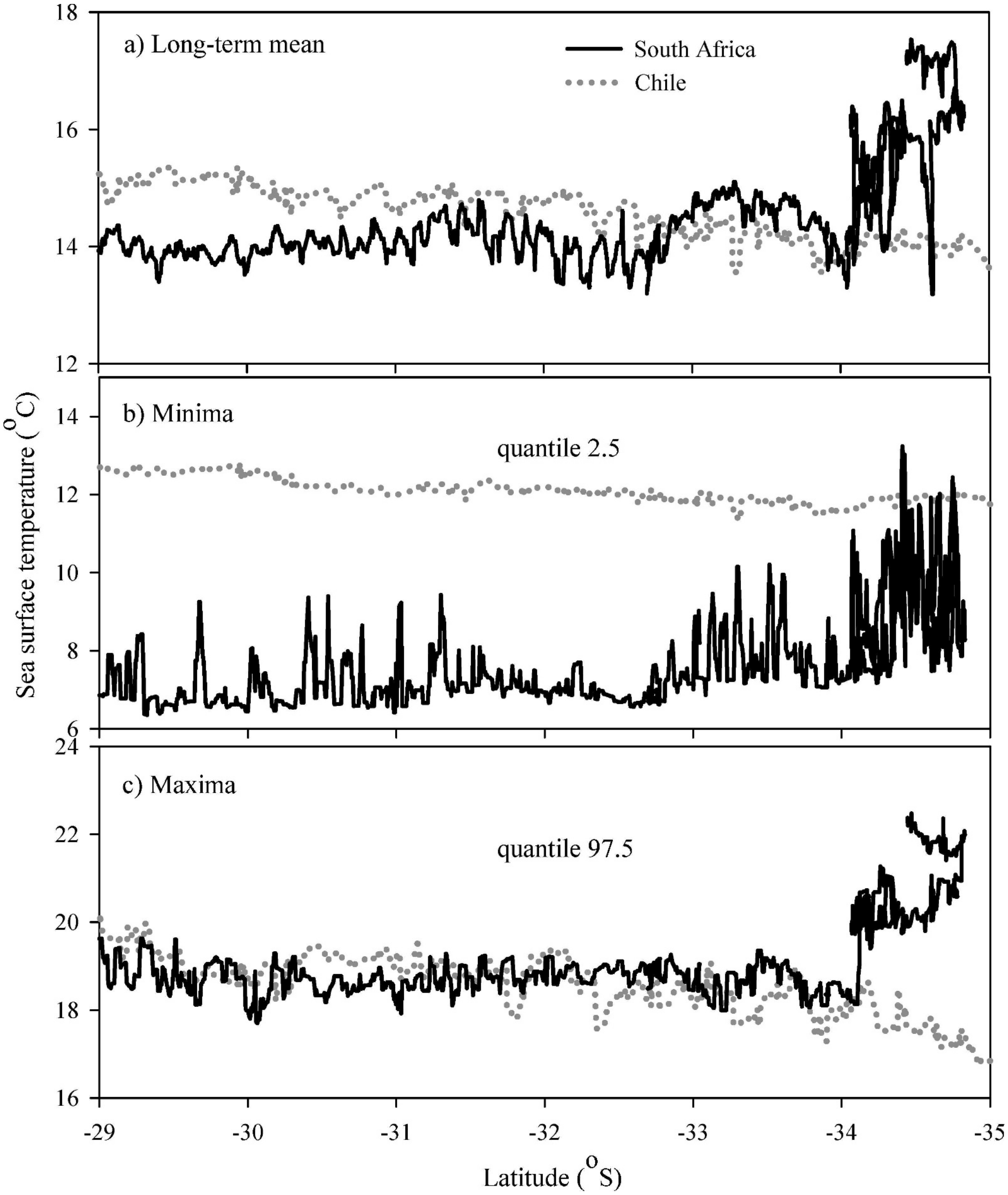

Fig. 2. Alongshore variation in long-term (a) mean, (b) minima, and (c) maxima SST in South Africa and Chile.

we calculated *r*-Pearson pairwise correlations between the raw estimates of functional group biomass and individual SST variables and the first three principal components of SST and raw functional group biomass, and then the first three principal components of community biomass.

Results

Oceanographic conditions—The simplest approximation of oceanographic conditions—long-term mean SST—exhibited opposite latitudinal trends between coasts, with temperature gradually declining poleward in Chile but sharply increasing poleward of 34°S in South Africa (Fig. 2a). South Africa was colder north of about 33°S (Fig. 2a) and experienced more extreme and more variable minima across all latitudes (Fig. 2b). Maximum temperatures were similar between systems until south of 34°S (Fig. 2c). In general, South Africa was characterized by greater spatial variability in SST (compare fluctuations of lines in Fig. 2).

The temporal dynamics of nearshore thermal conditions were strikingly different between the two systems (Fig. 3). South Africa was consistently more variable, as depicted by total variance over the entire 16-yr time series (Fig. 3a). Overall, among-site changes in temporal variance were greater in South Africa than those observed along Chile, where a trend of increasing stability to the south was apparent.

A well-defined spatial structure of different temporal variables characterized both systems. Across South Africa, a strong discontinuity at about 32°S (approx. 600 km in

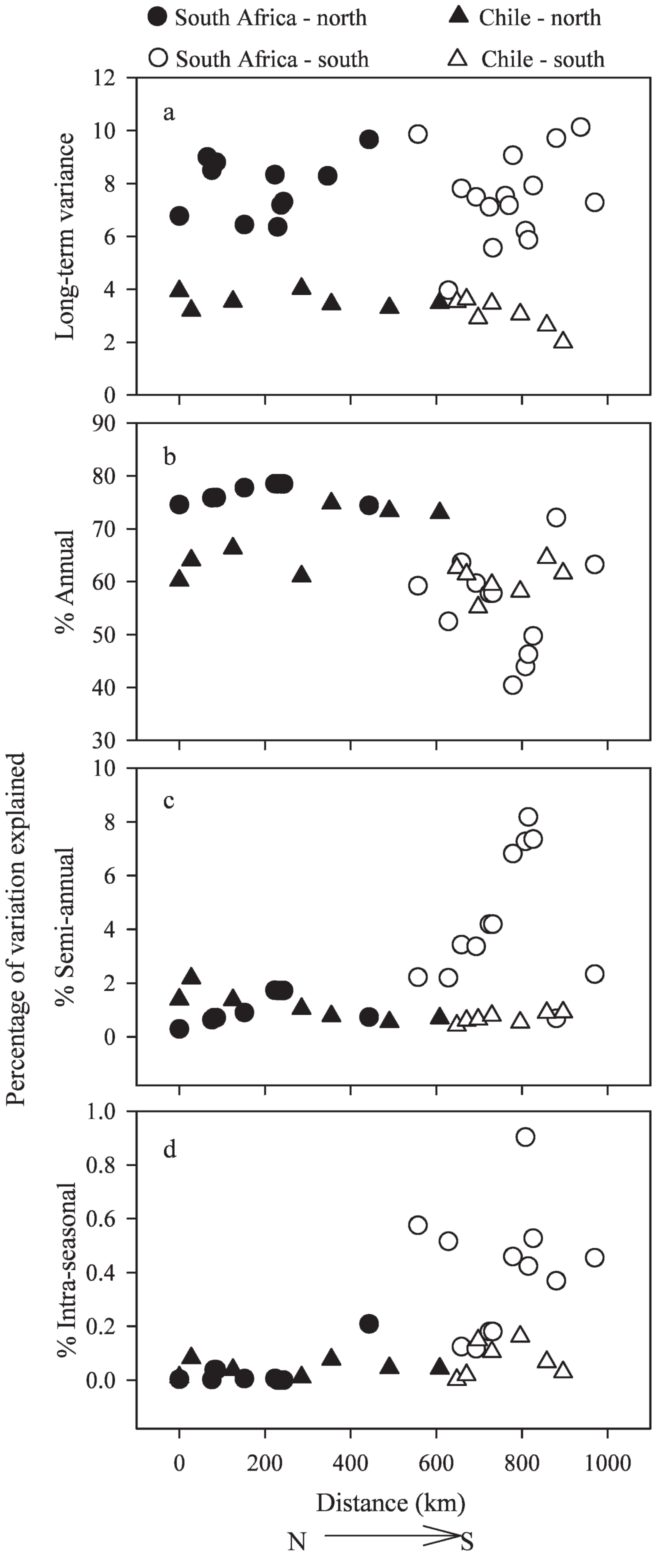

Fig. 3. Alongshore variation in temporal variables of SST for South Africa (circles) and Chile (diamonds). Solid symbols are sites north of 32°S, open symbols are sites south of that. Distance is north to south.

Fig. 3) partitioned the coast into two distinct regions. The northern region was dominated by a strong annual cycle in SST, which explained up to 79% of local variation (Fig. 3b). In contrast, relatively weaker annual signals that varied among sites were observed to the south. Moreover, the semiannual cycle, which was positively correlated with summer and autumn mean temperatures (Pearson $r = 0.70$, $p = 0.01$), represented a larger fraction of temperature variation poleward, culminating at the southern end of the Cape Peninsula (Fig. 3c). Likewise, the progression of variation within seasons was relatively stronger, yet variable among sites, south of 32°S (Fig. 3d). Similar to South Africa, Chile was characterized by a clear spatial structure of thermal regimes. The strength of the annual signal was greatest to the north and peaked toward the center of the study region (~32°S; Fig. 3b). The semiannual and intraseasonal cycles were more uniformly distributed along the coast, although they were slightly stronger at the northern and southern extremes, respectively (Figs. 3c,d). In general, the contrast between north and south so evident in South Africa was less apparent in Chile.

There were striking differences in the autocorrelation functions between Chile and South Africa (compare slopes of lines in Fig. 4a). The decorrelation scales of approximately 35 d in South Africa and 95 d in Chile were significantly different ($p < 0.001$), suggesting that SST dynamics across South Africa are dominated by "high-frequency" variability. The spatial (alongshore) distribution of autocorrelation estimates indicated that all sites in Chile were less variable than those in South Africa (Fig. 4b). Moreover, South Africa was characterized by greater among-site variation in short-term stability of local conditions, particularly south of 32°S, where relatively more persistent conditions described sites with warmer average temperatures (Pearson $r = 0.76$, $p = 0.003$). Short-term SST variability was not correlated to mean temperature conditions across central Chile (Pearson $r = 0.14$, $p = 0.64$). To determine whether site-to-site variation in weekly dynamics was related to the spatial anomaly of mean temperature, we examined correlations between local autocorrelation estimates and residuals of mean SST from the regional trends in SST. Autocorrelation patterns were related to warm conditions in South Africa (Pearson $r = 0.70$, $p = 0.0003$), whereas in Chile they showed the opposite pattern (Pearson $r = -0.71$, $p = 0.0044$).

The multivariate characterization of SST variability outlined the structure of relationships between SST components, with striking differences between Chile and South Africa (Fig. 5a). First, the spread of sites in multivariate space was greater in South Africa than in Chile. Second, differences between regions north and south of ~32°S were apparent within each system, but more pronounced in South Africa. Third, sites lying in the south were more different from each other than in the north, particularly in South Africa. The relative positions of points (sites) in Fig. 5a highlight similarities and differences in local nearshore SST regimes, with groups separated primarily on component 1 and, secondarily, on component 2. Further inspection of spatial distributions of principal components for each system revealed opposing alongshore

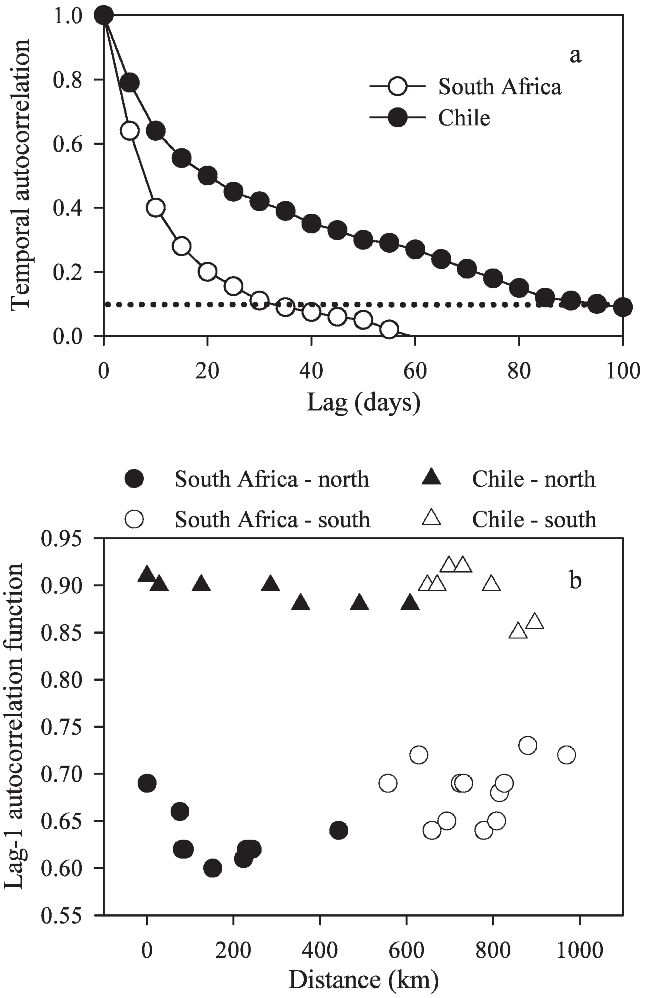

Fig. 4. (a) Temporal autocorrelation functions of sea surface temperature (SST) for average of time series at South Africa (open circles) and Chile (solid circles). Dotted horizontal line is Bonferroni-corrected ($\alpha = 0.05$) confidence interval for significant autocorrelation. (b) Alongshore variation in high-frequency (weekly) fluctuations in SST. Solid symbols are sites north of 32°S, open symbols are sites south of that. Distance is north to south.

gradients of contrasting slopes for component 1 (Fig. 5b), whereas spatial discontinuities and the particularly large variation among sites in the southern portion of South Africa were evident in component 2 (Fig. 5c). The geographic discontinuity was generally weaker and less spatially acute in Chile than in South Africa. The first three principal components (PC1, PC2, and PC3) cumulatively accounted for 52%, 85%, and 92% of the observed variability. The temporal dynamics were evenly weighted by short-term and long-term temperature pulsing (Table 1a). Weights were similarly high for all temporal descriptors except the annual cycle for PC1, whereas PC2 was most strongly weighted by the strength of the annual cycle. Weights for mean SST and the annual cycle were weak for PC3.

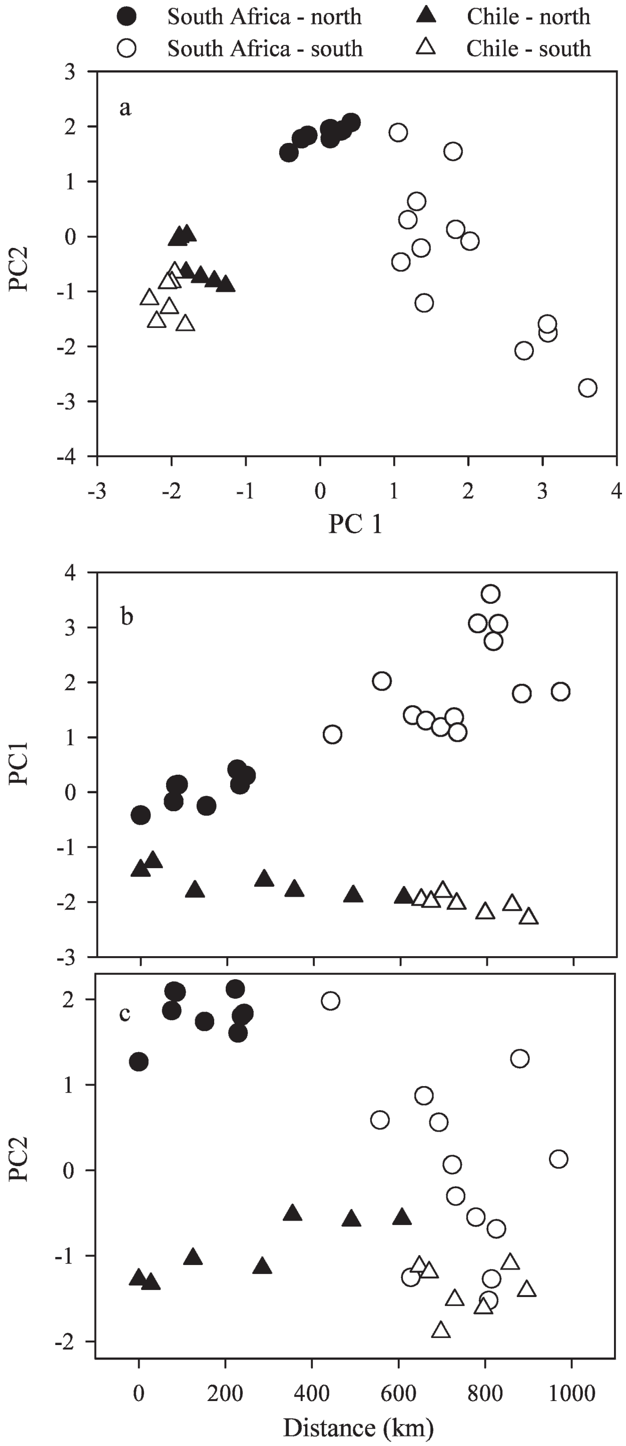

Fig. 5. (a) Relationships for the first two principal components obtained from principal component analysis (PCA) of sea surface temperature across both South Africa (circles) and Chile (triangles). Solid symbols are sites north of 32°S, open symbols are sites south of that. Alongshore variability in PC1 (b) and PC2 (c) from north to south.

Patterns of functional group biomass—The rocky shores of Chile supported consistently higher total biomass than South Africa in the low intertidal zone ($F_{1,38} = 101.44$, mean square [MS] = 35.44, $p < 0.0001$), but South African shores maintained higher biomass in the mid zone ($F_{1,39} = 2.59$, MS = 5.57, $p = 0.023$). Most functional groups had a

Table 1. Weights and statistics of principal components for (a) SST regimes and (b) community biomass structure across the South African and Chilean coasts.

(a) SST regimes

	PC1	PC2	PC3
Eigenvalue	3.13	1.98	0.40
Percentage	52.17	33.06	6.60
Cumulative percentage	52.17	85.23	91.83
Lag-1 autocorrelation	−0.43	−0.38	0.43
% intraseasonal	0.43	−0.35	0.47
% semiannual	0.44	−0.34	−0.50
% annual	−0.21	0.63	0.12
Long-term variance	0.42	0.22	0.56
Mean SST	0.46	0.40	−0.09

(b) Community biomass structure

	Low zone			Mid zone		
	PC1	PC2	PC3	PC1	PC2	PC3
Eigenvalue	2.10	1.56	1.00	2.29	1.36	0.80
Percentage	34.92	25.94	16.68	38.13	22.71	13.27
Cumulative percentage	34.92	60.86	77.54	38.13	60.83	74.10
Ephemerals	0.30	0.35	0.66	0.47	−0.20	0.14
Corticated	0.39	0.44	0.16	0.56	0.18	0.20
Kelp	−0.34	0.63	0.04	0.44	0.30	0.48
Filter feeders	0.32	−0.51	0.48	−0.44	0.05	0.68
Predators	−0.50	−0.11	0.44	−0.07	−0.69	0.45
Herbivores	0.54	0.09	−0.33	−0.27	0.59	0.21

similar range of biomass values along each coast, but between-system differences existed: whereas Chile was characterized by relatively higher biomass of kelp, mid-zone algae, and low-zone predators, South Africa was characterized by higher biomass of filter feeders and herbivores.

Spatial community-level structure was also observed in across-system multivariate characterization of biomass in terms of the first two components of PCA (Fig. 6). The two ecosystems were strikingly segregated in multivariate space and the spread of points (variation among sites) was again greater in South Africa than in Chile. Moreover, differences between regions north and south of 32°S were apparent within each system in the low zone, as well as the mid zone in Chile. Strong separation among groups was observed across low zones, which were primarily separated on PC1 (Fig. 6a). Relatively weaker separation occurred for mid zones (Fig. 6b). The first three components explained 78% and 74% of observed variation on low and mid shores, respectively. However, components represented different biomass structure in the two shore levels (Table 1b). On low shores, PC1 was strongly weighted by consumers (predators and herbivores), whereas kelp and filter feeders were prominent components of PC2. On mid shores, macroalgae (kelp, corticated and ephemeral algae) dominated PC1 and consumers dominated PC2. PC3 mostly reflected a combination of filter feeders and predators, as well as ephemerals (low zone) and kelp (mid zone).

Benthic–pelagic links: Functional group biomass and temperature variation—Between-system differences in biomass of functional groups were not correlated with long-term mean SST (Pearson $r < 0.25$, $p > 0.1$ for all functional groups). In contrast, biomass was strongly and significantly correlated with individual and aggregate measures of the regime of temporal variability in SST (Figs. 7, 8). For individual (univariate) variables of temporal dynamics, biomass responses to total variance and weekly stability were the most consistent, as all functional groups showed significant association to these scales of temporal variability (Fig. 7). Similarly, all groups were coupled to one or both of the first two principal components of multivariate characterization of thermal variability (Fig. 8). The strength and direction of relationships varied among functional groups. Although some groups, such as kelp, filter feeders, and herbivores, showed consistent patterns between tidal heights, patterns for other groups differed between the low and mid intertidal zones. These differences were most notable for corticated algae, which showed significant but opposite correlations with PC1 of SST in the low and mid zones.

The first principal component of SST variability explained significant structure and between-system differences observed in the multivariate characterization of low and mid intertidal communities (Fig. 9). In general, PC1 of community biomass was strongly associated with PC1 of temperature dynamics: positively across low shores and negatively across mid shores. The sequential ordering of regions for the two EBCEs was striking, especially for the mid zone (Fig. 9b).

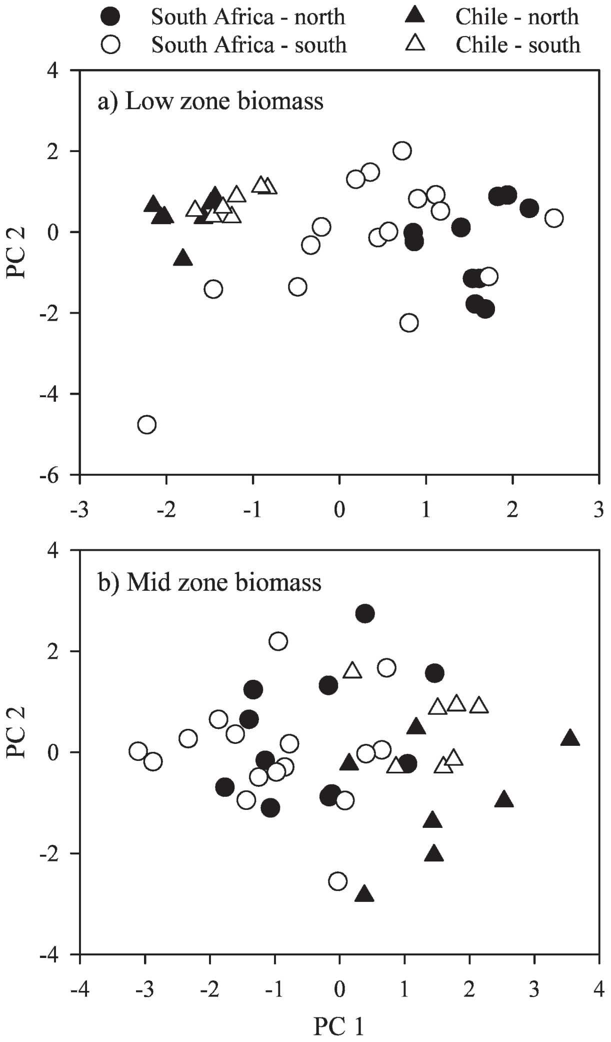

Fig. 6. Relationships for the first two principal components obtained from principal component analysis (PCA) of community biomass across both South Africa (circles) and Chile (triangles) for (a) low and (b) mid intertidal zones. Solid symbols are sites north of 32°S, open symbols are sites south of that.

Discussion

Our results show that the intensity and relative importance of different components of temporal variability in coastal oceanographic conditions differ between the west coasts of South Africa and central Chile, generating quite unique thermal regimes in both shores. Therefore, biological responses of benthic communities are expected to differ between these EBCEs. However, the spatial structure of patterns of temporal variability within each system creates coincident discontinuities at ~32°S. Differences in the physical environment between regions north and south of this latitude were most pronounced in South Africa but were also evident in Chile. This is the first quantitative comparison of multiscale time–space dynamics in the temporal regime of nearshore SST fluctuations in the Southern-Hemisphere EBCEs. Patterns in the biomass of rocky intertidal communities were unrelated to mean SST, but coupled to the spatial structure of temporal SST variability. These results suggest that nearshore hydrographic processes may promote inter-EBCE and regional patterns of benthic community structure.

Comparative nearshore SST regimes—Striking differences in hydrographic conditions, as estimated by SST, were observed between the two EBCE systems examined, as well as between regions north and south of ~32°S within each system. First, temperatures declined from north to south in Chile, but increased on the west coast of South Africa. Second, there was much more spatial variability in South Africa than in Chile. Third, Chile is characterized by relatively more stable dynamics, mainly influenced by fluctuations of relatively longer timescales (in the order of several months). Previous studies have shown that coastal SST fluctuations at these latitudes in Chile can indeed be strongly forced by large-scale oceanic or atmospheric circulation that produces important low-frequency variability and strongly modifies nearshore oceanographic conditions (Hormazabal et al. 2001). In contrast, South Africa is generally colder in the north and experiences greater extremes in thermal conditions that are more strongly pulsed over shorter timescales. These results are in agreement with previous studies showing that local forcing plays a prominent role in South Africa, particularly in the southern Benguela (Hardman-Mountford et al. 2003).

Shared discontinuity in spatial structure—Within both the South African and central Chilean EBCEs, shifts in the relative strength of annual and intraseasonal cycles in SST create latitudinal gradients and discontinuities. The regions north and south of ~32°S showed distinctive SST regimes that were clearly identified by PCA (Fig. 5a). These results reflected the contrasting seasonal cycles in wind imposed by shifts in the high-pressure systems lying north of our study regions, the South Atlantic and Pacific anticyclones. Indeed, winds and offshore Ekman transport in both systems are persistently upwelling favorable throughout the year north of 32°S, whereas poleward of that they are typically downwelling favorable during the austral winter (Shannon 1985; Navarrete et al. 2005).

Differences between regions north and south of 32°S are most pronounced in South Africa, where the southern region is characterized by greater within-season variability and a broader range of thermal dynamics. These patterns likely reflect the effect of the diverse, transient, synoptic-scale weather systems (e.g., troughs, coastal lows, etc.) that become trapped by the complex topography and coastal mountains of the south and can substantially modify upwelling-favorable winds and propagate as a type of Kelvin wave around the coast (Reason and Jury 1990; Risien et al. 2004). Warm-water tongues or advected eddies and rings from Agulhas origin can also modulate temperature at timescales from days to several months, but seldom penetrate north of 33°S (Shannon and Nelson 1996). In addition, Risien et al. (2004) observed intraseasonal variability (centered at around 40 d) in mid-latitude wind stress in the southern Benguela, which they suggest is

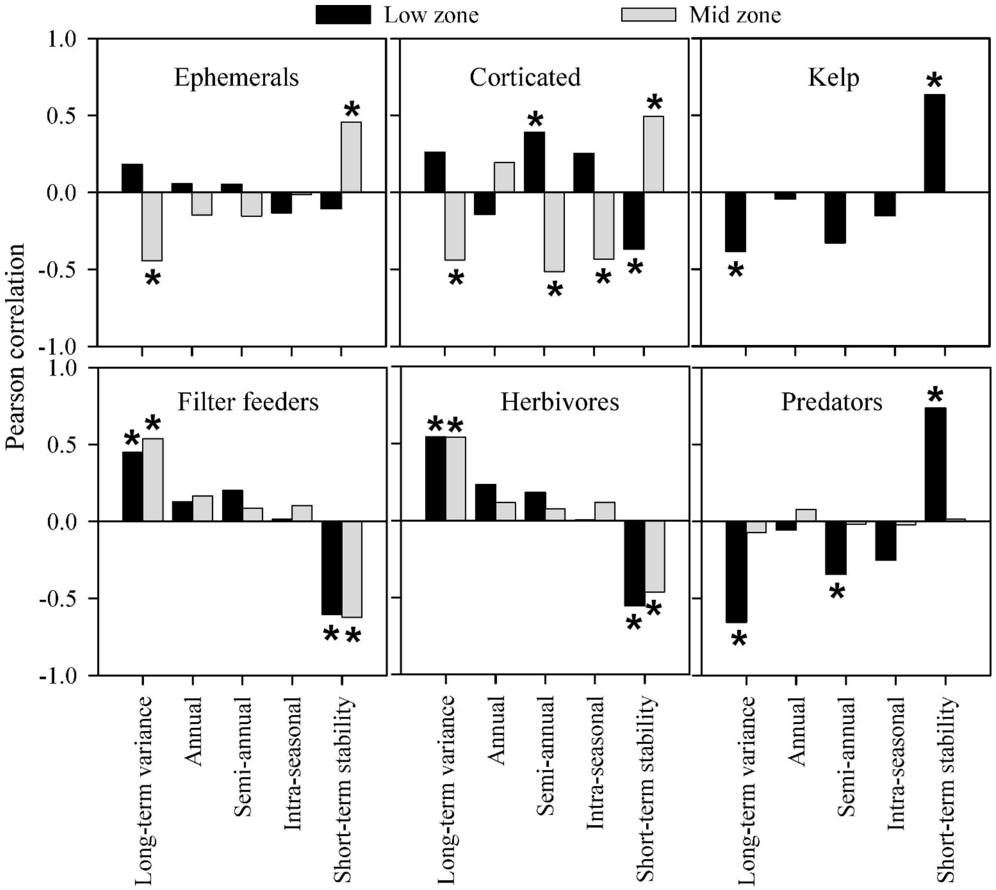

Fig. 7. Correlation coefficients between temporal variables of SST and biomass of individual functional groups on low (black bars) and mid (gray bars) shores across both South Africa and Chile. Stars indicate significant correlations ($p < 0.05$).

forced by wind events originating over eastern South America and propagating eastward across the Atlantic. It is worth noting that the mean decorrelation scale of SST detected by our analyses was around 35–40 d (Fig. 4).

Intraseasonal oscillations along the coast of Chile are associated with free, coastal-trapped waves of equatorial origin propagating poleward (Shaffer et al. 1997; Hormazabal et al. 2001). These have frequencies of 50–120 d, which matches well the relatively longer decorrelation scales observed across Chile in our study (Fig. 4). The gradual change in the importance of such low-frequency signals south of ~32°S is likely related to the westward initiation of Rossby waves documented to occur around 33°S (Hormazabal et al. 2004). As Kelvin waves impinge upon the coast at the equator, they also cause local wind disturbances that propagate toward the south, generally at scales of about a month.

Contrasting hydrographic conditions north and south of 32°S in South Africa are also influenced by more pronounced changes in "static" temperature conditions. Shannon (1985) suggested that modified Agulhas central water may upwell on the west coast at least as far north as 30°S. Therefore, differences in source water, in combination with the weaker and more variable wind-driven upwelling intensity that may alter depths from which water is drawn, may further contribute to the overall warmer and spatially variable SST conditions in the south.

Biomass responses to SST dynamics across EBCEs—Wave-exposed rocky intertidal communities of South Africa and Chile showed distinctly different biomass characteristics, but at the same time they showed coincident divergences at ~32°S. Individual functional groups and multivariate descriptors of biomass variability were consistently correlated with SST dynamics (Figs. 7–9), suggesting that within (regional) and between EBCE differences in nearshore oceanographic processes may promote the observed changes in biomass patterns. Correlation analyses between aggregate measures of community structure and SST dynamics were based on principal components, which explained a relatively low percentage of the total variation (35–52%), and thus, results should be interpreted with caution. However, the striking concordance between univariate and multivariate estimates strengthen our interpretation. In general, short-scale (e.g., intraseasonal, weekly) temporal fluctuations in SST, as well as the large differences in total variation, were most important. However, whether this variability was positively or

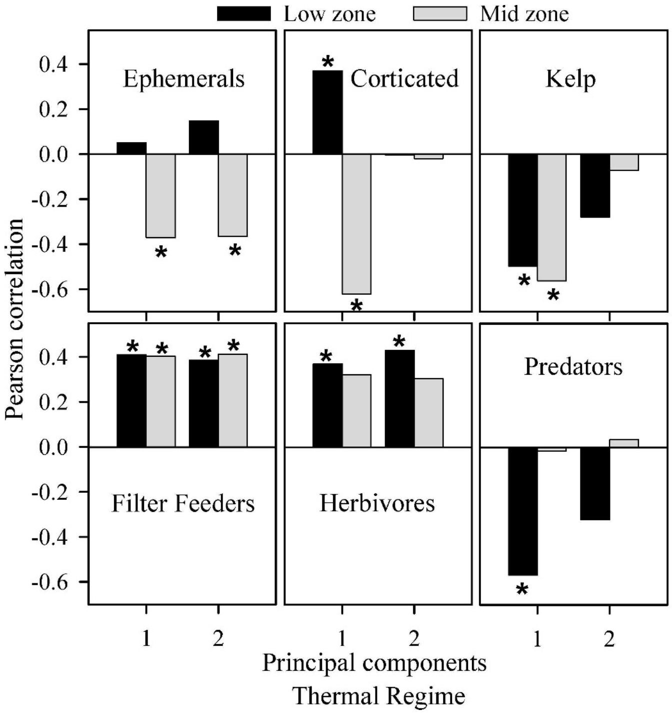

Fig. 8. Correlation coefficients between the first two principal components of the thermal regime and biomass of individual functional groups on low (black bars) and mid (gray bars) shores across both South Africa and Chile. Stars indicate significant correlations ($p < 0.05$).

negatively associated with biomass depended upon the functional group (Fig. 8) and tidal height (Figs. 8, 9) considered.

Since the broad scale of our study precludes true replication, care must be taken when seeking causation to observed patterns. With this caveat in mind, we discuss plausible and testable hypotheses about the processes and mechanisms behind these patterns. Coastal upwelling dynamics can have important implications for inshore nutrient replenishment (Wieters 2005), as well as for larval supply to the shore (Botsford 2001; Navarrete et al. 2005). In both EBCEs, temporal variability from synoptic to intraseasonal scales (e.g., coastal trapped waves) can change the depth of the thermocline and nutricline, modulating the effectiveness of nutrient pumping into the euphotic zone during upwelling events (Shannon 1985; Shaffer et al. 1997; Hormazabal et al. 2001). The fact that weekly and lower-frequency SST variability had generally negative effects on macroalgal biomass (*see* Figs. 8, 9b) could be a result of this type of variation in nutrient supply. On the other hand, persistent, year-round upwelling must provide a sustained source of nutrients and therefore primary production should rarely be nutrient limited. Indeed, long exposure to elevated nutrients is usually necessary to increase macroalgal growth and production (Pedersen and Borum 1996; Worm et al. 2000), whereas greater temporal variability in nutrient supply can limit growth responses of some algae (Rosenberg et al. 1984; Worm and Sommer 2000).

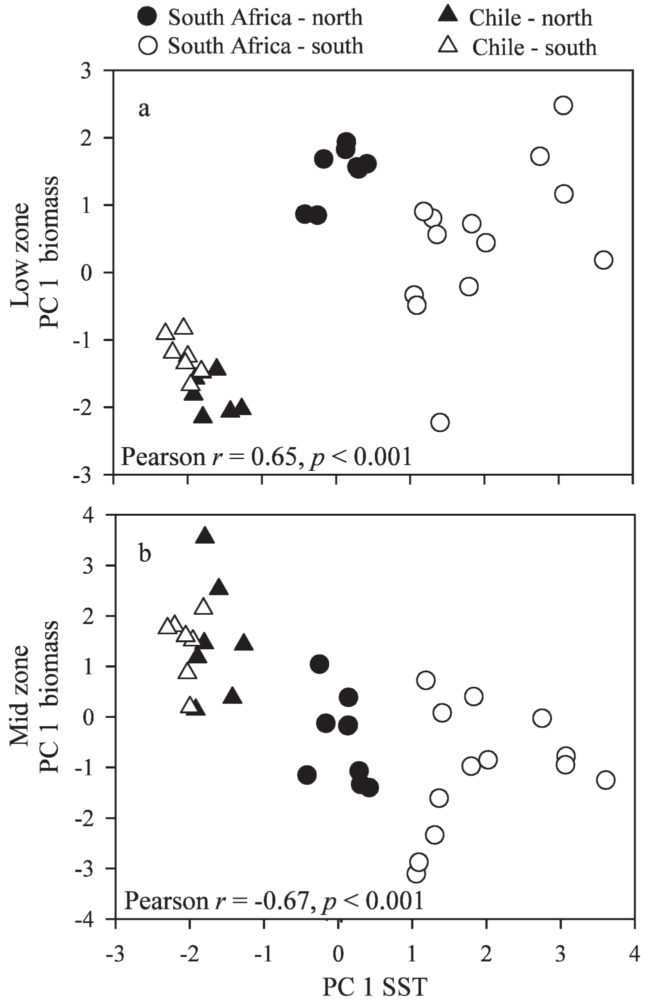

Fig. 9. Relationships between the first principal component of SST variability and the first principal component of community biomass variability on (a) low and (b) mid shores across both South Africa (circles) and Chile (triangles). Solid symbols are sites north of 32°S, open symbols are sites south of that.

Nutrient availability can not only have direct effects on algal growth but also interact with light conditions to influence algal performance. Resistance to solar radiation is modulated by nutrient availability (Santelices 1991) and, in turn, nutrient uptake is altered by exposure to ultraviolet radiation (Gómez et al. 1998). Therefore, changes in nutrient regimes are expected to directly and indirectly affect algal functional groups differentially because they differ in requirements, morphology, tissue chemistry, sensitivity of the photosynthetic system, and ability to store nutrients. Modification of upwelling intensity and temporal regimes may enhance growth and reproduction of some algal functional groups, which can then limit others either through exploitation and local nutrient depletion or by space competition. Such complex interactions are likely to constrain low-shore corticated algae, kelp, and ephemeral algae, which exhibit contrasting nutrient physiologies and commonly compete for space (Santelices 1991; Nielsen and Navarrete 2004).

Since SST variability is largely driven by physical processes producing alongshore and cross-shore advection, this variability may be indicative of different onshore larval transport conditions (Shanks et al. 2000; Botsford 2001). Larvae of many invertebrate species can be entrained in offshore-moving, newly upwelled waters, so that their delivery and settlement on shore occurs when upwelling relaxes and the fronts approach the coast (Farrell et al. 1991; Shanks et al. 2000) or when flow reversals occur (Wing et al. 1995). Other larvae can avoid the moving front by vertical migration and can be transported onshore during upwelling (Poulin et al. 2002). Persistent year-round upwelling could thus create fewer opportunities for onshore transport of surface-dwelling larvae over extensive regions of the coast (Connolly et al. 2001; Navarrete et al. 2005) and be responsible for some of the patterns of sessile invertebrate abundance reported here. Indeed, filter feeders (predominantly mussels and barnacles) were most abundant where SST variability was greatest (associated with PC1 and PC2 in Fig. 8), suggesting that persistent SST conditions lead to lower recruitment. Differences in mean recruitment rates between the two EBCEs may reflect differences in total population size of the species, reproductive output, larval retention, or larval survival and deserve further investigation.

The negative association between predator biomass and different SST regimes is not likely to be a simple consequence of larval retention in areas of different SST variability because although the predators along central Chile have pelagic larvae with long-distance dispersal (Wieters et al. 2008), the predator species in South Africa are direct developer whelks (i.e., *Nucella* and *Burnupena*) lacking a free-swimming larval stage. The relationship is probably linked to predators' performance (consumption rates) under different temperature regimes, as suggested by field studies on the effects of upwelling-driven SST variation on prey consumption rates by key intertidal predators (Sanford 2002).

The convention of analogous physical environments along coasts of EBCEs, such as the west coasts of South Africa and Chile, was built on common broad features associated with wind-driven upwelling dynamics. However, these coarsely similar dynamics are modulated by different coastal and bottom topographies and by cyclic, low-frequency annual (seasonal), semiannual, and intraseasonal oscillations, which strongly interact to produce disparate regimes of temporal variability in oceanographic conditions. Although long-term mean SSTs were generally similar between the two coasts, the relative importance of the different timescales for thermal fluctuations differed markedly: Chile is characterized by relatively warmer, more stable dynamics influenced by fluctuations of relatively longer timescales, whereas South Africa experiences greater extremes in thermal conditions that are more strongly pulsed over shorter timescales. Debunking the assumption of analogy, the spatial structure in temporal variability of SST revealed strong and similar spatial discontinuities in thermal regimes at about 32°S in both systems. We submit that major changes in the temporal variability of oceanographic conditions promote inter-EBCE and regional (within EBCE) differences in major patterns of benthic community biomass structure, which can have far-reaching consequences on regulation of these communities. Indeed the relative importance of species interactions along the coast of Chile shows a sharp change north and south of 32°S (Navarrete et al. 2005). Considerations of how the pattern of temporal variability in oceanographic conditions (and not just average conditions) produce major changes in the structure of biological communities must be incorporated into models and predictions of climate change, as well as policies for the conservation and sustainable management of marine resources. Comparative experimental studies in conjunction with detailed nearshore oceanographic studies will provide mechanistic understanding of these links and improve our ecological models.

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References

Blanco, J. L., A. C. Thomas, E. Carr, and P. T. Strub. 2001. Seasonal climatology of hydrographic conditions in the upwelling region off northern Chile. J. Geophys. Res. **106:** 11451–11467.

Botsford, L. W. 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. ICES J. Mar. Sci. **58:** 1081–1091.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation in southern Pacific intertidal communities. Mar. Ecol. Prog. Ser. **224:** 21–34.

Buishand, T. A., and J. J. Beersma. 1993. Jackknife tests for differences in autocorrelation between climate time series. J. Clim. **6:** 2490–2495.

Bustamante, R. H., and G. M. Branch. 1996. Large-scale patterns and trophic structure of southern African rocky shores: The role of geographic variation and wave exposure. J. Biogeogr. **23:** 339–351.

———, and others. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationship with consumer biomass. Oecologia **102:** 189–201.

Carr, M. E., and E. J. Kearns. 2003. Production regimes in four Eastern Boundary Current systems. Deep Sea Res. II **50:** 3199–3221.

Chavez, F., and J. R. Toggweiler. 1995. Physical estimates of global new production: The upwelling contribution, p. 313–320. *In* C. P. Summerhayes, K.-C. Emeis, M. V. Angel, R. L. Smith and B. Zeitschel [eds.], Upwelling in the ocean: Modern processes and ancient records. Wiley.

Connolly, S., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the Northeast Pacific Ocean. Ecology **82:** 1799–1813.

Connolly, S. R., and J. Roughgarden. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory. Am. Nat. **151:** 311–326.

Cury, P., A. Bakun, R. J. M. Crawford, A. Jarre, R. A. Quiñones, L. J. Shannon, and H. M. Verheye. 2000. Small pelagics in upwelling systems: Patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J. Mar. Sci. **57:** 603–618.

Farrell, T. M., D. Bracher, and J. Roughgarden. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. Limnol. Oceanogr. **36:** 279–288.

Fernández, M., R. Calderón, J. M. Cancino, and K. Jeno. 2007. The effect of temperature on the development of encapsulated embryos of *Concholepas concholepas* along a latitudinal cline. Mar. Ecol. Prog. Ser. **384:** 229–237.

Field, J. G., and F. A. Shillington. 2006. Variability of the Benguela current system (16,E), p. 835–863. *In* A. R. Robinson and K. H. Brinks [eds.], The sea: The global coastal ocean: Interdisciplinary regional studies and syntheses, Vol. 14. Harvard University.

Gómez, I., E. Pérez-Rodriguez, B. Viñegla, F. L. Figueroa, and U. Karsten. 1998. Effects of solar radiation on photosynthesis, UV-absorbing compounds and enzyme activities of the green alga *Dasycladus vermicularis* from southern Spain. J. Photochem. Photobiol. B. **47:** 46–57.

Hardman-Mountford, N. J., A. J. Richardson, J. J. Agenbag, E. Hagen, L. Nykjaer, F. A. Shillington, and C. Villacastin. 2003. Ocean climate of the South East Atlantic observed from satellite data and wind models. Prog. Oceanogr. **59:** 181–241.

Hill, A., B. M. Hickey, F. A. Shillington, P. T. Strub, K. H. Brink, E. D. Barton, and A. C. Thomas. 1998. Eastern ocean boundaries coastal segment (E), p. 29–67. *In* A. R. Robinson and K. H. Brink [eds.], The sea. Wiley.

Holt, R. D. 2008. Theoretical perspectives on resource pulses. Ecology **89:** 671–681.

Hormazabal, S., G. Shaffer, J. Letelier, and O. Ulloa. 2001. Local and remote forcing of sea surface temperature in the coastal upwelling system off Chile. J. Geophys. Res. **106:** 16657–16671.

———, ———, and O. Leth. 2004. Coastal transition zone off Chile. J. Geophys. Res. **109:** C01021, doi:10.1029/2003JC001956.

Lagos, N. A., S. A. Navarrete, F. Véliz, A. Masuero, and J. C. Castilla. 2005. Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along the coast of central Chile. Mar. Ecol. Prog. Ser. **290:** 165–178.

Leibold, M. A. 1995. The niche concept revisited: Mechanistic models and community context. Ecology **76:** 1371–1382.

Lluch-Belda, D., R. J. M. Crawford, T. Kawasaki, A. D. MacCall, R. H. Parrish, R. A. Schwartzlose, and P. E. Smith. 1989. World-wide fluctuations of sardines and anchovy stocks: The regime problem. S. Afr. J. Mar. Sci. **8:** 195–205.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic–pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proc. Natl. Acad. Sci. USA **94:** 14530–14535.

———, and others. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proc. Natl. Acad. Sci. USA **100:** 12229–12234.

Navarrete, S. A., E. A. Wieters, B. R. Broitman, and J. C. Castilla. 2005. Scales of benthic–pelagic coupling and the intensity of species interactions: From recruitment limitation to top down control. Proc. Natl. Acad. Sci. USA **102:** 18046–48051.

Nielsen, K. J. 2003. Nutrient loading and consumers: Agents of change in open-coast macrophyte assemblages. Proc. Natl. Acad. Sci. USA **100:** 1660–1665.

———, and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up: Intertidal interactions between consumers and upwelling. Ecol. Lett. **7:** 31–41.

Parrish, R. H., A. Bakun, D. M. Husby, and C. S. Nelson. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish production, p. 731–778. *In* G. D. Sharp and J. Csirke [eds.], Proceedings of the expert consultation to examine changes in abundance and species of neritic fish resources, Vol. 291. FAO.

Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. Nature **374:** 255–257.

Pedersen, M. F., and J. Borum. 1996. Nutrient control of algal growth in estuarine waters: Nutrient limitation and nitrogen storage among phytoplankton and species of macroalgae. Mar. Ecol. Prog. Ser. **142:** 261–272.

Pickett, M. H., and J. D. Paduan. 2003. Ekman transport and pumping in the California Current based on the U.S. Navy's high-resolution atmospheric model (COAMPS). J. Geophys. Res. **108:** 3327, doi:10.1029/2003JC001902.

Poulin, E., A. T. Palma, G. Leiva, D. Narváez, R. Pacheco, S. A. Navarrete, and J. C. Castilla. 2002. Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in central Chile. Limnol. Oceanogr. **47:** 1248–1255.

Reason, C. J. C., and M. R. Jury. 1990. On the generation and propagation of the southern African coastal low. Q. J. R. Meteor. Soc. **116:** 1133–1151.

Ricklefs, R. E. 1987. Community diversity: Relative roles of local and regional processes. Science **235:** 167–171.

Risien, C. M., C. J. C. Reason, F. A. Shillington, and D. B. Chelton. 2004. Variability in satellite winds over the Benguela upwelling system during 1999–2000. J. Geophys. Res. **109:** CO301, doi:10.1029/2003JC001880.

Rosenberg, G., T. A. Probyn, and K. H. Mann. 1984. Nutrient uptake and growth kinetics in brown seaweeds: Response to continuous and single additions of ammonium. J. Exp. Mar. Biol. Ecol. **80:** 125–146.

Roughgarden, 2006. Foreward. p. xvii–xx. *In* J. Kritzer and P. Sale [eds.], Marine metapopulations. Elsevier.

Sanford, E. 2002. Water temperature, predation, and the neglected role of physiological rate effects in rocky intertidal communities. Integr. Comp. Biol. **42:** 881–891.

Santelices, B. 1991. Production ecology of *Gelidium*. Hydrobiologia **221:** 31–44.

Shaffer, G., O. Pizarro, L. Djurfeldt, S. Salinas, and J. Rutllant. 1997. Circulation and low frequency variability near the Chile coast: Remotely forced fluctuations during the 1991–1992 El Niño. J. Phys. Oceanogr. **27:** 217–235.

Shanks, A. L., J. Largier, L. Brink, J. Brubaker, and R. Hooff. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol. Oceanogr. **45:** 230–236.

Shannon, L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. Oceanogr. Mar. Biol. Annu. Rev. **23:** 105–182.

———, and G. Nelson. 1996. The Benguela: Large-scale features and processes and system variability, p. 163–210. *In* G. Wefer, W. H. Berger, G. Siedler and D. J. Webb [eds.], The South Atlantic: Present and past circulation. Springer.

Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. Proc. Natl. Acad. Sci. USA **105:** 8974–8979.

Smith, W. O., G. W. Heburn, R. T. Barber, and J. J. O'Brien. 1983. Regulation of phytoplankton communities by physical processes in upwelling systems. J. Mar. Res. **41:** 539–556.

Strub, P. T., J. M. Mesías, V. Montecinos, J. Rutllant, and S. Salinas. 1998. Coastal ocean circulation off western South America, p. 273–315. *In* A. R. Robinson and K. H. Brink [eds.], The global coastal ocean: Regional studies and syntheses. Wiley.

Thomas, A. C., M. E. Carr, and P. T. Strub. 2001. Chlorophyll variability in eastern boundary currents. Geophys. Res. Lett. **28:** 3421–3424.

Wieters, E. 2005. Upwelling-control of positive interactions over mesoscales: A new path linking bottom-up and top-down processes. Mar. Ecol. Prog. Ser. **301:** 43–54.

———. 2006. Benthic–pelagic coupling: Rocky intertidal communities and nearshore oceanographic conditions across multiple scales. Ph.D. thesis. Univ. of Cape Town.

Wieters, E. A., S. D. Gaines, S. A. Navarrete, C. A. Blanchette, and B. A. Menge. 2008. Scales of dispersal and the biogeography of marine predator–prey interactions. Am. Nat. **171:** 405–417.

Wing, S., J. L. Largier, L. W. Botsford, and J. F. Quinn. 1995. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol. Oceanogr. **40:** 316–329.

Worm, B., H. K. Lotze, and U. Sommer. 2000. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. Limnol. Oceanogr. **45:** 339–349.

———, and U. Sommer. 2000. Rapid direct and indirect effects of a single nutrient pulse in a seaweed–epiphyte–grazer system. Mar. Ecol. Prog. Ser. **202:** 283–288.

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