Benthic-pelagic coupling: rocky intertidal communities and nearshore oceanographic conditions across multiple scales

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Declaration

I hereby declare that all of the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

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Date

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Abstract

In Chapter 1, I characterize geographic patterns in rocky intertidal communities across 6° of latitude along the west coast of South Africa and examine the spatial structure of functional group biomass in relation to wave action and upwelling intensity. Despite between-habitat differences in biomass, most functional groups showed similar regional trends in exposed and sheltered habitats, but weaker non-significant between-habitat associations were observed when considering differences due to site. Diverse geographic trends were observed, with only specialized kelp-trapping limpets showing a smoothly decreasing trend with latitude. Abrupt changes in the abundance of several species were observed at about 32°S or near 34.5°S. Correlations between functional groups were strongest in the low (exposed) and mid (sheltered) shores, and supported the possibility that species interactions, particularly (1) competitive dominance by filter feeders and gardening limpets and (2) habitat facilitation by filter feeders partially account for local differences in functional-group abundances. Nearshore oceanographic conditions were characterized using satellite-measured sea surface temperature (SST), verification by *in situ* loggers, and analysis of Offshore Ekman Transport (OET) indices. A clear discontinuity at about 32°S partitioned the coast into a northern region characterized by consistently strong and spatially homogenous upwelling, and a southern region distinguished by significant meso-scale variation in seasonal upwelling intensity among sites, with clear upwelling centers alternating with "downstream" areas only weakly influenced by upwelling. Functional group relationships with SST differed between north and south regions. Local abundances were generally more variable in the south, where greater biomass of ephemeral and corticated macroalgae, as well as specialized gardening and kelp-trapping limpets, were associated with upwelling centers. In contrast, high-shore filter-feeder and predator biomasses were significantly greater at downstream sites. These results suggest that oceanographic discontinuities around 32°S may frame community dynamics and that upwelling intensity influences community structure and generates regular spatial differences in interaction webs along the South West Cape. This study represents the critical first step to identifying spatial scales at which processes regulate communities, and

provides a series of testable hypotheses that can be evaluated by experimental comparative approaches.

Quantitative comparisons of different systems offer opportunities to evaluate the generality of large-scale patterns and putative processes. In Chapter 2, I compare the spatial relationships of key rocky intertidal functional groups to the temporal dynamics of nearshore thermal regimes across mid-latitude regions (29°-34.5°S) of the Benguela and Humboldt systems on the west coasts of South Africa and Chile. To characterize and compare nearshore oceanographic conditions, spatial structure in the temporal dynamics of thermal regimes were compared using a 16-year time series (1987-2003) of satellite-measured SST. In general, South Africa is relatively colder, particularly north of about 32°S, experiences more extreme thermal conditions and exhibits greater spatial variability in SST. Latitudinal trends between the two countries were diametrically opposite, declining southwards in Chile but increasing in South Africa. The intensity and relative importance of different temporal components of SST fluctuations also differed, producing unique thermal regimes. In general, Chile had greater long-term stability, with increasing stability poleward. Background SST dynamics across South Africa were dominated by greater high-frequency variability. Despite these differences, similar spatial structure in the relative strength of different "pulsing" frequencies was observed in both systems, with strong and coincident discontinuities observed at about 32°S. Site-to-site variations in both SST and local biomass of most functional groups were generally greater in South Africa. Multivariate characterization of community biomass revealed striking differences between South Africa and Chile, as well as between regions north and south of 32°S within each system. Between-system differences in biomass were largely unrelated to mean SST, but strongly correlated with the temporal dynamics of the thermal regimes. Nearshore hydrographic processes seem important drivers of between-system and inter-regional patterns of community structure. Within each coast, site-to-site variation in biomass of most functional groups was significantly correlated with local individual temporal components of SST dynamics, although associations often differed with tidal height and among functional groups. Moreover, the relative importance of the different temperature signals differed north or south of 32°S. Thus, local regimes may reflect very different mechanisms influencing nutrient replenishment, primary productivity, physiological stress,

and/or particle transport. This is the first study to quantitatively compare (1) the spatial structure of mean thermal states between the west coasts of South Africa and central Chile, (2) the relative importance of weekly to inter-annual dynamics of nearshore sea surface temperature, (3) the magnitudes of spatial variation in rocky intertidal community structure among-sites and between regions and (4) the degree of coupling between biomass and nearshore SST dynamics across different spatial scales.

A critical limitation to our ability to generalize and "scale up" results of locally-derived ecological models is the lack of information on how variation in large-scale processes, such as those identified in Chapters 1 and 2, modify local ecological processes (e.g. predation, competition, facilitation). Dependence of positive species interactions on the traits of individuals has rarely been explored, particularly in marine communities. In Chapter 3, transplant experiments and surveys at 14 sites spanning ~900 km of the central Chilean coast demonstrate that upwelling intensity explains among-site differences in growth rates of the turf-forming alga *Gelidium chilense*. At upwelling centers, turf algae grew faster, attained taller heights and inhibited recruitment of the mussel *Perumytilus purpuratus*, whereas short turf at downstream sites enhanced mussel recruitment. By determining the supply of mussels to higher trophic levels, upwelling-controlled facilitation has important consequences for community regulation. This is the first study to identify upwelling as a mechanism (1) controlling trait-dependent habitat modification and (2) regulating the relative importance of facilitation in marine rocky intertidal communities.

General Introduction

Benthic marine ecologists working on rocky intertidal shores have been extraordinarily successful in disentangling complex multi-species interactions and developing community theory. Empowered by rigorous experimental methods, numerous studies have revealed strong "top-down" effects, where predators and/or herbivores are capable of controlling prey assemblages and shaping local communities (e.g. Paine 1966, Lubchenco & Gaines 1981, Castilla & Paine 1987, Branch & Griffiths 1988, Menge et al. 1994, Robles et al. 1995, Menge 2000b, Underwood 2000, Menge & Branch 2001). Likewise, the primacy of competition for space or food in maintaining distributional limits, regulating abundance or body size, and determining the composition of species has been repeatedly documented (e.g. Connell 1961, Branch 1981, Hawkins & Hartnoll 1983, Branch 1984, Underwood 1986, Hall 1988). Although receiving relatively less attention, the positive effects of habitat-modifying species can also play a critical structuring role in marine systems (see reviews by Bruno & Bertness 2001, Stachowicz 2001, Bruno et al. 2003).

Early on it was clear that key environmental factors mediate species interactions to predictably alter community structure. Most notably, gradients in wave exposure and desiccation/heat stress differentially inhibit or favor species, which not only leads to systematic changes in distributional limits, but also alters whether biological interactions (e.g. predation, competition, facilitation) or physical disturbance controls local communities (e.g. Baker 1909, Lewis 1964, Dayton 1971, 1975, Stephenson & Stephenson 1972, Menge 1976, 1978a, b, McQuaid 1982, Denny 1985, McQuaid & Branch 1985,

Lubchenco 1986, Blanchette 1994, Brosnan 1994, Leonard et al. 1998). Thus, community structure was largely thought to depend upon these short-term ecological processes and environmental stressors. However, due to the nature of experimental methods, most work was necessarily restricted to small spatial scales, often occurring over few-100s of meters within a single site. While this allowed critical testing of ideas and clearly advanced our understanding of community dynamics, it also led to several misconceptions regarding the scales over which different processes vary and precluded our ability to generalize (Menge 1992, 2000b).

Recent empirical work incorporating variation that occurs over larger spatial scales and longer temporal scales than traditionally tackled has identified a new suite of physical and ecological processes involved in sculpting communities, expanding our understanding of connections among populations, communities, and adjacent ecosystems (e.g. Tegner & Dayton 1987, Gaines & Bertness 1993, Bustamante et al. 1995b, Bustamante & Branch 1996b, Polis & Hurd 1996, Connolly & Roughgarden 1998, Dayton et al. 1999, Menge et al. 2003, Coleman et al. 2006). Although few, these studies highlight the importance of nearshore oceanographic processes in driving transport pathways that supply nutrients, food particles and larvae to benthic habitats. Moreover, it now appears that hydrodynamically-driven thermal fluctuations can also alter physiological performance of organisms. These effects can modify the strength of key species interactions, translating into important consequences for benthic community dynamics (e.g. Sanford 1999, 2002b). Since persistent spatial structure is often observed in oceanographic variability, such as that exhibited in satellite imagery, linkages to community dynamics may be predictable. For example, Navarrete et al. (2005) documented a sharp, regional-scale discontinuity in upwelling regimes that produces abrupt and persistent changes in offshore surface

chlorophyll-a and onshore recruitment rates of competitively dominant species, which consequently set bounds to the strength of species interactions. Such studies have clearly broadened our perspective and allowed us to begin to match the scale of knowledge with that of pressing environmental problems. Yet, we still know little about the magnitude, nature, interdependence and generality of benthic-pelagic coupling in driving community patterns. To address such questions, a multi-scale approach utilizing a combination of diverse techniques that integrate physical, chemical, and biological information is needed (Levin 1989, 1992, Gaines & Bertness 1993).

Over large spatial scales, correlation has been widely used to detect similar changes between paired spatial series and generate hypotheses about the effects of environmental forcing on geographic community patterns. However, they are generally weak in determining causes of variation (Diamond 1986, Lubchenco & Real 1991). Given that controlled experimentation of processes acting over large scales is usually impossible, comparisons of natural variation in existing conditions and phenomena can help to refine hypotheses. An even more powerful approach is that of combining small-scale and large-scale approaches, such as replicating local-scale experiments at multiple sites of contrasting conditions (i.e. the comparative-experimental approach). While each technique has its limitation, a combination of approaches can expand understanding, place results into context, and offer important insight into the scale-dependency of processes. In this thesis, I use all these tools to try and identify environmental processes to which benthic communities are most sensitive, to examine the potential effects of large-scale nearshore oceanographic conditions on rocky intertidal communities.

The coastal environments of eastern boundary current ecosystems of the world are of particular interest due to the intense wind-driven upwelling that injects nutrients into the

euphotic zone and fuels anomalously high primary and secondary production (Small & Menzies 1981, Huyer 1983). These systems are defined by complex physical and chemical dynamics that interact over a variety of spatial and temporal scales. Inspection of sea surface temperature (SST) and ocean color imagery reveals a rich structure of meso-scale features, such as focused centers, filaments, eddies, and jets. These features are superimposed on larger regional and basin-scale shifts in water mass properties, atmospheric forcing, and coastal morphology (Parrish et al. 1981, Huyer 1983, Hickey 1998). Many of the recent ecological studies documenting strong biophysical coupling have been carried out in different coastal upwelling systems.

Along the extensive coasts of South Africa and Chile, the two major southern-hemisphere eastern-boundary current ecosystems, the study of biological and physical processes structuring rocky intertidal communities at just a few sites has been the main focus of ecological research. Over the past two to three decades, this scientific endeavor has led to the recognition of these coasts as among the best studied marine systems of the world, and examples of studies in both systems now appear in basic ecological textbooks (e.g. Raffaelli & Hawkins 1996, Barnes & Hughes 1999, Bertness et al. 2001). The main patterns of zonation and regulatory processes were first placed in a descriptive framework by Stephenson and Stephenson (1949) and are summarized in reviews by Branch and Griffiths (1988) for South Africa and Fernandez et al. (2000) for Chile. As is the case for most coasts of the world, the majority of knowledge about the dynamics of these intertidal systems has been built upon a handful of geographically restricted experimental studies (Branch & Griffiths 1988, Santelices 1990, Camus 1998, Fernandez et al. 2000).

Experimental studies along the west coast of South Africa were among the first to demonstrate that variation in bottom-up effects (nutrients/productivity) could have strong

and cascading influences on the dynamics of rocky intertidal communities. In this case, variation in nutrient inputs associated with seabird colonies (Bosman et al. 1986, Bosman & Hockey 1986, Branch et al. 1987) or plant and detrital subsidies from adjacent subtidal kelp beds (Field et al. 1980a,b, 1981, Koop et al. 1982, Linley & Field 1982, Newell et al. 1982, Bustamante et al. 1995a, Bustamante & Branch 1996a) set the stage for complex dynamics reliant upon both top-down and bottom-up processes. These studies prompted large-scale surveys across South Africa (several thousands of km) that identified biogeographic regions and gradients in onshore nutrient concentrations and benthic primary productivity that are associated with changes in upwelling intensity as move around the west, south, and east coasts (Emanuel et al. 1992, Bustamante et al. 1995b). Over this sub-continental scale, increased grazer and filter feeder biomass were associated with increased productivity. Patterns of spatial variation in community structure that occur over meso-scales (sites 10s – 100s km apart) within the west coast have yet to be identified, but holds the promise of integrating the rich ecological information derived from previous local and biogeographic studies (Menge & Olson 1990, Connolly & Roughgarden 1998, Broitman et al. 2001).

This thesis constitutes a series of studies directed at understanding the scales over which ecological processes and community structure are coupled to nearshore oceanographic environmental variability, as represented by sea surface temperature. Large, quantitative data sets were gathered to describe patterns of community structure, and are certainly amenable to exploring a diverse array of questions regarding composition, diversity, distributional ranges, etc. However, for the purposes here, I have tried to constrain my questions/analyses to alongshore spatial patterns in biomass of functional groups. Biomass values are generally representative of energy flow through a community

(Field 1983, McQuaid & Branch 1985). Likewise, functional groups tend to highlight species attributes related to performance and are based on productivity and disturbance potentials (e.g. Steneck & Dethier 1994). More detailed analysis of species richness and composition will follow in future analyses.

In Chapter 1, I characterize alongshore spatial patterns in biomass of different functional groups across wave-exposed and sheltered rocky intertidal habitats of the west coast of South Africa. I then examine their relationship with regional and meso-scale coastal oceanographic conditions, with particular attention to spatial variability of coastal upwelling centers. I conducted quantitative surveys of assemblages occupying four main shore heights within matched exposed and sheltered habitats at 43 sites spaced between 29°S and 34.5°S latitude. Spatial variability in nearshore oceanographic conditions was assimilated from both satellite-measured and *in situ* sea surface temperatures, as well as estimates of Offshore Ekman Transport (OET) that were obtained from the National Oceanic and Atmospheric Administration (NOAA). From this, I hoped to identify the most important scales of biological-physical couplings, provide a series of testable hypotheses and construct a predictive framework that incorporates local interspecific interactions and physical forcing mechanisms in driving alongshore changes in community structure.

Global eastern-boundary current ecosystems are forced by both shared physical characteristics/features common to all coastal upwelling systems, as well as by individual basin-scale circulation patterns and atmospheric connections. In Chapter 2, I use the comparative analysis approach to begin to evaluate the generality and/or context-dependency of large-scale patterns in benthic-pelagic coupling. First, I quantify and evaluate the similarities and differences of spatial patterns in temporal dynamics of nearshore thermal regimes across mid-latitude regions (29°-34.5°S) of the Benguela and

Humboldt systems. Characterizations of spatio-temporal dynamics were based on 16-year time series of sea surface temperature derived from thermal imagery. I then asked whether biomasses of key intertidal functional groups were coupled to environmental variability within or between eastern boundary coastal ecosystems. Identical surveys of low- and mid-shore assemblages on wave-exposed shores at 27 South African and 16 Chilean sites were conducted across the same latitudinal range within each system. Surveys in central Chile built upon and expanded a previously-existing, long-term dataset first presented in Broitman et al. (2001).

A critical limitation to our current ability to generalize and "scale up" results of locally-derived ecological models is the lack of information on how large-scale processes, such as those identified in Chapters 1 and 2, modify those acting over local scales. In Chapter 3, I use the comparative-experimental approach to ask whether alongshore, meso-scale variation in upwelling intensity that occurs over ~900 km of the central Chilean coast impacts local growth rates and morphology of dominant turf-forming macroalgae and regulates the relative importance of facilitation in regulating these rocky intertidal communities. This study consisted of a series of experiments and surveys conducted at 14 sites, which were chosen for their proximity to major upwelling centers.

The final chapter synthesizes the results of my studies and provides general conclusions regarding biological-physical linkages over meso-, regional-, and basin-wide scales.

Chapter 1

Geographic variation in rocky intertidal community structure along the oceanographically variable west coast of South Africa: evidence for the modifying influences of upwelling and wave action

1.1 Introduction

There is growing evidence that the dynamics of local communities cannot be fully understood unless considered within the context of regional phenomena (Ricklefs 1987, Ricklefs et al. 2004). To achieve this, integration of information from a wide variety of disciplines over a broad range of spatial and temporal scales is required. Through rigorous experimental tests, marine ecologists have had considerable success in unraveling the dynamics of local systems, providing critical insight into multi-species interactions and the relative importance of different processes in regulating communities (for reviews see Raffaelli & Hawkins 1996, Fernandez et al. 2000, Menge 2000, Underwood 2000, Underwood et al. 2000, Menge & Branch 2001). However, due to the nature of experimental methods, most work has been necessarily restricted to small spatial scales, often occurring over a few 10s of meters within a single or a few sites (Wiens 1989, Steele & Forrester 2005). A large gap exists when the scale of questions is expanded to incorporate processes operating among habitats or regions. Description of large-scale patterns, as well as an understanding of their proximate causes, is critical to our ability to

generalize and "scale up" our experimentally-derived understanding of community dynamics, and to answer impinging conservation questions.

Community patterns reflect the outcome of interacting physical and biological processes acting across multiple scales. An important challenge, therefore, is to examine mechanisms that relate processes at one scale to patterns at another (Levin 1992). Recent studies show that local biological interactions can give rise to large-scale patterns (Wootton 2001, Kerr et al. 2002, Pearman 2002, Guichard et al. 2003, Steele & Forrester 2005). Therefore, description of such patterns may offer insight into regularities, causes of change, and the degree to which local interspecific interactions, such as facilitation, competition and predation, can give rise to predictable patterns over larger spatial scales. Similarly, strong gradients and discontinuities or breaks in community patterns can be an indication of the limits under which locally-derived models apply (Navarrete et al. 2005). Alternatively, regional processes may overshadow the influence of such local processes on assemblage structure (Ricklefs 1987, Van Dorp & Opdam 1987, Pearson 1993). For example, fragmentation of habitats may limit dispersal or survival of some functional groups, but not others (e.g. Robinson et al. 1992), or promote instability (e.g. Boulinier et al. 1998). Examining associations among community patterns and the physical environment can thereby offer insight into the mechanisms responsible for determining community structure, and provide testable hypotheses about the relative importance of these processes over space.

In rocky intertidal and shallow subtidal habitats, there is growing evidence that nearshore oceanographic processes can dictate the strength of interspecific interactions and can be of overriding importance in determining large- to meso-scale variability in community structure (Menge et al. 1994, Menge et al. 1997a, Connolly & Roughgarden

1998, Menge et al. 2003, Menge et al. 2004, Navarrete et al. 2005). For example, Connolly and Roughgarden (1998), Connolly et al. (2001) and Menge et al. (2004) argue that coastline topography and associated changes in offshore extension of upwelling fronts produce latitudinal gradients in recruitment of mussels and barnacles along the coasts of Oregon and California, which ultimately drives regional differences in community structure. Likewise, a sharp regional discontinuity in oceanographic regime along the coast of Chile produces a geographic break in recruitment and abundance of mussels and barnacles, and dictates the relative importance of top-down control of these benthic communities (Navarrete et al. 2005).

Alongshore variation in nearshore oceanographic conditions also occurs within regions over meso-scales of 10s of kilometers. For example, localized centers of coastal upwelling are often associated with headlands and capes (Jury 1985), while relatively warm-water areas not directly affected by upwelling occur between upwelling centers (Kelly 1985, Graham & Largier 1997, Broitman et al. 2001). Such alongshore variation in upwelling influences nutrient levels and primary productivity. Low chlorophyll and high nutrient concentrations in the euphotic zone seem to be consistently associated with newly upwelled water (Andrews & Hutchings 1980, Field et al. 1980b, Barlow 1982, Hutchings et al. 1983, Olivieri 1983, Brown & Field 1985, Wieters et al. 2003), and levels of available nutrients in onshore waters can directly affect benthic macroalgae (Fujita et al. 1989, Bustamante et al. 1995b, Menge et al. 1997a, Nielsen & Navarrete 2004). In contrast, high phytoplankton production and distinct bloom events are often observed downstream from upwelling centers (Shannon et al. 1983, Brown 1984, Marin et al. 1993, Masotti et al. 1998, Wieters et al. 2003), increasing the availability of food for benthic filter-feeders (Page & Hubbard 1987, Duggins et al. 1989, Smaal & Van Stralen 1990, Bertness et al. 1991,

Leichter et al. 1998, Sanford & Menge 2000) and pelagic larvae (Barnes 1956, Hentschel & Emlet 2000, but see Vargas et al. in press). Likewise, spatial variation in upwelling can influence advection and retention of larval stages of benthic invertebrates, such that their delivery and settlement onshore is concentrated downstream from upwelling centers when upwelling relaxes (Small & Menzies 1981, Roughgarden et al. 1991, Shanks 1995, Wing et al. 1995a, Wing et al. 1995b, Shanks et al. 2000). Under these conditions and over these scales, the supply-side ecology of benthic populations is probably dominated by differences in upwelling intensity.

Upwelling effects can potentially interact with or be modified by local habitat characteristics to differentially affect local communities. On rocky shores, differences in wave exposure have long been known to be a critical factor on community composition and species abundance, largely attributed to differences in physical stresses, food supply and disturbance that alter survival and species interactions (Lewis 1964, Dayton 1971, 1975, Stephenson & Stephenson 1972, Menge 1976, 1978a, b, McQuaid 1982, McQuaid & Branch 1984, Denny 1985, McQuaid & Branch 1985, Menge & Sutherland 1987). Wave exposure also modifies water flux and residence times, which can determine nutrient and gas exchange rates (e.g. Leigh et al. 1987), as well as supply rates of particles (Field et al. 1980b, 1981, Gaines et al. 1985, Menge 1992, Bustamante & Branch 1996a, Menge et al. 1997b). Thus, the relative importance of upwelling and wave exposure warrants consideration.

In South Africa, strong upwelling on the west coast and weak or no upwelling on south and east coasts corresponds to different biogeographic provinces and creates an oceanographic gradient in productivity (Stephenson 1936, 1939, 1943, 1944, 1947, Stephenson et al. 1940, Emanuel et al. 1992, Bustamante et al. 1995b, Bustamante &

Branch 1996b, Bolton & Stegenga 2002). Along this gradient, intertidal nutrients, benthic chlorophyll-a production and mean biomass of grazers and filter feeders are all greater on the west coast and decline toward the east (Bustamante et al. 1995b). These studies have contributed tremendously to our understanding of the biological effects of physical oceanographic features and help to explain how biological productivity varies over sub-continental scales, leading to among-coast differences in benthic communities. However, whether alongshore differences in coastal upwelling over smaller meso-scales are associated with similar differences in community organization within biogeographic provinces is less well documented. Yet, it is these intermediate scales that are most relevant for managers and such information is critical to identify priority areas for conservation.

Here, I present geographic patterns in the structure of rocky intertidal communities across 6° of latitude along the west coast of South Africa as a descriptive part of a long-term study on the dynamics of nearshore marine ecosystems. Since the goal is to characterize broad patterns of abundance and resource utilization across the region, I examine variation, and co-variation, in biomass of different functional groups and correlations with environmental factors. I address spatial patterns both across the entire region (regional trends) and those due to smaller (site) scales. I evaluate the effects of regional and meso-scale upwelling intensity on patterns of community biomass and provide testable hypotheses that can be evaluated in the future by experimental comparative approaches.

1.2 **Methods**

Study Region and Sites

Field surveys of rocky intertidal communities were conducted, during spring months of 2001-2003, at 43 sites (10s-100s km apart) stretched between 29°S and 34.5°S along the west coast of South Africa, encompassing a broad range of meso- and large-scale variation in environmental conditions (Fig. 1.1, Table 1.1). Namaqualand (28°S - 31°S), together with the principal upwelling center further north at Lüderitz, Namibia (27°S), constitutes an "environmental barrier" (sensu Shannon 1985) and a discontinuity in oceanographic conditions that essentially divides the Benguela system into two distinct regions. Here, the coastline is uniform, devoid of significant embayments, and distinguished by an arid coastal belt of low relief. The wind field exhibits little seasonal variability, so coastal upwelling persists throughout the year and cold water is present during most seasons (Shannon 1985, DeMarcq et al. 2003). South of 32°S to approximately 34.5°S, where the poleward extent of the Benguela is sharply confined by warm waters of the Agulhas Current (Shannon & Nelson 1996, Shillington 1998), alongshore winds and upwelling are highly seasonal, with maximum upwelling occurring in austral spring and summer (September - March, Andrews & Hutchings 1980, Nelson & Hutchings 1983a, Shannon 1985). The Southwest Cape is characterized by complex topography; an irregular coastline produces striking capes and bays and, in places, mountains abut against the shore. These features shear the wind-stress field (Jury 1985) and, in combination with a variable yet relatively narrow coastal shelf (30- 40 km), beget strong, alongshore spatial variability in coastal upwelling (Jury 1985, Shannon 1985). Thus, upwelling occurs at localized centers associated with capes.

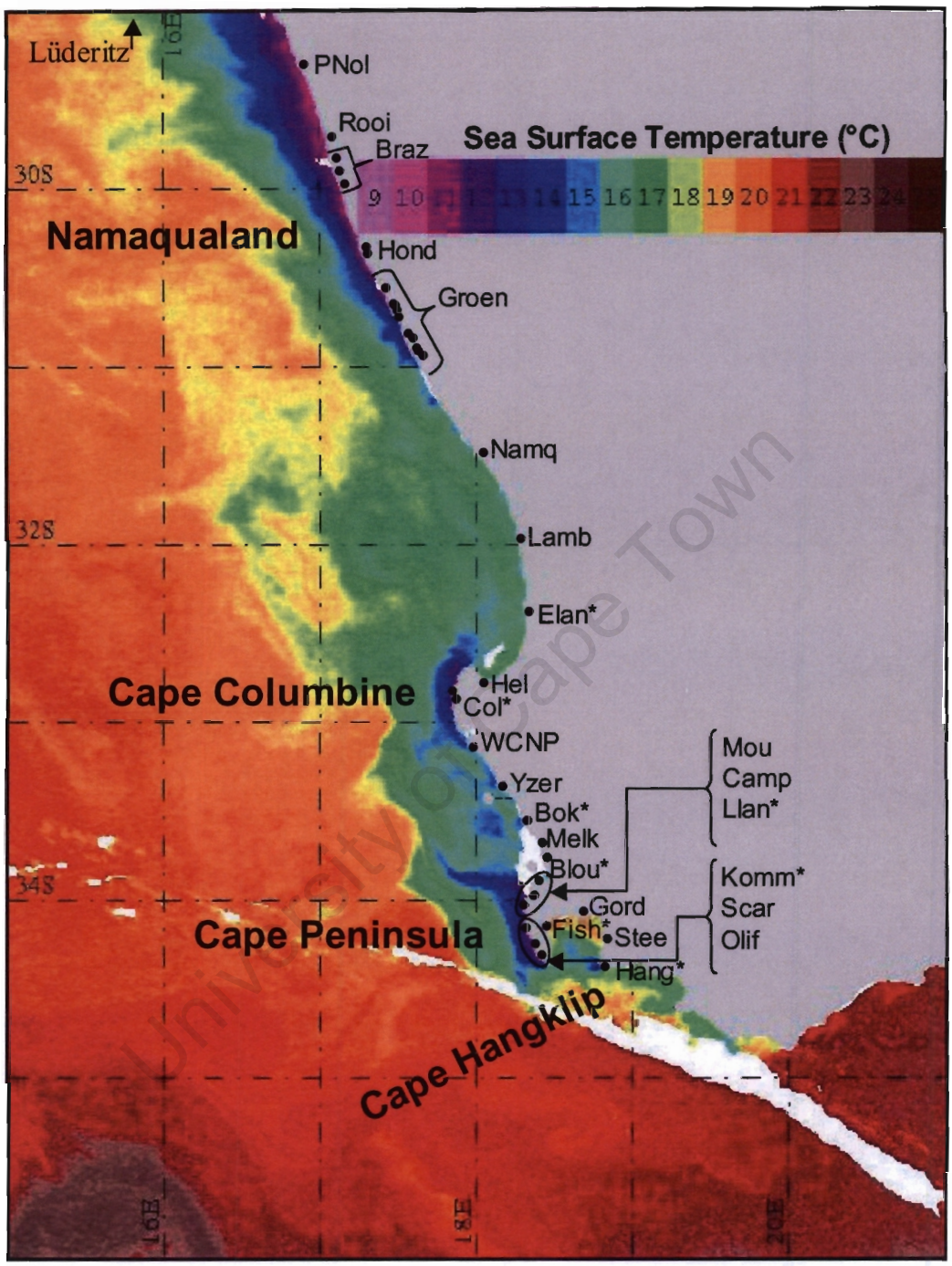


Fig. 1.1. Selected AVHRR (Advanced Very High Resolution Radiometer) satellite image of sea surface temperature, also showing locations of field sites. Alongshore variation in temperature reflects the existence of cold upwelling centers with warm downstream areas in between. Asterisks indicate sites with *in situ* temperature loggers. See Table 1.1 for interpretation of site name abbreviations.

Study sites were variably spaced along the coast. Across the Northwest Cape, most sites were distributed northwards from 31°S due to limited roads and restricted access to private diamond-mining lands. Near Groenrivier (30.5°S), sampling was more intensive, with 16 sites covering approximately 25 km. In the Southwest Cape, I selected study sites within and downstream of upwelling centers. The most intense and large upwelling centers occur off Cape Columbine (2 sites) and the Cape Peninsula (6 sites), with a smaller one at Hangklip (1 site) (reviewed by Shannon 1985). In contrast, relatively warmer, more passive upwelling conditions occur downstream in the lee of such capes, and therefore I sampled three such sites within False Bay, two in Table Bay, and two adjacent to St. Helena Bay.

Despite differences in large-scale coastline topography, most sites along the coast exhibit a similar, broad range of wave exposure over scales of 10s to 100s of meters. The role of wave action has clearly been demonstrated to be an important structuring agent in South African intertidal communities (Stephenson 1943, Stephenson & Stephenson 1972, McQuaid 1981, McQuaid & Branch 1984, McQuaid & Branch 1985, Field & Griffiths 1991, Emanuel et al. 1992, Bustamante & Branch 1996b). However, whether larger-scale upwelling processes interact with or modify the effects of wave action is not known. Therefore, whenever possible, I sampled two contrasting levels of wave exposure (wave exposed and sheltered) nested within sites with different intensities of upwelling, rendering a total of 73 sampling localities.

Community Structure

To characterize alongshore patterns in rocky intertidal community structure, I conducted quantitative surveys of the four major tidal zones recognized at wave-exposed and wave-protected habitats at each site (Branch & Branch 1981). Platforms were selected to be comparable in exposure to wave action. Percentage cover of macroscopic sessile flora and fauna within a minimum of six 0.25 m^2 quadrats was sampled at haphazard intervals (1-5 m) along 20-50 m long transects stretched parallel to the shore in each zone. At most sites, 2-3 transects (30-100 m apart) were sampled per zone. Visual estimates of percentage cover were aided by a monofilament grid of twenty-five 10 x 10 cm squares (i.e. 4% cover each). This sampling method provides an adequate and consistent estimate of abundance of common species (Dethier et al. 1993, Bustamante et al. 1997), but can be less accurate for species with low cover (i.e. <2%). All species covering less than 1% of quadrat area were scored as 0.5% cover. Covers of species inhabiting primary space (attached to the rock surface) and secondary space (atop other organisms) were estimated separately, so total cover could exceed 100%.

Numbers of all mobile invertebrates were counted within each quadrat. In addition, individual patellid limpets of the genera *Scutellastra* and *Cymbula*, which can reach up to 100 mm in length, were classed according to size and distinguished according to whether they occupied primary or secondary space. Three size-classes were employed and similarly defined for most species: recruits (shell length < 10 mm), juveniles (10-30 mm) and adults (>30 mm). Because *S. argenvillei* and *C. granatina* switch from general grazing to trapping kelp at about 40 mm shell length (Bustamante et al. 1995a), "adults" of these species were considered to be individuals > 40 mm. To characterize size frequency

distributions of *S. argenvillei*, *C. granatina*, and *S. granularis* in greater detail, lengths of all individuals found in 8-10 quadrats were measured to the nearest mm.

Biomass (wet weight) per species was calculated for each quadrat using area/mass and length/mass regressions for sessile and mobile species, respectively. To obtain site-specific conversion equations for all dominant sessile species (> 5 % cover), I collected a minimum of 5 samples per species from each site. For each species, measured patches of 100% primary cover were randomly selected and all material within them removed, rinsed, blotted dry, and weighed to the nearest 0.01g. Mean mass per unit area for each species was then multiplied by percentage cover to derive biomass for the quadrat. To obtain site-specific length/mass regressions for mobile species, I collected a minimum of 50 individuals that spanned the size range observed at each site. Individuals were measured to the nearest 0.1 mm and weighed to the nearest 0.01g. These regressions were then applied to the size-frequency data to derive average biomass.

Since broad-scale comparisons among functional groups can focus attention on key regulating factors (Hay 1994, Steneck & Dethier 1994, Duarte et al. 1995), species abundances were pooled into functional groups (Table 1.2). Functional groups of algae were based upon morphological and anatomical characteristics that are associated with differences in productivity potential and susceptibility/resistance to herbivory and mainly followed classifications developed by Steneck and Dethier (1994) and modified by Broitman et al. (2001). Invertebrate classification was based on trophic position and foraging strategy and distinguished "gardeners" that form territorial patches of algae and "trappers" that trap either drift algae or fronds of living kelp from other more conventional grazers because their functional effects on the ecosystem differ (Branch & Griffiths 1988). Other than than the special cases presented by "gardeners" and "trappers" (*Cymbula* and

Scutellastra), differences in functional group do not generally occur between congenerics. Whenever individual species presented discontinuous patterns across the region, I examined their individual abundances. A more comprehensive 'species-based' analysis will be presented elsewhere.

Physical environment

To characterize alongshore-variation in the physical environment and classify sites according to upwelling intensity, 17 high-resolution (1 km) AVHRR (Advanced Very High Resolution Radiometer) thermal images from the summer upwelling season (Jan – March) of 2003 were analyzed. Using image-processing techniques, I extracted a nearshore transect parallel to the shoreline (about 2-3 km offshore), as well as transects perpendicular to the shore at each site. At each site, the mean differences between sea surface temperature (SST) nearshore (within 2-3 km) and that 25, 40, 60, 80, and 100 km directly offshore were calculated. Sites with onshore waters persistently colder than offshore waters in all images were defined as "upwelling centers", while onshore waters consistently warmer or similar ($\leq 0°C$) to offshore waters were defined as "downstream" sites with weak upwelling (see also Broitman et al. 2001). To simplify presentation, here I show mean differences in SST at 25 km, which provided the greatest spatial and temporal coverage (least data loss due to cloud cover) and avoided the influence of offshore variation due to Agulhas eddies and rings. To corroborate the classification of sites obtained this way, direct measurements of SST were made with onshore temperature loggers (Tidbit Stowaway, ONSET) placed *in situ* at ~1 m depth at eight sites that were expected to vary in upwelling intensity (indicated by * in Fig. 1.1). *In situ* loggers recorded SST at 5 min intervals from 2001 to present. Daily and 5-day composite means of *in situ* SST were

compared to estimates based on the 17 high-resolution satellite images, as well as a longer time series (1987-2003) of 5-day composites derived from low spatial resolution (4.5 km) NOAA AVHRR, Global area coverage (GAC) that were kindly provided by Herve Demarcq. To further evaluate latitudinal variation in seasonal upwelling intensity, seasonal means of the 1-degree lat/long squares of Upwelling Index downloaded from the National Oceanographic and Atmospheric Administration (NOAA) website (http://www.pfeg.noaa.gov/) were calculated.

Data analyses:

To compare site-level biomass (sum of mean biomass ($g/0.25m^2$) per zone) of functional groups between habitats, 1-way ANOVAs, with wave exposure considered as a fixed factor and abundance per site as replicates, were used. Data were transformed (ln [x+1]) to meet model assumptions, which were checked by visual inspection of the residuals and tested using a Shapiro-Wilks test for normality. A completely factorial design with wave exposure and tidal height was not possible due to incomplete information for several sites. To then evaluate the spatial consistency of differences in biomass across tidal heights (zones) and sites, a 2-way ANOVA was used, with tidal height considered as fixed factor and sites considered a random factor, with separate analyses being undertaken for wave-exposed and sheltered habitats. In all cases a log (n + 1) transformation was applied to meet ANOVA assumptions. Significant 2-way-interactions required tidal heights to be considered separately in further analyses of spatial patterns in functional group abundance (see Results).

To distinguish spatial correlation resulting from regional or latitudinal trends from those due to among-sites (meso-scale) variation, I decomposed the spatial variation in SST

and functional group biomass and abundance (percentage cover or density) into its trend (i.e. variation common to several sites adjusted throughout the region) and the residual variation (local variation not accounted for by the larger, regional trend). A LOcally WEighted Scatterplot Smoothing (LOWESS: Cleveland 1979) was fitted to the spatial pattern in biomass and abundance (log n + 1) as a function of distance from the southernmost study site (Hangklip). To determine how much smoothing to allow, the process was repeated for several values of the f-factor, and final selection for analysis was that producing normal LOWESS residuals and independence from geographical distance (Kolmogorov-Smirnov tests, $p > 0.05$; Trexel & Travis 1993). For each LOWESS regression, I retained the predicted values for each focal point (Ys) and the local residuals, which provided three descriptors of biomass and abundance: 1) the fitted LOWESS values (hereafter, regional trend), 2) the local residuals (hereafter, meso-scale variation) and 3) the observed means at each site (hereafter, raw data). See Lagos et al. (2005) and Navarrete et al. (2005) for similar applications.

As a first step to examine whether patterns of functional group biomass in wave exposed and sheltered habitats were spatially coupled along the coast, correlation (Spearman rank r_s) between habitats was calculated for each descriptor of biomass. Rank correlations were preferred because I was interested in whether the areas of relatively high/low biomass were the same for both habitats. Due to the distinct species composition of communities occupying exposed and sheltered habitats, comparisons were based on overall site-level biomass, which was estimated as the sum of means for each intertidal zone. However, data for all four tidal heights were not available for all sites, largely due to variation in local geomorphology, and therefore I restricted analyses only to those sites presenting dependable estimates of all functional groups in all four tidal zones.

To explore potential species or functional group interactions, I calculated correlations among functional groups using r-Pearson correlations for LOWESS residual abundance and biomass of functional groups. In this manner, strong positive or negative correlations among sites were not confounded with regional trends. Because competitive hierarchies in space-use are prevalent in these communities (Branch 1984), correlations were calculated based on cover and density, as well as biomass. Separate analyses were performed for wave exposed and sheltered habitats. Sequential Bonferroni corrections were applied to adjust significance levels for multiple comparisons (Legendre & Legendre 1998, Peres-Neto 1999).

To evaluate the effects of regional and local variation in SST on the spatial patterns of biomass and abundance across wave exposed and sheltered habitats, I used simple linear regression analyses. To further evaluate the effects of meso-scale spatial variation in upwelling intensity on local variation in functional group abundance and biomass, I restricted analyses to sites falling within the southern region, which is characterized by clear variation in upwelling conditions over meso-scales (see below). From the LOWESS regressions, local residual biomass for each functional group was analyzed using one-way ANOVA, with upwelling condition considered as a fixed factor. Visual inspection of the residuals plotted against predicted values revealed variances were homogeneous, and normality was tested using Shapiro-Wilks W test. Similar analyses were performed for each tidal height and wave exposure habitat.

1.3 **Results**

Physical environment: SST & upwelling

Although mean onshore *in situ* measured SST was approximately 2°C colder than that obtained from satellite images, both showed similar spatial patterns of variation and were strongly and positively correlated across the study region (Fig. 1.2a, see also Lagos et al. 2005 for a similar result on the coast of Chile). The pattern of mean satellite-derived SST during upwelling seasons exhibited a significant spatial structure, with a clear latitudinal trend of increasing temperature toward the south (Fig. 1.2b). The significant positive relation with latitude was also clear when long-term means were considered (1987-2003, $r^2 = 0.46$, $P = 0.0005$). Average offshore-onshore difference in SST for the study sites revealed further spatial structure along the coast (Fig. 1.2c). A positive difference indicates the presence of a cold, coastal water mass relative to offshore, which is interpreted as upwelling. Two distinct regions of the coast were apparent: north of about 32°S (Site no. 22 on Fig. 1.2c), strong and spatially homogenous upwelling characterized the region, whereas significant meso-scale variation distinguished the area south of that, with clear upwelling centers alternating with "downstream" areas of weak or indirect effects of upwelling. These differences were obvious despite the substantial variation observed among sites within upwelling categories. A clear latitudinal trend in upwelling intensity and persistence, as measured by upwelling indices, was also observed, with seasonal means in offshore transport weakening toward the south, where upwelling favorable conditions are less consistent and seasonally variable (Fig. 1.3).

Two important patterns therefore emerge: (1) a general increase in temperature from north to south, and (2) spatially homogenous sustained upwelling north of 32°S but

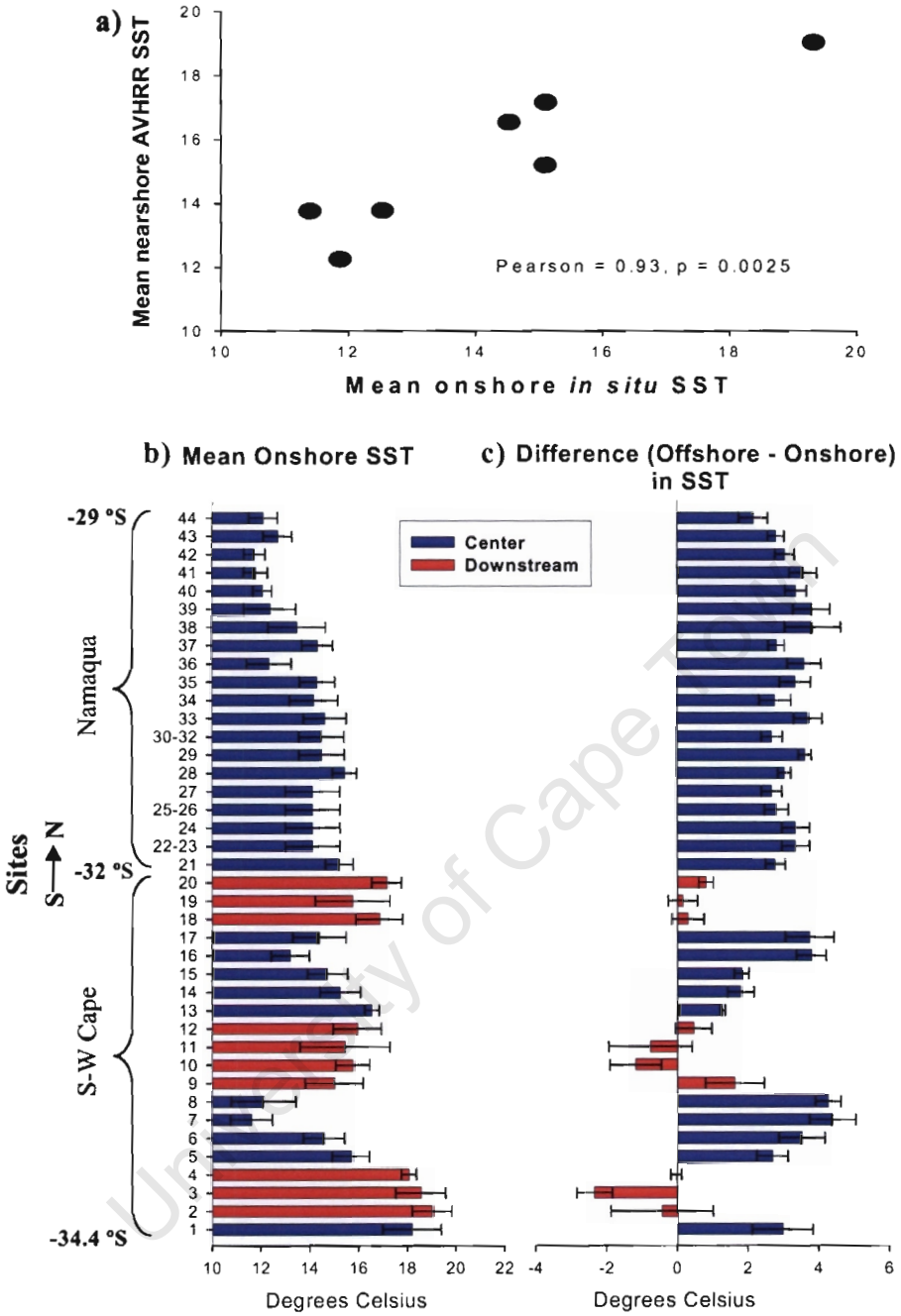


Fig. 1.2. a) Relationship between onshore mean *in situ* sea surface temperature (SST) and nearshore mean satellite-measured SST. Pearson correlation coefficient was statistically significant at P = 0.0025. b) Mean daily onshore SST in front of each study site c) Mean difference in SST between pixels 25 km offshore from each study site and SST 2 km offshore. Positive values indicate water nearshore was colder then offshore. Blue bars = upwelling centers, red bar = downstream sites. Names of sites corresponding to site numbers appear in Table 1.1. Due to satellite resolution, there are some cases where a bar represents more than one site.

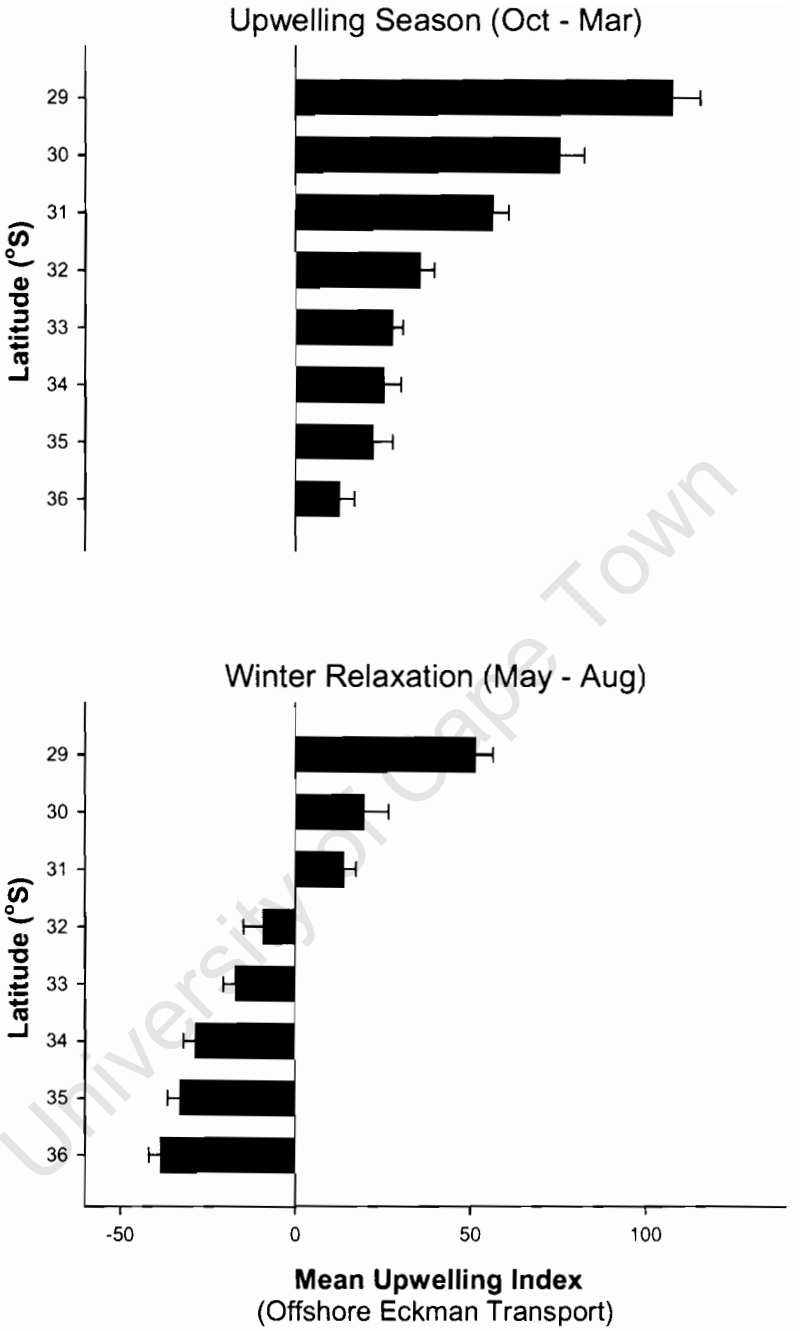


Fig. 1.3. Seasonal means of 1-degree lat/long squares of Offshore Eckman Transport indices obtained from the National Oceanographic and Atmospheric Administration (NOAA).

spatially heterogeneous alternation of upwelling centers and downstream sites and a concentration of upwelling in summer to the south of that.

Patterns of biomass

Total site-level biomass (sum of mean biomass (g / 0.25m^2) per zone, all functional groups pooled) was similar on wave exposed and sheltered shores (Fig. 1.4a: $F_{1,67} = 0.269$, MS = 0.165, p = 0.606), but the relative contribution of functional groups differed. Sessile filter feeders dominated exposed shores, whereas macroalgae dominated sheltered shores (Fig. 1.4a, insert). Moreover, exposed shores supported significantly greater biomass of kelp, gardening limpets, and anemones, while sheltered shores supported greater biomass of ephemeral algae and trapping limpets.

Regional LOWESS-adjusted trends in site-level biomass of most functional groups were significantly, positively correlated between wave exposed and sheltered habitats (Fig. 1.4b), suggesting that both habitats respond in similar ways to larger-scale processes. Across both habitats, ephemeral algae (mostly *Ceramium*, *Centroceras*, and *Cladophora* in exposed; but *Aeodes* and *Ulva* in sheltered) and corticated macroalgae (primarily *Champia* and *Gigartina*), as well as kelp, presented oscillating patterns of biomass alongshore, with a striking trough occurring at sites towards the center of the region, from about 30.5°S to 31°-32°S (sites 21-37; Fig. 1.5). Here, ephemeral and corticated algae were overall small and less robust than other parts of the coast, leading to low biomass values even at sites with relatively high average percentage cover (40-60 %). The relatively low biomass of kelp in this same region reflected low kelp cover (mean ± SE = 0.63 ± 0.36). Specialized, kelp-trapping limpets exhibited clear latitudinal trends, with increasing biomass that reached extraordinary levels (up to 5.2 kg/m^2) towards the north in both exposed and sheltered

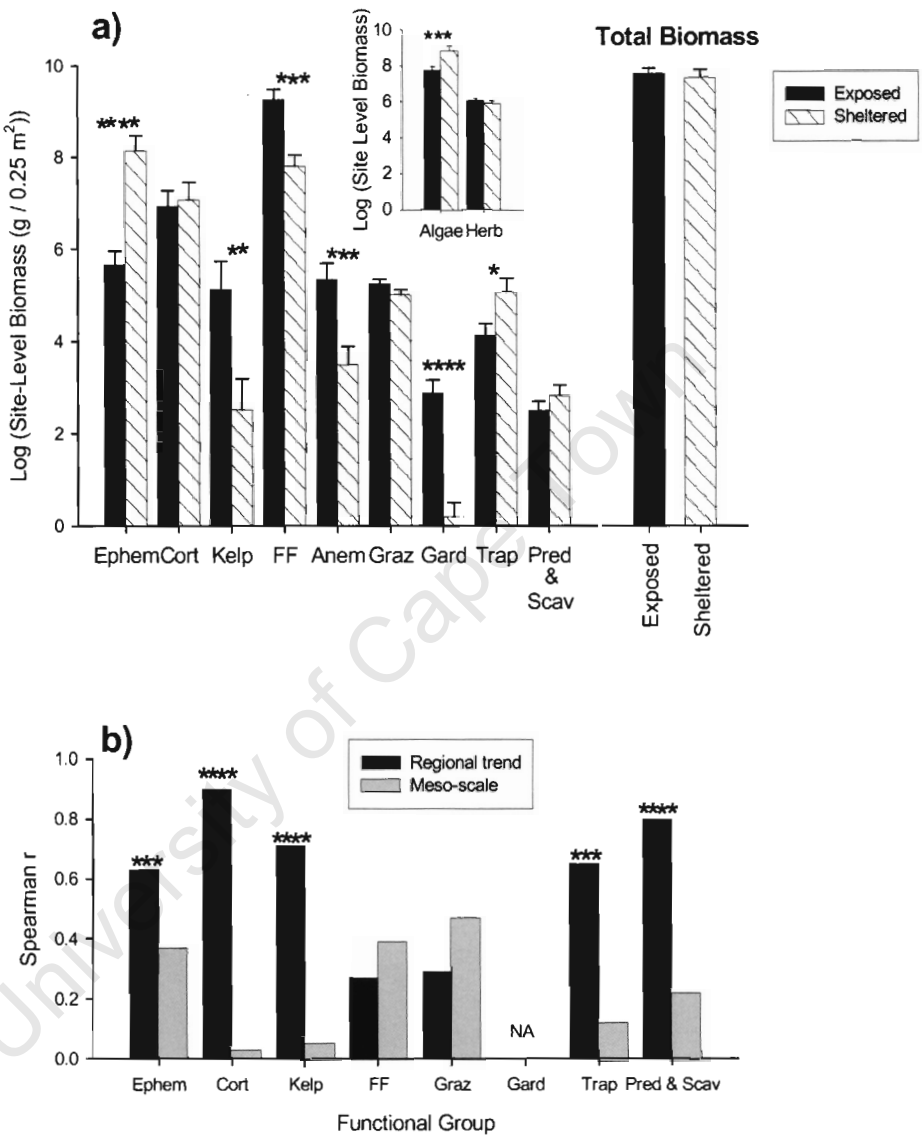


Fig. 1.4. a) Log of mean site-level biomass (g/0.25 m^2) for separate functional groups and total biomass across wave-exposed (solid bar) and sheltered (hatched bars) shores. b) Spearman correlation coefficient for biomass of functional groups on wave-exposed and sheltered shores. Black bars = regional trends, Grey bars = meso-scale variation. Asterisks indicate levels of significance: * = P<0.05; ** = P<0.01; *** = P<0.001; **** = P<0.0001.

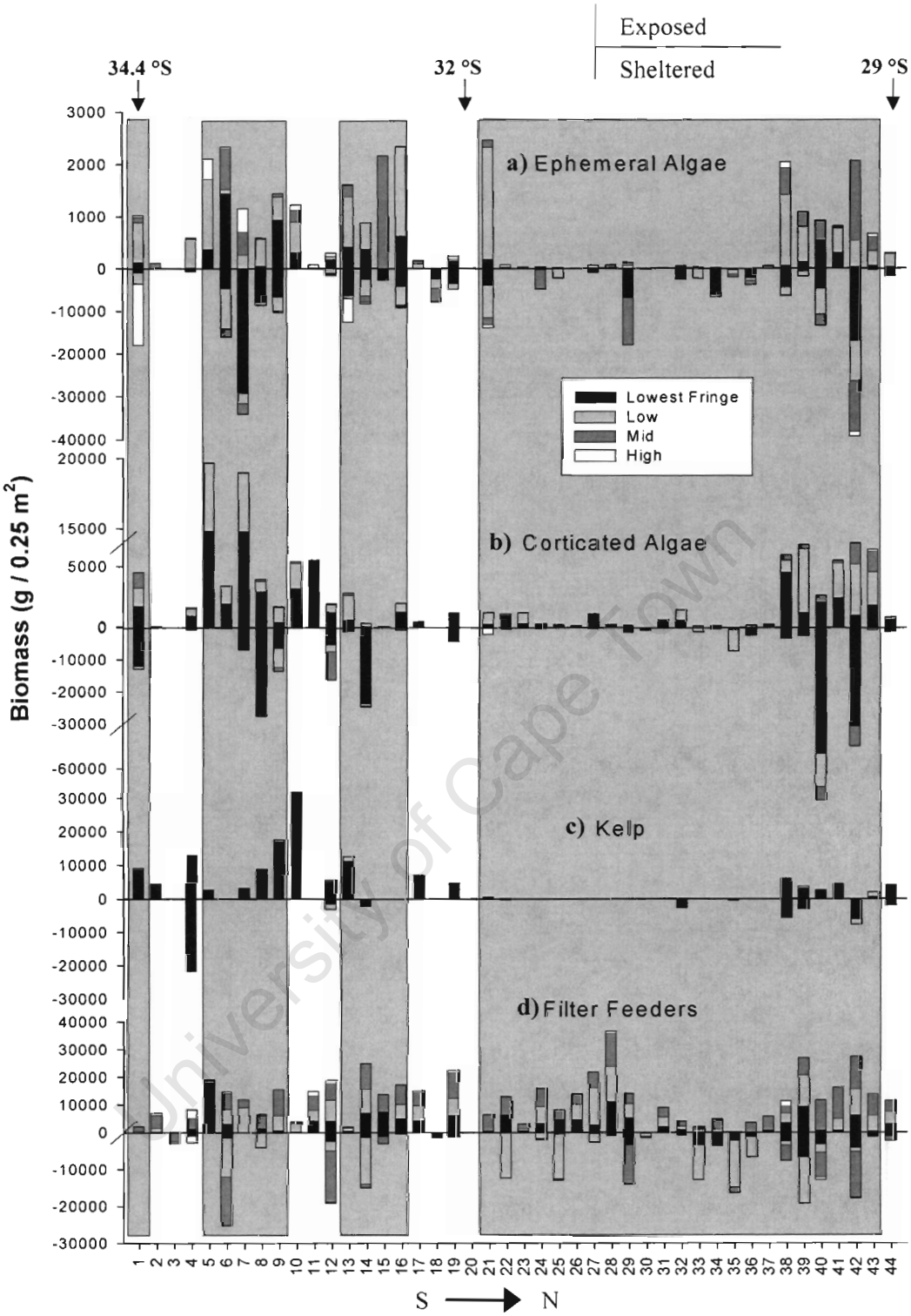


Fig. 1.5. Mean biomass of dominant functional groups at four tidal heights: a) ephemeral algae, b) corticated algae, c) kelp, d) filter feeders, e) grazers, f) gardeners, g) trappers, h) predators/scavengers. Positive values indicate wave-exposed habitats, whereas negative values indicate sheltered habitats. Note different y-axis scales. The shaded background indicates sites strongly influenced by coastal upwelling. Sites are listed from south (left) to north (right).

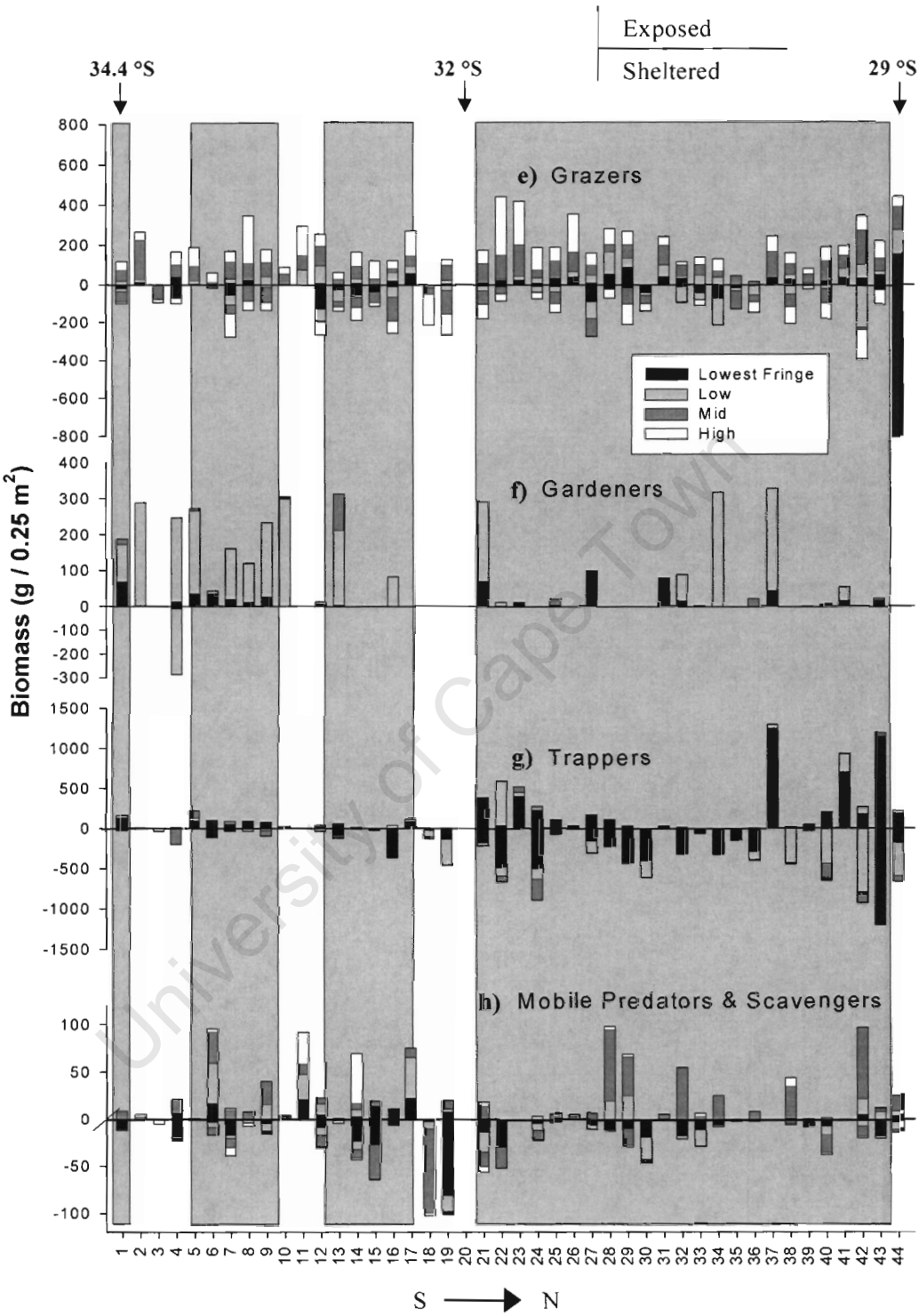


Fig. 1.5 (continued).

habitats (Fig. 1.5g). No clear regional trends were observed for mobile predators and scavengers, though both habitats presented similar oscillating patterns in biomass variation.

Patterns of regional variation in site-level biomass of filter feeders, grazers, and gardeners were not correlated between habitats (Figs. 1.4b, 1.5). No clear regional trends were observed for filter feeders in either habitat (primarily *M. galloprovincialis* in exposed, but *Gunnarea* in sheltered). While grazer biomass in wave-exposed habitats significantly increased in a step-like fashion towards the north of the region, primarily as result of lowest-fringe and low-shore trends (e.g. black and light grey bars in Fig 1.5e), an oscillating pattern was observed in sheltered habitats. Territorial gardening limpets were more frequently observed in the south, although scattered populations of high biomass occurred in the north (Fig. 1.5f). In terms of biomass, gardeners were essentially absent from wave-protected habitats (Fig 1.4a).

Functional group biomass in exposed and sheltered habitats responded differently to local, within-site conditions. Overall, weaker between-habitat associations were observed when considering meso-scale residual variation, with non-significant correlations (after Bonferroni adjustment) for all functional groups.

Besides the latitudinal trends observed for herbivore functional groups across the region, striking discontinuities in biomass were observed for several species when considered in isolation (Fig. 1.6). The most abrupt changes occurred with several species of barnacles (*Octomeris angulosa*, *Tetraclita serrata*, *Notomegabalanus algicola*, and *Chthamalus dentatus*), the tunicate *Pyura stolonifera*, and the pulmonate limpets *Siphonaria* spp., all of which have biogeographic ranges that extend beyond the study region, to the southeast and north (Branch et al. 1994, Wieters and Branch, unpublished data). These groups were regular components of southern communities, but only scarce

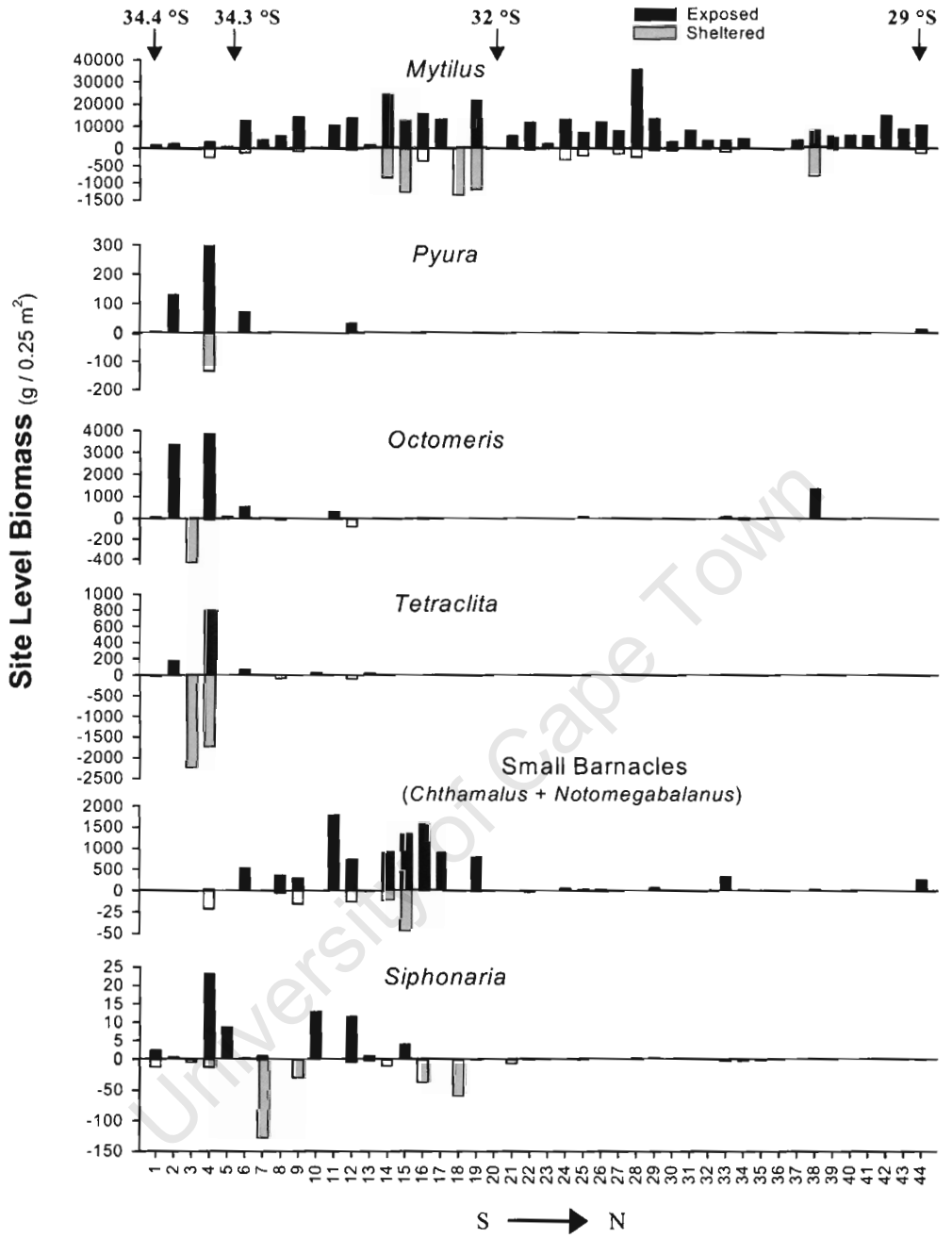


Fig. 1.6. Site-level biomass of selected species: a) *Mytilus galloprovincialis*, b) *Pyura stolonifera*, c) *Octomeris angulosa*, d) *Tetraclita serrata*, e) small barnacles, d) *Siphonaria* spp. Positive values and black bars indicate wave-exposed habitats, whereas negative values and grey bars indicate sheltered habitats. Note different y-axis scales. Sites are listed from south (left) to north (right).

individuals could be found to the north ($p < 0.05$ for all latitudinal correlations). The small, common barnacles (*C. dentatus* and *N. algicola*), as well as *Siphonaria*, presented a sharp discontinuity at Elandsbaai, at about 32°S, while the tunicate and the large barnacles (*O. angulosa* and *T. serrata*) attained relatively high biomass only in False Bay. The dominant filter feeder, *Mytilus galloprovincialis*, presented no clear pattern.

In both exposed and sheltered habitats, biomass of each functional group differed significantly across tidal zones (significant Zone effect: two-way mixed linear model, $p < 0.0001$ in all cases), but these differences were not consistent across sites (significant Site x Zone interactions: $p < 0.0001$ in all cases). Therefore, zones were considered separately in further analyses of spatial patterns.

Correlations Between Functional Groups – Meso-Scale Variation

When considering alongshore patterns in residual variation of biomass (after removing the regional trends through LOWESS regression), spatial correlation between functional groups was strongest in the low and mid zone of wave exposed and sheltered shores, respectively (Figs. 1.7). Ephemeral and corticated macroalgae were tightly coupled among sites, with significant positive correlations observed in both habitats in all zones. This means that local, within-site conditions seem to affect these two functional groups similarly. Conversely, both ephemerals and corticated algae were consistently negatively associated with grazers in both habitats and in all zones. Gardening limpets were absent from sheltered shores, but on exposed shores, residual biomass of gardening limpets was negatively correlated with that of filter feeders, grazers and predators/scavengers across sites. In turn, residual biomasses of filter feeders and predators/scavengers were consistently positively correlated with one another, and filter feeders with gazers on

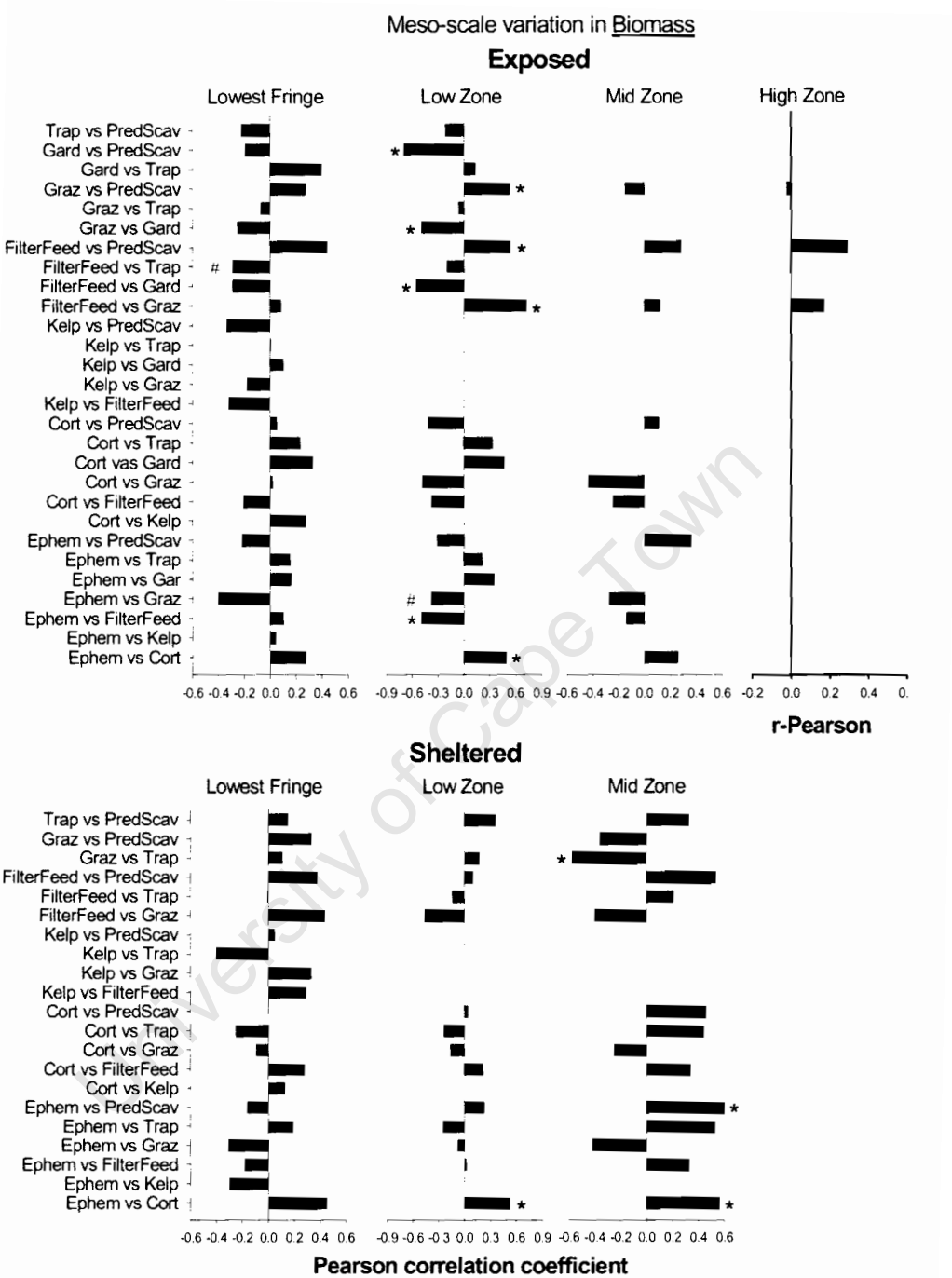


Fig. 1.7. Pearson correlation coefficients for relationships between meso-scale variation in biomass of functional groups in wave-exposed and sheltered shores. Asterisks indicate significant linear correlation after Bonferroni correction ($p < 0.05$); # indicates coefficients that were significant when comparing cover (sessile organisms) and density (mobile organisms). High, sheltered shores lacked significant correlations.

exposed shores. Moreover, significant negative associations were observed between filter feeders and ephemeral algae. On exposed shores where filter feeders were dominant, their biomass was negatively correlated with that of corticated algae, but on sheltered shores where they are scarcer, the relationship was positive. Trapping limpets that achieve high densities on exposed shores where they capture live kelp fronds on the lowest fringes of such shores had a strong, negative relationship with the amount of space occupied by filter feeders. In mid, sheltered shores, among-site variation in biomass of predators/scavengers varied in accordance with that of ephemeral macroalgae. In this same zone, significant negative correlations were observed between grazers and specialized limpets that trap drift kelp.

Additional insight into the relative importance of functional group interactions in driving patterns of among-site variation can be gained by examining cover of sessile species, particularly for crustose forms with low biomass and space-occupying anemones (Fig. 1.8). Density of mobile predators and scavengers consistently followed among-site variation in cover of anemones across most tidal heights in both wave-exposure habitats, probably as a secondary consequence of a strong positive correlation between anemones and filter feeders. Cover of crustose algae on lower shores was negatively correlated with cover of sessile invertebrates (filter feeders, anemones), but mirrored among-site variation in the densities of trapping and gardening limpets. Cover of crustose algae was associated negatively with grazer densities and positively with both corticated and ephemeral algal cover.

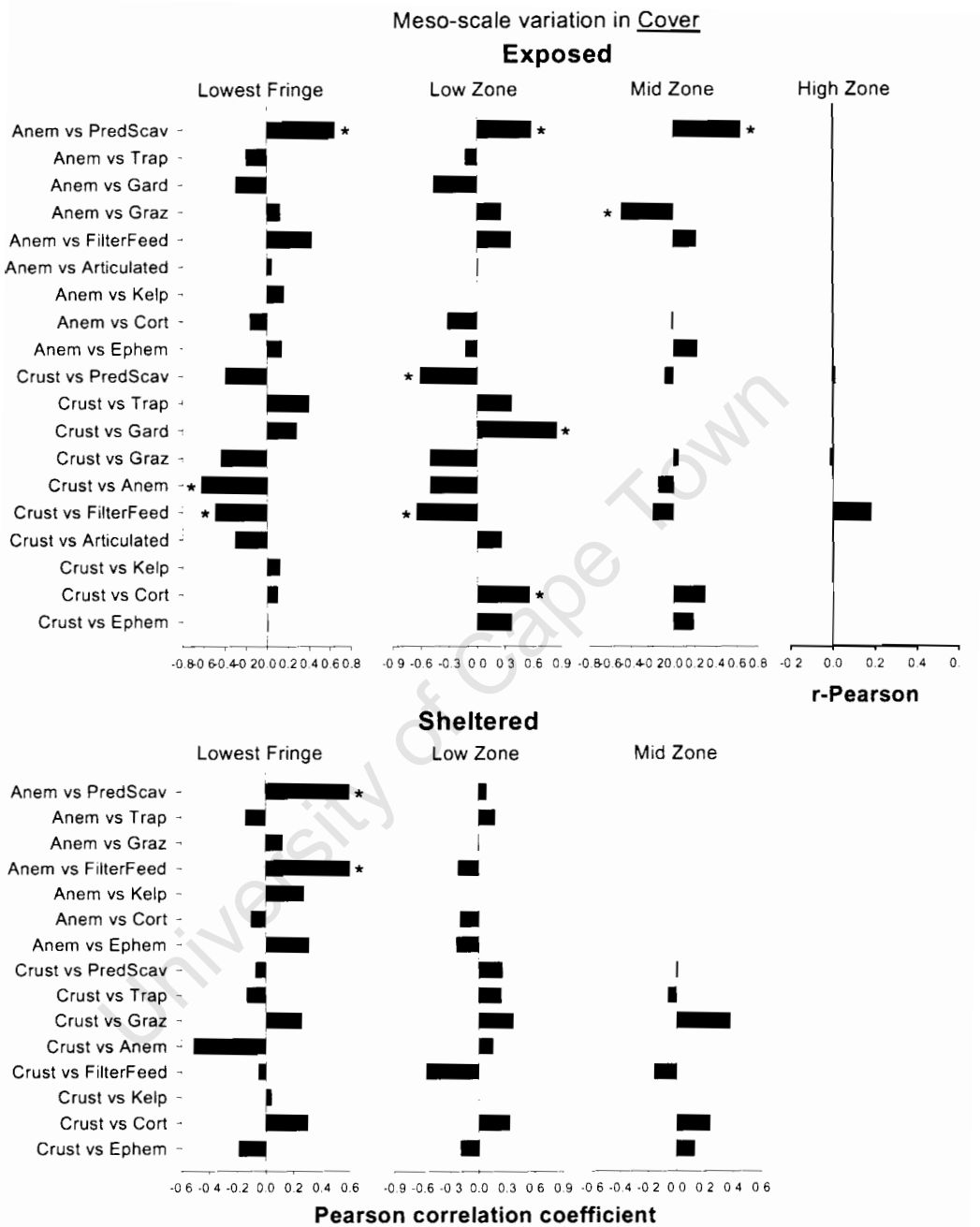


Fig. 1.8. Pearson correlation coefficients for relationships between meso-scale variation in cover of anemones and crustose algae in relation to cover or density of sessile or mobile functional groups, respectively, on wave-exposed and sheltered shores. Asterisks indicate significant linear correlation after Bonferroni correction ($p < 0.05$). High, sheltered shores lacked significant correlations.

Variances between North and South Regions

As a first step to determine whether among-site changes in abundance are more/less variable in regions characterized by relatively heterogeneous or spatially consistent upwelling conditions, I compared the coefficients of variation for meso-scale, residual variation between regions north and south of 32°S for both wave exposed and wave sheltered habitats (Fig. 1.9). The most consistent pattern among functional groups was observed in the low zone of wave-exposed shores, where most functional groups had greater variability in abundance in the southern region. When considering patterns of individual functional groups across tidal zones, filter feeders, crusts, kelp, and ephemeral macroalgae on sheltered shores had generally greater variability in the south. Likewise, filter feeder biomass on wave exposed shores was also consistently more variable in the south.

Functional Groups & SST

To shed light on the influences of nearshore oceanographic conditions on spatial variation in community structure, I examined the relationship between mean SST and functional group biomass. For both wave-exposed and sheltered habitats, regional trends in nearshore SST accounted for a high and significant proportion of the large-scale regional variation in biomass of functional groups (Table 1.3). The most broad and consistent relationships with SST, those groups for which SST explained significant variation in biomass across all occupied tidal heights, were exhibited by filter feeders, gardeners, and kelp-trappers, as well as mobile predators and scavengers in sheltered habitats. For other groups, the strength of associations with SST depended on tidal height.

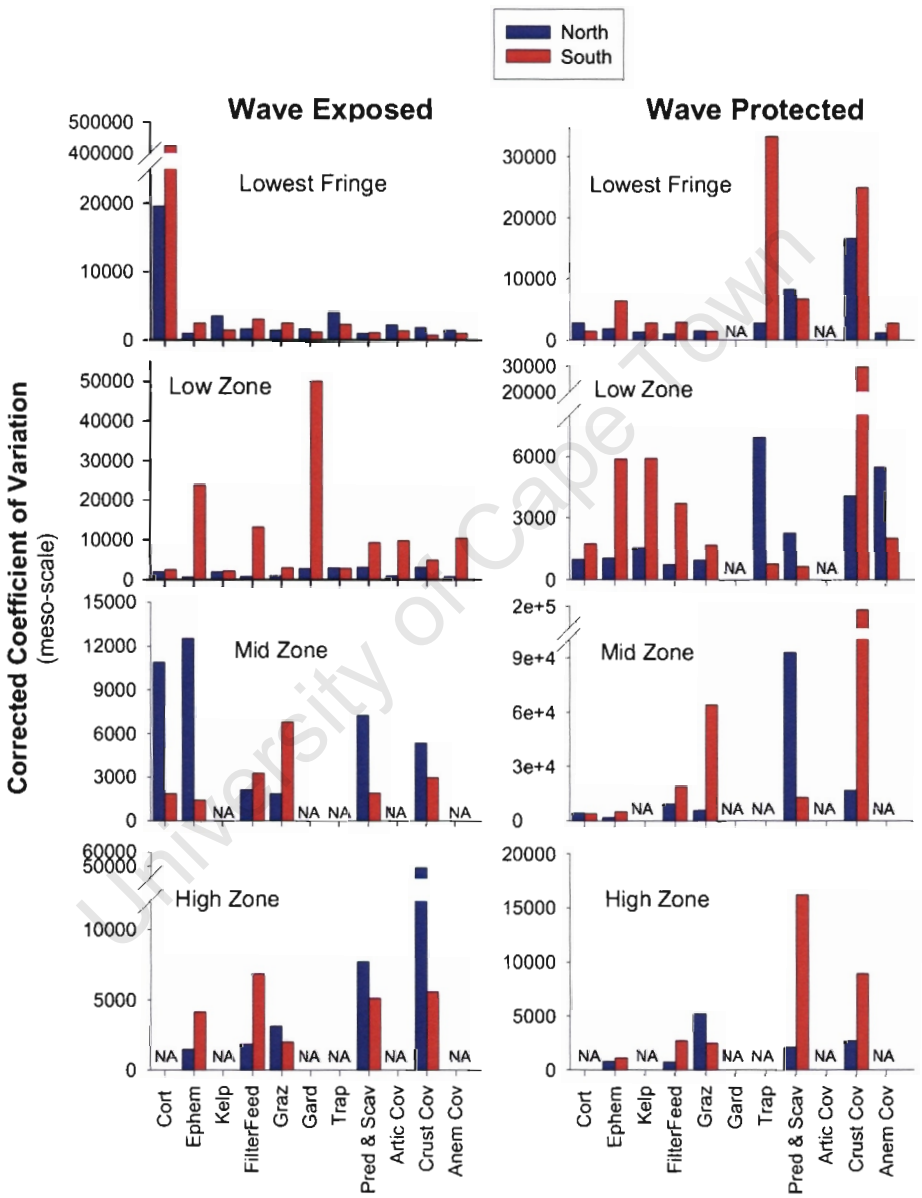


Fig. 1.9. Corrected coefficient of variation in meso-scale, residual abundance calculated across sites within a region for dominant functional groups at each tidal height and habitat. Blue bars = north of 32°S, Red bars = south of 32°S.

Interestingly, responses of most functional groups to large-scale variation in SST often differed between the regions north and south of about 32°S, as defined by the described change in oceanographic regime (Figs. 1.10, 1.11). For example, on wave exposed shores the biomass of corticated algae and kelp decreased significantly with SST in the north, but presented either no clear linear relationship or significantly increased with SST in the south. Ephemeral biomass, on the other hand, decreased with SST on lower shores in both regions, albeit more gradually in the south. However, significant and opposing responses to SST were observed across the mid shore (Fig. 1.10). Strong negative responses to SST were observed for filter feeder biomass in all but the mid zone in the south, while similar significant responses were observed only for the low and mid zone in the north. Grazer biomass exhibited significant and opposing directional responses to SST between regions on mid and high shores. Likewise, specialized kelp-trapping limpets displayed negative responses to SST in the north, but no clear relationship was apparent in the south. Responses of predator and scavenger biomass to SST also differed between the north and the south in the mid and high shore.

Between-region differences in the degree and/or direction of functional group responses to SST were similarly observed on sheltered shores (Fig. 1.11).

Associations with SST were overall weaker and usually non-significant when considering meso-scale residual variation or raw data (Table 1.3). No clear differences in functional group response to SST were observed between the north and south regions when considering meso-scale residual variation.

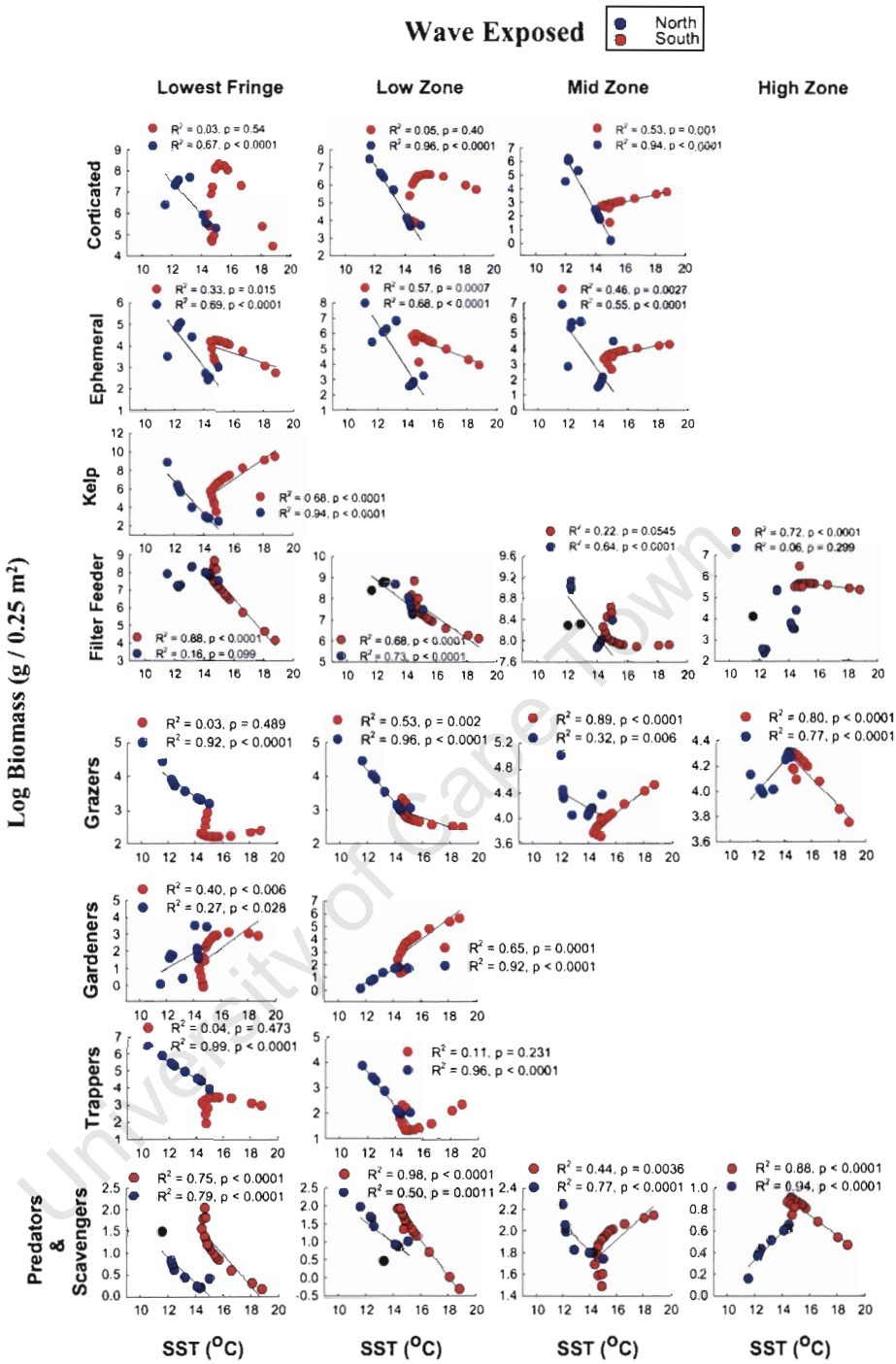


Fig. 1.10. Scatterplots of regional variation in mean sea surface temperature (SST) and dominant functional group biomass across different tidal heights for wave-exposed shores. Blue circles = north of 32°S, red circle = south of 32°S. The R^2 values correspond to linear regressions. Lines indicate significant relationships at $p < 0.05$.

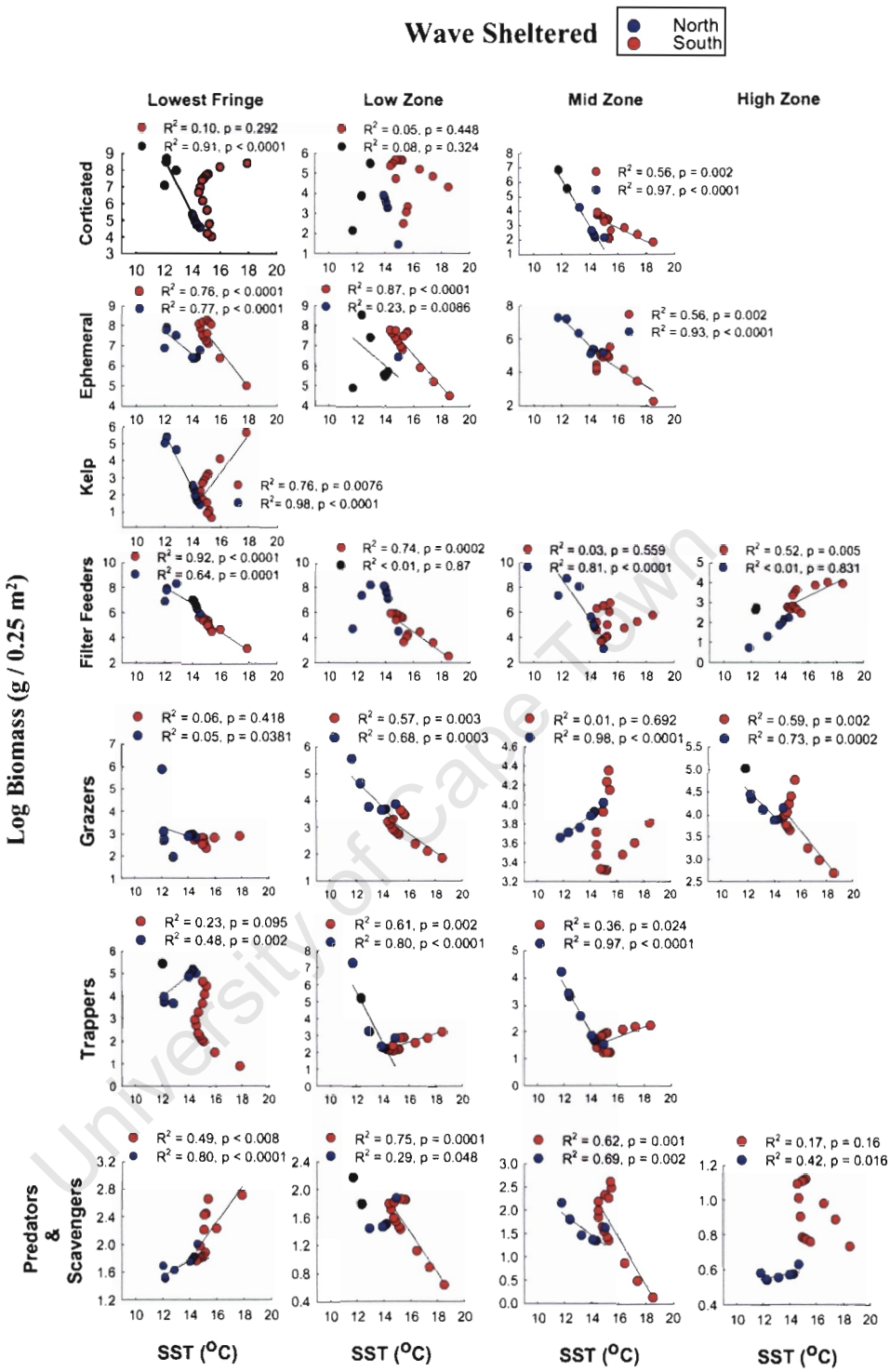


Fig. 1.11. Scatterplots of regional variation in mean sea surface temperature (SST) and dominant functional group biomass across different tidal heights of sheltered shores. Blue circles = north of 32°S, red circle = south of 32°S. The R^2 values correspond to linear regressions. Lines indicate significant relationships at $p < 0.05$.

Effects of upwelling variation south of 32°S

The geographic pattern of meso-scale residual variation of most functional groups matched alongshore differences in relative upwelling intensity (Fig. 1.12). Biomasses of corticated and ephemeral algae were significantly greater at upwelling centers than at downstream sites on low exposed shores and in the lowest fringe of sheltered shores (Fig. 1.12a, b). There was no clear patterns for kelp (Fig. 1.12c), but filter feeder biomass was always greater downstream than at upwelling centers, most obviously in the high shore where barnacles were the major contributor (Fig. 1.12d). Grazers were inconsistent, but in exposed shores where they were most abundant, kelp trappers and territorial limpets achieved greater biomass at upwelling centers, particularly in the lowest fringe (Fig 1.12e-g). Highest biomass of predators (excluding scavengers) inhabiting the high zone of exposed habitats was observed at downstream sites (Fig. 1.12h insert).

1.4. **Discussion**

This is the first quantitative description of alongshore variation of intertidal community structure within the Benguela ecosystem of the west coast of South Africa. Spatial patterns of functional group biomass emerged that coincided with differences in oceanographic conditions, with both wave-exposed and sheltered communities responding similarly to larger-scale processes. Physical conditions exhibited two main patterns. First, the coast north of about 32°S was typified by spatially uniform year-round upwelling, whereas south of that, the coast was spatially heterogeneous with upwelling being focused at capes by coastline topography to produce clear variation in intensity. Second, upwelling was sustained year-round in the north, but concentrated in summer and pulsed in the south. At both regional scales (over 100s of km) and meso-scales (10s of km) spatial and temporal

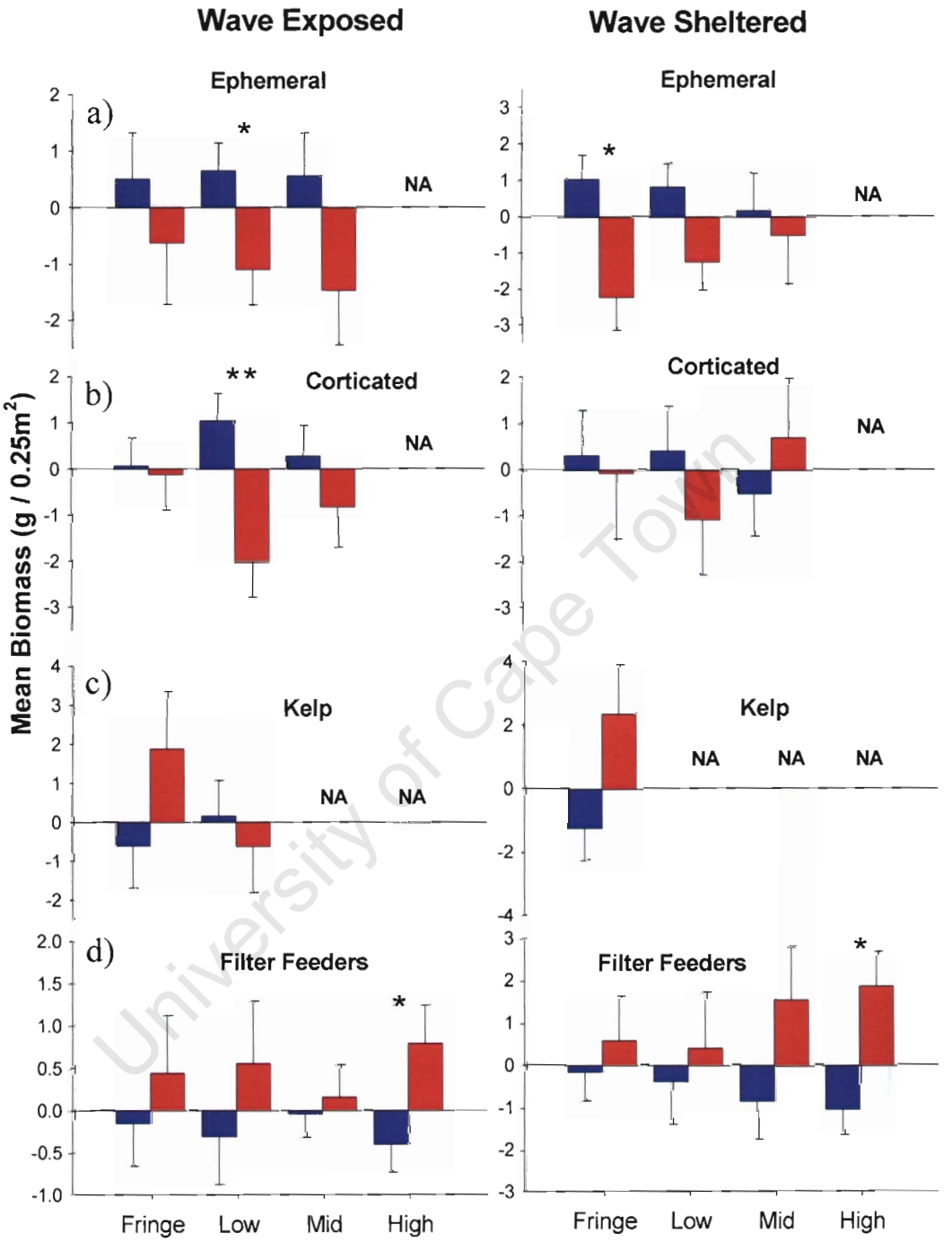


Fig. 1.12. Average biomass of a) ephemeral algae, b) corticated algae, c) kelp, d) filter feeders, e) grazers, f) gardeners, g) trappers, and h) predators/scavengers at upwelling centers (blue bars) and downstream sites (red bars) in each tidal height and habitat, after removing the regional trend in the data using LOWESS regression (residuals). Error bars represent variation across sites within each upwelling category. Asterisks indicate significance: * = $P<0.05$; ** = $P<0.01$.

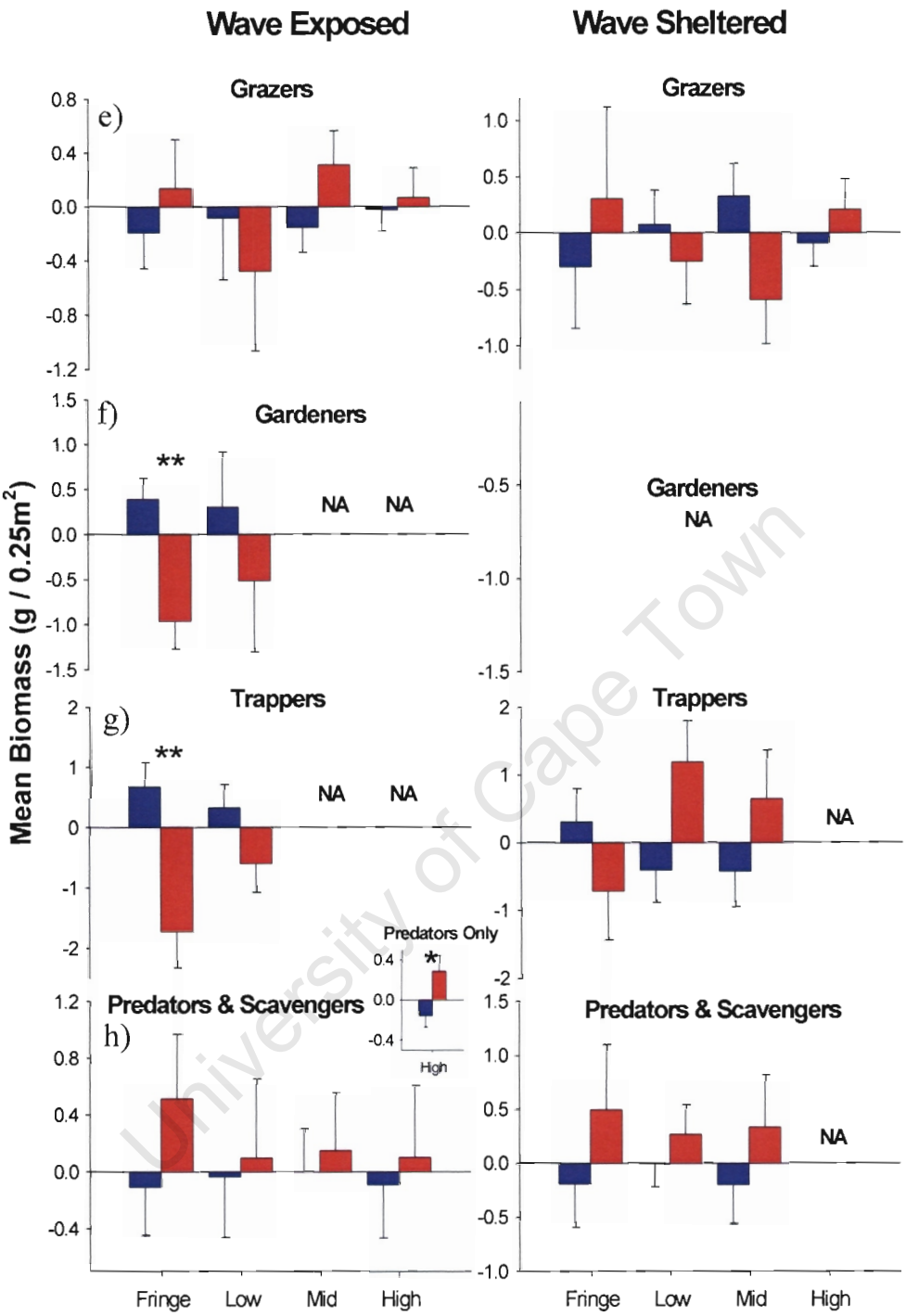


Fig. 1.12 (continued).

structure in SST and upwelling intensity were thus evident. Similar oceanographic patterns have been recorded before (e.g. Andrews & Hutchings 1980, Hutchings et al. 1983, Shannon et al. 1983, Jury 1985, Shannon 1985), but no one has explored whether this translates into differences in intertidal community structure on rocky shores.

The sharp discontinuity in hydrographic regimes at ~32°S coincided with abrupt breaks in the abundance of several species, as well as marked differences in many relationships of functional-group biomass with SST. The biota in the oceanographically more variable southern region exhibited greater among-site variability in abundance, particularly on low, wave-exposed shores. Here, too, meso-scale variation in the intensity of upwelling produced predictable change in the biomass of key functional groups: macroalgae and specialized gardening and kelp-trapping herbivores were more abundant at upwelling centers, while filter feeders and their predators and scavengers had higher biomass at relatively warm downstream sites. Regional trends in functional group biomass at wave-exposed and sheltered shores were highly correlated, while site-residuals were not, suggesting that habitats are similarly affected by regional-scale processes, but not by local, site-specific factors. As in any comparative study, care must be taken when attributing causes to observed patterns. Below, I amplify on these patterns and introduce plausible and testable hypotheses relating to the causes of these patterns.

Identifying links and critical areas

The abrupt break in abundance of small barnacles and *Siphonaria* spp. observed at about 32°S suggests a corresponding change in biological or environmental conditions that regulate their abundance. One potential explanation is that the change in upwelling regimes at 32°S, with greater and persistent offshore transport occurring to the north, leads to

differences in larval delivery rates such that relatively few opportunities for settlement occur to the north. Indeed, similar discontinuities in large-scale oceanographic regimes along the coast of central Chile and the west coast of the US produce sharp breaks in recruitment rates of mussels and barnacles, which then determined geographic patterns of adult abundance of these species (Connolly & Roughgarden 1998, Connolly et al. 2001). Alternatively, increases in abundance of trapping limpets that occur north of 32°S (Fig. 1.5) could potentially lead to higher rates of biotic disturbance (e.g. bulldozing) and/or competition. Numerous studies have demonstrated a strong influence of limpets on barnacle colonization and their role in maintaining free space (e.g. Dayton 1971, Hawkins 1983, Berlow & Navarrete 1997). These hypotheses could be tested by quantifying recruitment rates and survival of barnacles and limpets in the presence/absence of other herbivores north and south of 32°S.

Similar mechanisms may drive the abrupt breaks in abundance of large barnacles (*Octomeris*, *Tetraclita*) and the tunicate *Pyura stolonifera* that were observed at about 34.3°S (False Bay), which marks a well-documented change in species composition and biogeographic provinces (Emanuel et al. 1992). The ranges of all these species extend throughout the study region and beyond into Namibia (Branch et al. 1994, G. M. Branch and E. Wieters, unpubl. data), and therefore the discontinuity in abundance is not related to species approaching the end of their distribution.

The rather dramatic differences in many functional group relationships with SST in regions north or south of approximately 32°S (Figs. 1.10, 1.11) shows they respond quite differently to large-scale oceanographic conditions in these two regions. One explanation for the regional differences may be that organisms north and south of 32°S are differentially acclimated or adapted to differences in mean temperatures. Previous studies

have revealed that environmental variation along coastlines can influence the genetic structure of populations, particularly that associated with enzyme activity (Hilbish 1985, Hilbish & Koehn 1985, Johannesson et al. 1995, Davison & Pearson 1996, Hilbish 1996), which can lead to different physiological characteristics even in conspecifics. Temperature alone can limit algal species distributions (e.g. van den Hoek 1982, Yarish et al. 1986, Stegenga et al. 1997) and its effects on growth and survival are well known (see reviews by Geider 1987, Raven & Geider 1988). Moreover, temperature plays a key role in controlling the rate of photosynthesis, and the ability of algae to acclimate their photosynthetic apparatus to changes in thermal environment is well established (see Davison 1991 for review). Thus, different photosynthetic-temperature ecotypes are possible (e.g. Moore et al. 1998). Acclimation-induced variation in tolerance of thermal stress and rates of physiological processes has also been observed in rocky intertidal invertebrates (Stillman & Somero 1996, Tomanek & Somero 1999, Dahlhoff et al. 2001, Halpin et al. 2002, Helmuth et al. 2002). These differences can lead to trade-offs in performance or fitness that alter species interactions and community dynamics (e.g. Sanford 1999, 2002a, b). Whether thermal tolerances, photosynthetic optima or physiological rates differ along the west coast of South Africa is unknown, but future studies testing the existence of ecotypes could have important consequences for our understanding of benthic-pelagic links and how these are mediated by physiology.

Alternatively, the regional differences in responses of functional groups to large-scale SST may be because alongshore variation in nutrient availability is differentially linked with average thermal conditions north and south of 32°S. Nitrate is considered the main limiting nutrient in the Benguela (Chapman & Shannon 1985). Similar to the situation observed in other upwelling systems (Strub et al. 1998, Blanco et al. 2001, Kearns

& Carr 2003), Waldron & Probyn (1992) documented strong, inverse relationships between temperature and nitrate supply for the west coast of South Africa and Namibia. Whether differences in nutrient concentrations exist between the Namaqua and Southwest Cape regions is unknown and appropriate inshore nutrient data are scarce. However, nutrient influx is driven by upwelling events, and the temporal and spatial stability of the system is expected to affect nutrient input (see Chapman & Shannon 1985 for review). South of 32°S, where the coastline is irregular and the topography shears the wind stress to produce marked alongshore variability in upwelling, typical wind reversals pulse the system both seasonally and on a time scale of about six days. This contrasts sharply with the Namaqua region north of 32°S, which is characterized by relatively consistent, or quasi-stable, upwelling-favorable conditions that form an environmental barrier in the Benguela and divide the system into two (Chapman & Shannon 1985, Shannon 1985). Little inshore oceanographic information is available for this "barrier region", so it is difficult to compare it with the relatively well-studied Southwest Cape. However, the stabilities of the regions can differentially impact nutrient limitation/depletion (Chapman & Shannon 1985) and we may expect that coupling between average nutrient-temperature conditions is greater to the north.

The consistent and strong negative relationships observed between regional variation in SST and biomass of algae (ephemeral, corticated, and kelps) and their consumers (grazers and trappers) in the Namaqua region (blue circles, Figs. 1.10 and 1.11) may thus result from enhanced bottom-up effects. Growth, reproduction, and propagule survival of many macrophyte species is greatest in cold, nutrient-rich waters (Luning & Freshwater 1988, Dayton et al. 1999, Blanchette et al. 2002, Nielsen & Navarrete 2004). Therefore, enhanced performance may account for the higher algal biomass observed in

northern Namaqualand. On offshore islands along the west coast, elevation of nutrient input by seabirds is known to enhance algal growth and biomass (Bosman et al. 1986, Bosman & Hockey 1986), with important consequences for the structure of the entire community (Branch et al. 1987, Bustamante et al. 1995b, Bustamante & Branch 1996a, Nielsen & Navarrete 2004). In addition, experimental manipulations in northern Namaqualand have shown that survival and biomass of kelp-trapping limpets strongly depend upon availability of their kelp food source (Bustamante et al. 1995a). Therefore, bottom-up factors are known to have important effects on the structure and dynamics of communities north of about 32°S.

In contrast to the more stable conditions observed north of 32°S, the average latitudinal trend in SST captured relatively little of the upwelling dynamics that control nutrient influx in the Southwest Cape, south of 32°S. Indeed, residual variation of SST after de-trending was obviously greater towards the south, and analyses of a 16-year time series of nearshore satellite-derived SST at these same study sites revealed that shorter-frequency events explained a greater percentage of the overall variation towards the south (see Fig. 2.3 in Chapter 2). Moreover, *in situ* nutrient data also suggest that similar nitrate concentrations are observed in freshly upwelled water across numerous locations in the southern Benguela, regardless of differences in SST (Chapman & Shannon 1985). Therefore, the Southwest Cape offers a unique opportunity to begin to tease apart the effects of the latitudinal trend in temperature and input of nutrients as evidence suggests that they are relatively weakly coupled over these scales in this region. Strong and significant positive relationships with SST were observed for trends in low-shore kelp and gardeners, as well as mid zone macroalgae and grazers. A testable hypothesis is that performance of these groups is significantly affected by temperature.

Coincident with the regional change in upwelling regimes, recent evidence indicates that a shift in species composition also occurs near 32°S, particularly for macroalgal assemblages (Bolton & Anderson 1997), attributable to an increasing presence of warm-water Agulhas species as one approaches the southern limit of the Benguela system (Bolton & Stegenga 2002). This apparent "overlap" between marine provinces was the basis for separating the west coast of South Africa into two distinct bioregions in a recent national marine biodiversity assessment (Lombard & Strauss 2004). Thus, the regional differences in functional group responses to mean SST observed in this study could potentially reflect compositional changes, with species that have higher temperature tolerances and optima dominating the south. However, the species that dominated biomass patterns were those common to both regions. Relatively few species accounted for the biomass of functional groups and dominance was unrelated to species richness, as observed in previous studies (McQuaid & Branch 1984, McQuaid & Branch 1985, Bustamante & Branch 1996b, Wieters, unpubl. data). For all these reasons, I consider it unlikely that species composition was responsible for the patterns observed north and south of 32°S.

Meso-scale Variation in Upwelling South of 32°S

As evidenced by satellite imagery and confirmed by *in situ* temperature records, clear alongshore, meso-scale variation in upwelling intensity occurs along the south-western section of the west coast. Localized centers of coastal upwelling are associated with headlands and capes (Jury 1985), with downstream warmer-water areas that are not directly affected by upwelling being located between these centers (Kelly 1985, Shannon 1985, Graham & Largier 1997, Broitman et al. 2001). Such alongshore variation in upwelling can influence nutrient levels and primary productivity, as portrayed by the low

chlorophyll and high nutrient concentrations that seem to be consistently associated with newly upwelled water in the euphotic zone (Andrews & Hutchings 1980, Field et al. 1980b, Barlow 1982, Hutchings et al. 1983, Olivieri 1983, Brown & Field 1985). Consistent with this pattern, biomass of corticated and ephemeral macroalgae on low shores was significantly greater at centers of intense upwelling than at downstream sites, both in wave-exposed and, for ephemerals, sheltered habitats (Fig. 1.12a, b). Indeed, upwelling-controlled levels of available nutrients in onshore waters can directly affect benthic macroalgae and lead to among-site variation in abundance (Fujita et al. 1989, Nielsen & Navarrete 2004). Along the upwelling coast of central Chile, corticated algae grow faster and are more abundant at strong upwelling sites, but ephemeral algae are more abundant where upwelling is weak (Broitman et al. 2001, Nielsen & Navarrete 2004). These differences appear to be due to nutrient-modified competitive abilities between these two groups, with corticated algae out-competing ephemerals where productivity is high. The similar responses of low-shore ephemeral and corticated algae to among-site variation in upwelling and SST along the Southwest Cape suggest that such competitive interactions are absent or less important here. However, competitive abilities may play a relatively more important role in the Namaqua region since space occupancy (but not biomass) of these groups showed opposite patterns in response to SST north of 32°S. These questions are amenable to experimental testing.

The greater abundance of filter feeders observed at downstream sites (particularly the abundance of barnacles in the high shore) is likely to be a result of enhanced larval recruitment and/or performance. According to the upwelling-relaxation model (Connolly & Roughgarden 1998), larvae and phytoplankton entrained in offshore-moving waters during active upwelling accumulate at offshore upwelling fronts, which then get pushed

back onto shore when winds reverse and upwelling relaxes (Field et al. 1980b, Farrell et al. 1991, Roughgarden et al. 1991, Botsford et al. 1994, Alexander & Roughgarden 1996, Wieters et al. 2003). Given alongshore currents, collision of these fronts with the coast would be expected downstream from upwelling centers, thus producing the distinct phytoplankton bloom events that are often observed in the lee of capes (Shannon et al. 1983, Brown 1984, Marin et al. 1993, Masotti et al. 1998, Wieters et al. 2003). Indeed, three years of monthly barnacle settlement rates measured at eight of my study sites revealed significantly higher barnacle recruitment at downstream sites relative to upwelling centers (Pfaff et al., unpubl. data). In addition, filter feeder growth is often positively correlated with temperature (Seed 1976, McDonald & Kohen 1988, Blanchette et al. in press). To date, we have no information regarding variation in barnacle growth along the South West Cape. Along the coast of Oregon, barnacle growth was found to vary with upwelling intensity, with highest growth at the site of relatively weak upwelling (Sanford & Menge 2000). Alternatively, adult barnacle mortality may differ according to upwelling intensity, but this seems unlikely since predators were more abundant where their barnacle prey were abundant.

The mussel *Mytilus galloprovincialis* has been shown to grow faster at upwelling centers than at downstream sites, and Xavier et al. (in prep.) argue this may be due to greater concentrations of particulate kelp at upwelling centers – although I did not find any evidence of greater kelp abundance there.

Predatory whelks inhabiting the high shore (largely *Nucella dubia* and *N. cingulata*) were also significantly more abundant at warmer downstream sites. Since these whelks are direct developers that lay benthic egg capsules with juveniles that crawl-away and live within the same habitat as the adults (Bokenham & Neugebauer 1938), increased

reproductive output can lead to higher local densities. Thus, the higher densities observed downstream are likely due to higher production of their main barnacle prey, as suggested by apparent positive correlation between abundances and recruitment of barnacles (Pfaff et al. unpubl. data). Predator-prey models that take into account life-history of interacting species predicts that geographic variation in abundance of predators with relatively restricted dispersal (closed populations) should scale with geographic variation in the settlement of their broadly-dispersing prey (open populations), and most of the variation in *Nucella* population sizes along the west coast of North America is explained by a simple measure of prey recruitment (Wieters et al. in review).

Similar bottom-up effects may at least partly be responsible for the significantly higher abundance and biomass of gardening limpets found at upwelling centers. The size of defended gardens is known to scale with their productivity, such that smaller gardens are needed at more productive sites (Branch et al. 1992). Smaller gardens then allow denser packing of adults on primary surface, which can lead to overall greater biomass. Greater garden productivity may also lead to increased growth and reproduction, which can result in numerical response. While little is known about the larval phase of *Scutellastra cochlear*, recruits have never been found away from adult habitat (Branch 1975b, Branch et al. 1994), suggesting limited dispersal or strong settlement cues associated with adults. Likewise, abundance and biomass of trapping limpets were higher at cold, nutrient-rich upwelling centers. Previous experimental studies have shown that the biomass and survival of trapping limpets depend upon both competitive interactions with mussels and the availability of the live kelp fronds upon which they feed (Bustamante et al. 1995a, Steffani & Branch 2005). The lack of correlation between trappers and kelp may suggest kelp is of

little importance, but concomitant top-down effects of trappers on kelp may be important within the localized confines of the intertidal zone.

Scaling-up experimental results: Insight into biological interactions

Competition for space and/or food and the top-down effects of grazing and predation may constrain local abundance of functional groups and lead to among-site variability. The significant negative correlation between meso-scale variation in densities of kelp-trappers and cover of filter feeders (but not kelp) suggests that direct competition for space plays a relatively more important role than food limitation in determining among-site variability of these trapping limpets along the coast. Previous local experiments and surveys conducted in the lowest intertidal fringe demonstrated that filter feeders, particularly the invasive mussel *Mytilus galloprovincialis*, competitively exclude sedentary adults of the indigenous, kelp-trapping limpet *S. argenvillei* on wave-exposed shores (Steffani & Branch 2005). Here, mussels rapidly acquire space and form dense mussel beds, which directly limit the access of limpets to rock space. They also compete for space with live kelp, the fronds of which are the principal food source for adult *Scutellastra argenvillei* (Bustamante et al. 1995a). Likewise, biomasses of grazers, as well as the abundance and biomass of filter feeders and mobile predators and scavengers, were inversely correlated with those of the territorial, gardening limpet *Scutellastra cochlear*, which is likely a consequence of both direct aggressive interference and exploitation competition by this territorial limpet, as demonstrated experimentally at sites in the southern region (Branch 1975a, b, 1976, 1981, Branch et al. 1992).

Across the entire coast, densities of grazers, as well as abundance and biomass of mobile predators and scavengers and the abundance of anemones were positively correlated

with cover of filter feeders. In addition to their well-documented competitive abilities (e.g. Paine 1966, Paine & Suchanek 1983), filter feeders, particularly mussels, also simultaneously provide complex habitat that benefits a diverse array of associated species by enhancing recruitment and/or providing refuge from enemies, physical forces, or physiological stresses (Suchanek 1980, Griffiths et al. 1992, Griffiths 1992, Lintas & Seed 1994, Seed 1996, Hammond & Griffiths 2004). Previous studies along the coast of South Africa documented positive effects of mussels on mussel recruits (Harris et al. 1998) and on juveniles of the grazers *Scutellastra granularis* and *S. argenvillei* (Griffiths et al. 1992, Hockey & Van Erkom Schurink 1992, Steffani & Branch 2005). Likewise, density of predatory whelks (*Nucella* spp.) has increased since the invasion of *M. galloprovincialis,* at least at some sites (Branch & Steffani 2004). Anemones capture wave-tumbled food (Kruger & Griffiths 1998) and are likely to be responding to the increased abundance of prey and protection from desiccation that mussels provide (Sebens & Paine 1979, Sebens 1981). Likewise, filter feeders and/or the grazers they harbor may provide additional food sources for mobile predators and scavengers. Experiments designed to evaluate the relative importance of habitat modification and food supply, and how these processes interact with one another to shape among-site variability across the coast would be insightful.

Dramatic effects of herbivores on the abundance and distribution of ephemeral and corticated algae have been experimentally demonstrated locally (Branch et al. 1987, Branch & Griffiths 1988, Branch et al. 1992), and therefore we might expect to find consistent, significant negative correlations between grazers and these algal groups. However, such results were only partially observed. Ephemeral algal biomass was always negatively associated with grazer biomass, in keeping with the strong effects of grazers demonstrated by their experimental removal (reviewed by Branch 1981). Corticated algae tended to

follow the same pattern on exposed but not sheltered shores, although their relationships with grazers were never significant. Although this could be construed as meaning that interactions between grazers and corticated algae are relatively weak across the coast, consumer effects may in reality be so strong that grazers uniformly deplete algae, resulting in the absence of any among-site correlations of standing stock. Again, experiments could distinguish between these alternatives.

Crustose algae were negatively correlated with space-occupying groups such as filter feeders and anemones. Unexpectedly, they were negatively associated with generalised grazers and positively associated with both ephemeral and corticated algae. Much previous work has shown crustose algae to be grazer-resistant and to actually depend on grazers to avoid overgrowth by foliose algae (Underwood 1980, Steneck et al. 1991, Dethier 1994). Both trapping and territorial herbivores, which can attain exceptionally high densities (Bustamante and Branch 1995a, Bustamante et al. 1995a) and exclude most foliose algae, were positively correlated with algal crusts.

Significant positive among-site correlations observed between the numerical abundance of grazers and mobile predators and scavengers (mainly *Nucella dubia*) in the high zone suggests that bottom-up effects may drive meso-scale variation in abundances of these groups. There are no experimental studies testing the effects of top intertidal predators on herbivores, so interactions are difficult to evaluate further. While the oystercatcher *Haematopus moquini* is a top predator in this system and is known to feed intensively on the dominant grazer, the limpet *S. granularis* (Hockey & Underhill 1984), the numbers of oystercatchers are too low on the mainland to effect limpet populations (Hockey and Bosman 1988).

Comparison of Habitats

The strong effects of wave exposure on local community composition and functional group biomass have received considerable attention in South Africa (Branch & Griffiths 1988). Results of my study are generally in agreement with previous findings, with filter feeders, gardening limpets, anemones and kelp being more abundant and algae less abundant on exposed shores (Fig. 1.4a). However, the main question addressed here is whether the different communities occupying wave-exposed and sheltered shores respond similarly to large- and meso-scale environmental variation across the coast. In general, regional trends of biomass were strongly correlated between exposed and sheltered shores (Fig. 1.4b), suggesting large-scale processes establish a framework that shapes these communities in similar ways. In contrast, between-habitat associations were weak when considering meso-scale, residual variation, which suggests that functional group biomass in exposed and sheltered habitats may respond differently to local, within-site conditions. Indeed, responses to local variation in SST and upwelling were often habitat dependent. Likewise, strong correlations between functional groups were also habitat-dependent, suggesting that wave exposure modifies the relative importance of biological interactions in shaping biomass. For example, although nutrient concentrations are expected to be higher at upwelling centers, water movement impacts rates of nutrient and gas exchange (Leigh et al. 1987). Thus, nutrient uptake rates may constrain growth of algae in sheltered habitats where water is retained for longer times (Bustamante & Branch 1996a), but be of little importance in wave exposed habitats where flow rates are higher. Whether such mechanisms are responsible for the different impacts that upwelling had on corticated algae in exposed and sheltered shores is unknown, but could be experimentally tested.

1.5. **Conclusions**

This study represents the first quantitative description of alongshore regional- and meso-scale variation in community structure for the west coast of South Africa. Patterns here offer a preliminary evaluation of the degree to which local interspecific interactions (e.g. herbivory, facilitation, competition) give rise to predictable patterns over larger spatial scales and how nearshore oceanographic processes can modify or overshadow these effects. Determination of underlying causal processes is beyond the scope of this study and requires future experiments and oceanographic studies across distant sites, but a major contribution of this work is the identification of the scales and locations at which controlling processes may be bounded. An abrupt regional change in the seasonality, intensity, and meso-scale variation in upwelling was observed at about 32°S, which coincided with differential meso-scale spatial heterogeneity in biomass, abrupt breaks in abundance of some species, and differential biomass responses to SST. These changes, which were consistent between wave-exposed and sheltered habitats, suggest that either regional differences in nutrient availability and/or acclimation-induced trade-offs in performance or fitness of organisms may frame species interactions and community dynamics. Results also suggest that meso-scale variation in upwelling intensity influences community structure and generates regular spatial variation in interaction webs along the coast, particularly across the South West Cape. A hypothesized interaction web incorporating some of the key links suggested by this study is presented in Fig. 1.13. At capes, where upwelling is strong, nutrients and offshore advection processes are expected to play a relatively more important role. Here, increased nutrient availability enhances algal growth rates, corticated and ephemeral algae attain higher biomass as they quickly reach a size escape from grazers, grazers play a relatively minor role, specialized territorial limpets attain higher biomass from increased

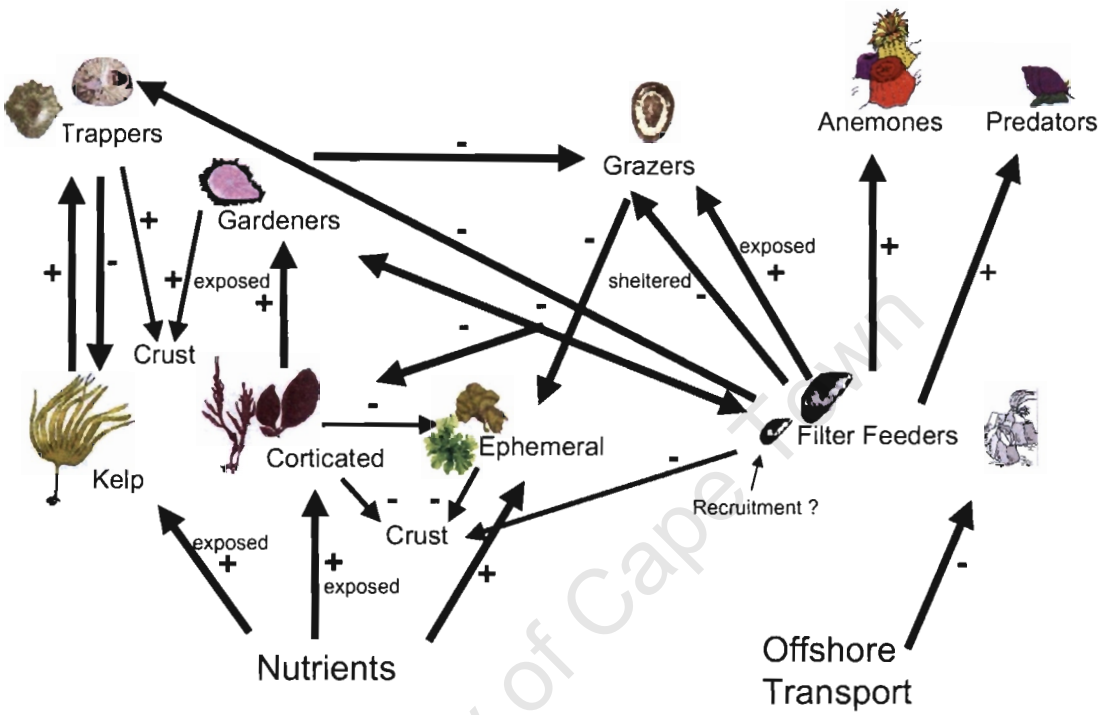


Fig. 1.13. Hypothesized interaction web under strong upwelling derived from results. +, positive effect; -, negative effect. Question mark indicates key interaction for which there is no current information available.

algal productivity, but only kelp-trappers become increasingly important in controlling algal (kelp) abundance, and grazers are suppressed by increased competition with gardening limpets. Enhanced offshore transport limits barnacle recruitment and suppresses predator biomass. Based on patterns in this study, wave exposure is suggested to potentially mediate upwelling effects and thus alter species interactions. For example, (a) where wave action is weak, mussel settlement is relatively weak and competition with trapping limpets diminished (Branch and Steffani 2004), and (b) gas exchange rates may limit positive effects of nutrient enhancement for corticated algae in wave sheltered habitats. My hope is that these patterns and suggested hypotheses will inspire future comparative and experimental studies and help begin to "scale up" our understanding of community dynamics.

Table 1.1 Names and locations of study sites.

Site N°.	Site Name	Abbreviation	Latitude (°S)	Longitude (°E)
1	Hangklip	Hang	-34.38	18.84
2	Steenbras	Stee	-34.20	18.82
3	Gordons Bay	Gord	-34.13	18.83
4	Fishoek	Fish	-34.13	18.45
5	Olifantsbos	Olif	-34.27	18.38
6	Scarborough	Scar	-34.19	18.34
7	Kommetjie	Komm	-34.15	18.35
8	Llandudno	Llan	-34.01	18.33
9	Camps Bay	Camp	-33.95	18.38
10	Mouille Point	Mou	-33.90	18.40
11	Blouberg	Blou	-33.80	18.46
12	Melkbos	Melk	-33.73	18.44
13	BokPunt	Bok	-33.56	18.30
14	Yzterfontein	Yzer	-33.36	18.15
15	West Coast N. P.	WCNP	-33.15	18.00
16	Columbine	Col	-32.82	17.84
17	Columbine 2	Col	-32.80	17.85
18	St. Helena Bay	Hel	-32.77	18.04
19	Elands Bay	Elan	-32.31	18.32
20	Lamberts Bay	Lamb	-31.90	18.31
21	Namaqua Sands	Namq	-31.61	18.30
22	Caravan South	Groen	-30.95	17.64
23	Caravan Granatina	Groen	-30.95	17.64
24	Seans	Groen	-30.94	17.63
25	Outhouse	Groen	-30.94	17.63
26	Esterhuizen	Groen	-30.94	17.63
27	Shell Beach	Groen	-30.94	17.63
28	Island Wreck	Groen	-30.92	17.60
29	Island Point	Groen	-30.92	17.60
30	Nina's Mystery	Groen	-30.92	17.61
31	Mussel Rock	Groen	-30.92	17.61
32	Tongue	Groen	-30.91	17.60
33	Shortcut	Groen	-30.91	17.59
34	Groen Lighthouse	Groen	-30.86	17.58
35	DeBeers Gate	Groen	-30.83	17.56
36	Moonbay Granatina	Groen	-30.82	17.56
37	Moonbay	Groen	-30.81	17.56
38	Hondeklip Wreck	Hond	-30.35	17.28
39	Hondeklip 2	Hond	-30.33	17.27
40	Brazil Snake	Braz	-29.85	17.09
41	Brazil Nelson	Braz	-29.89	17.10
42	Brazil North	Braz	-29.81	17.08
43	Rooiklippies	Rooi	-29.74	17.06
44	McDougalls	PNol	-29.29	16.88

Table. 1.2 Allocation of genera to functional groups

Ephemerals	Corticated	Kelp	Filter Feeders	Grazers	Mobile Predators & Scavengers
Aeodes	*Axillariella*	*Ecklonia*	*Aulacomya*	*Afrolittorina*	
Aristothamnion	*Bifurcaria*	*Laminaria*	*Balanus*	*Acanthochiton*	
Bryopsis	*Bifurcariopsis*		Bryozoa	*Chaetopleura*	*Argobuccinum*
Centrocerus	*Botryglossum*		*Choromytilus*	*Chiton*	*Burnupena*
Ceramium	*Botryocarpa*		*Chthamalus*	**Cymbula*	*Clionella*
Chaetomorpha	*Carpoblopheris*	**Articulated**	*Crepidula*	*Fissurella*	*Cymatium*
Cladophora	*Caulacanthus*	*Arthrocardia*	*Dendropoma*	*Gibbula*	Nudibranch
Enteromorpha	*Champia*	*Corallina*	*Haliclona*	*Haliotis*	*Nucella*
Polysiphonia	*Chordariaceae*	*Jania*	*Hymeniacedon*	*Helcion*	*Patiria*
Porphyra	*Chordariopsis*		*Ircinia*	*Ischnochiton*	
Scytosiphonia	*Chylocladia*		*Mytilus*	*Oxystele*	
Ulva	*Codium*	**Crusts**	*Notomegabalanus*	*Parechinus*	
	Colpomenia	Black crust	*Octomeris*	*Patiriella*	
	Desmarestia	*Heydrichia*	*Pentacta*	**Scutellastra*	
	Epymenia	*Hildenbrandia*	*Pyura*	*Siphonaria*	
	Gelidium	*Leptophytum*	*Roweia*	*Tricolia*	
	Gigartina	*Ralfsia*	*'Spirorbis'*	*Turbo*	
	Glossophora	*Spongites*	*Tetraclita*		
	Grateloupia	Ulvoid crust			
	Gymnogongrus		Hydrozoa		
	Halopteris		*Aglaophenia*	**Gardeners**	
	Hymenena		*Eudendrium*	*S. cochlear*	
	Hypnea		*Obelia*	*‡S. longicosta*	
	Ivengaria		*Salacia etc.*		
	Laurencia				
	Leathesia				
	Mazaella		**Anemones**	**Trappers**	
	Nemastoma		*Actinia*	*‡C. granatina*	
	Neuroglossum		*Anthothoe*	*†S. argenvillei*	
	Nothogenia		*Aulactinia*		
	Pachymenia		*Bunodosoma*		
	Phyllemenia		*Corynactis*		
	Plocamium		*Pseudactinia*		
	Polyopes				
	Prionitis				
	Pterosiphonia				
	Sarcodia				
	Schyzemenia				
	Splachnidium				
	Suhria				
	Thamnophyllis				
	Trematocarpus				

* Excluding specialized gardeners and trappers

† individuals > 4 cm

‡ individuals > 3 cm

Table 1.3. Explained variation (R^2) in the relationship between functional group biomass and mean nearshore sea surface temperature (AVHRR) on a) wave exposed and b) sheltered shores. Bold: significant linear relationship ($p<0.05$).

	Regional Trend				**Meso-Scale**				**Raw Data**			
	Lowest Fringe	Low Zone	Mid Zone	High Zone	Lowest Fringe	Low Zone	Mid Zone	High Zone	Lowest Fringe	Low Zone	Mid Zone	High Zone
a) Exposed												
Ephemeral	0.11	0.04	0.02	NA	0.01	0.03	0.01	NA	0.01	0.04	0.02	NA
Corticated	0.07	<0.01	**0.18**	NA	**0.14**	0.11	<0.01	NA	0.10	0.06	0.07	NA
Kelp	0.11	NA	NA	NA	0.01	NA	NA	NA	0.03	NA	NA	NA
Filter Feeders	**0.46**	**0.69**	**0.32**	**0.33**	0.08	0.02	0.02	0.03	0.03	0.03	0.06	**0.13**
Grazers	**0.59**	**0.74**	0.02	0.02	<0.01	0.01	0.01	0.06	0.10	0.02	<0.01	0.03
Gardeners	**0.24**	**0.78**	NA	NA	0.05	0.01	NA	NA	0.01	0.11	NA	NA
Kelp-trappers	**0.48**	**0.34**	NA	NA	0.08	0.04	NA	NA	**0.18**	0.08	NA	NA
Pred/Scavengers	0.01	**0.33**	<0.01	**0.20**	0.01	0.04	<0.01	0.02	<0.01	<0.01	<0.01	0.02
b) Sheltered												
Ephemeral	0.10	0.08	**0.81**	NA	**0.23**	0.05	<0.01	NA	**0.17**	0.07	0.09	NA
Corticated	0.05	0.03	**0.52**	NA	0.04	0.06	0.01	NA	0.08	0.04	0.04	NA
Kelp	**0.15**	NA	NA	NA	0.12	NA	NA	NA	0.01	NA	NA	NA
Filter Feeders	**0.85**	**0.52**	**0.24**	NA	0.04	<0.01	**0.22**	NA	0.09	0.14	0.01	NA
Grazers	0.06	**0.79**	<0.01	**0.60**	0.07	<0.01	0.11	0.03	0.01	**0.17**	0.03	**0.21**
Kelp-trappers	**0.23**	**0.26**	**0.33**	NA	0.01	<0.01	0.08	NA	0.04	0.03	<0.01	NA
Pred/Scavengers	**0.66**	**0.41**	**0.25**	**0.28**	0.03	0.01	0.01	<0.01	0.10	<0.01	<0.01	<0.01

Chapter 2

Between-system comparisons: benthic links to the temporal pulsing dynamics of thermal conditions

2.1. Introduction

Large-scale phenomena may construct the pathways, define the limits, and set the pace at which local interactions among organisms are played out (Connolly & Roughgarden 1998, Menge et al. 2003, Menge et al. 2004, Navarrete et al. 2005 and see Chapter 3). Thus, their influence in shaping community structure and dynamics is indisputable and highlights the need to integrate physical and biological information from a broad range of disciplines and scales. While recent efforts have begun to distinguish some of the driving factors of biological variability over large scales, we know little about their generality, context dependency, and interaction with other processes. Quantitative comparisons between different systems offer opportunities to evaluate the generality of patterns and putative processes.

Recent efforts to incorporate nearshore oceanographic variability into our understanding of benthic marine community dynamics have provided critical insight into the ways in which distant communities are connected via benthic-pelagic links and emphasize the influences of previously neglected bottom-up effects (Demers et al. 1989, Duggins et al. 1989, Bertness et al. 1991, Witman et al. 1993, Bustamante et al. 1995a, Bustamante & Branch 1996a, Leonard et al. 1998, Archambault & Bourget 1999,

Archambault et al. 1999, Smith & Witman 1999, Menge et al. 2004, Nielsen & Navarrete 2004, Navarrete et al. 2005). A good proportion of these studies have been conducted in Eastern Boundary Current Ecosystems (EBCEs), which share similar environmental dynamics that are embedded within a hierarchy of scales in space and time (Parrish et al. 1983, Ricklefs 1990). The four major EBCEs (i.e. Benguela, Canary, Humboldt, and California current systems) are characterized by narrow continental shelves, equatorward surface flow over a poleward undercurrent, equatorward wind stress, and coastal wind-driven upwelling. Upwelled water is generally cold, salty, nutrient-rich and oxygen poor inshore (Huyer et al. 1991, Strub et al. 1991, Hickey 1998). On a global scale, these similar physical characteristics appear to drive similar biological processes, as EBCEs account for a disproportionate amount of primary production (Chavez & Toggweiler 1995) and support similar zooplankton and pelagic fish faunal assemblages (Parrish et al. 1983, Ware 1992). Likewise, similarities have been observed in seasonal succession of phytoplankton, from diatoms to dinoflagellates (Shannon & Pillar 1986, Mitchell-Innes et al. 2000), and alternating shifts in dominance of fish species, anchoveta replacing sardine (Shackleton 1986, Lluch-Belda et al. 1989, Sherman 1992, Schwartzlose et al. 1999, Cury et al. 2000). Relative to adjacent non-upwelling oceanographic regimes, rocky intertidal communities of EBCEs appear to be characterized by higher primary productivity, higher larval recruitment rates of many invertebrates (but see Connolly et al. 2001), increased rates of species interactions, and greater abundances of key functional groups, but overall lower species diversity (Bustamante et al. 1995b, Bustamante & Branch 1996b, Harris et al. 1998, Menge et al. 1999, Menge et al. 2003, Blanchette et al. in press).

Within EBCEs, large-scale circulation patterns of ocean and atmosphere drive basin-scale pressure fields that modulate upwelling to create latitudinal gradients in

upwelling intensity, frequency, and duration (Hickey 1998, Hill et al. 1998, Shillington 1998). Regions at different latitudes are distinguished by differing seasonal cycles of equatorward coastal wind forcing (Bakun & Nelson 1991), as well as the influences of advection, turbulence, and buoyancy (Huyer et al. 1991, Hill et al. 1998, Strub et al. 1998). While our understanding of biological-physical co-variation across regions at the scale of 100s-1000s km is at its infancy, recent work suggests that regional differences in upwelling intensity can explain regional gradients in chlorophyll seasonal cycles and larval recruitment of benthic invertebrates, which may drive rates of species interactions and lead to differences in population and/or community structure (Connolly et al. 2001, Thomas et al. 2001a, Menge et al. 2004, Navarrete et al. 2005 and see Chapter 1).

Meso-scale dynamics, occurring over 10s-100s km, are also prevalent in EBCEs (e.g. Shannon 1985, Strub et al. 1991, Hickey 1998, Botsford 2001). Superimposed on the climate-controlled backdrop of basin- and regional-scale forcing, local topography and meteorology focus upwelling at fixed centers (Jury 1985, Kelly 1985, Strub et al. 1991, Longhurst 1998), which creates alternating patterns of strong and weak upwelling over the scale of capes and bays. These changes have been shown to be spatially linked to variation in populations or functional groups (Ebert & Russell 1988, Wing et al. 1995b, Broitman et al. 2001, Nielsen & Navarrete 2004, Lagos et al. 2005 and see Chapters 1 & 3).

The two southern hemisphere EBCEs, the Benguela and Humboldt, are the most productive of the coastal wind-driven upwelling systems of the world (Thomas et al. 2001b, Carr 2002, Kearns & Carr 2003). In conjunction with the environmental variability described above, a regional break in meso-scale features occurs at ~ 32°S in both these systems (Shannon 1985, Thomas 1999, Navarrete et al. 2005 and see Chapter 1). Reduced seasonality and persistent, year-round upwelling-favorable conditions 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 maxima in spring/summer but favoring downwelling in winter (Shannon 1985, Thomas et al. 2001b, Carr & Kearns 2003). In the southern sections of both systems, upwelling events occur on the scale of about a week (Shannon 1985, Strub et al. 1998). However, we do not know whether the intensities of shared physical forcing processes are similar between systems, nor do we understand how dominant these are relative to other local processes. We also lack information as to whether the changes observed across the different scales of space (e.g. regions, meso-scales) are of similar magnitude. For example, is the relative strength of seasonality in upwelling or temperature similar between systems and are the regional differences that occur along the coasts of similar magnitude? Such questions are critical in order to determine primacy of a particular class or scale of physical features in generating biological pattern, and whether responses of biological communities to environmental variation are general or context-dependent.

Here, I explore the spatial relationship between the spatial distribution of biomass of key intertidal functional groups and the dynamics of nearshore thermal regimes across the mid-latitude regions (29°-34.5°S) of the Benguela and Humboldt systems, which lie on the west coasts of South Africa and central Chile, respectively. As a first step, I answer simple, yet important questions regarding spatial patterns in biological and physical conditions along these coasts: (1) How similar is the spatial structure of mean thermal states between South Africa and Chile? (2) How does the relative importance of weekly to inter-annual dynamics of nearshore sea surface temperature vary along each coast and how similar are the thermal regimes of South Africa and Chile? (3) Do these systems present similar magnitudes of spatial variation in community structure among-sites and/or between

regions? (4) Is biomass on rocky intertidal shores spatially coupled with mean thermal conditions or temporal variability of sea surface temperature across or within EBCEs?

Understanding spatial variation within and between EBCEs has important consequences for ecosystems and economies due to their disproportionate contribution to the world's production and fisheries (Barber & Smith 1981, Pauly & Christensen 1995). Moreover, the strength and nature of biological-physical links are critical to determine the impact of potential changes in different forcing conditions, such as those associated with El Niño Southern Oscillation, Pacific Decadal Oscillation, North Atlantic Oscillation, and global warming.

2.2. **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 (Longhurst 1998). While the inner shelf width is similar along South Africa, the outer shelf is broad and extends 100-200+ km beyond the inner shelf, causing a much smoother slope (Shannon 1985). The shelf is narrowest to the south, but broadens north of 32°S to its widest point at the Orange River basin at the political border between South Africa and Namibia.

The Benguela is unique 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 Agulhas retroflection to the south (e.g. Shannon & Nelson 1996). Water for upwelling appears to

come from greater depth (>100-200m) along South Africa and is primarily South Atlantic Central Water (Stander 1964, Shannon 1966, Carmack & Aagaard 1977, Bailey 1985, Kearns & Carr 2003). In central Chile, Sub-Antarctic Water is upwelled from less than 50m (e.g. Blanco et al. 2001, Carr & Kearns 2003). These source waters are characterized by unique chemical properties. Current information suggests that Sub-Antarctic Water is more saline and nutrient rich. In particular, phosphate content of Chilean source water appears to be the highest of all EBCEs (Kearns & Carr 2003).

Community Structure

To obtain comparable data for rocky intertidal community structure along the west coast of South Africa and central Chile, identical field surveys were conducted at respectively 27 and 16 study sites, spaced 10s - 100s km apart and spread between 29°S and 34.5°S latitude (Fig. 2.1a). Surveys were conducted during austral spring-summer months between 2001 and 2004, with most sites surveyed in several years. Details of sampling methods are described in Chapter 1 and Broitman et al. (2001). Briefly, percentage cover and density of sessile and mobile species were estimated in a minimum of eight 0.25-m^2 quadrats haphazardly placed along 20 to 50-m transects stretched horizontally across the mid and low intertidal zones of 1-5 wave-exposed 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 x 7-m strips). Biomass (wet weight) per species was calculated for each quadrat using site-specific

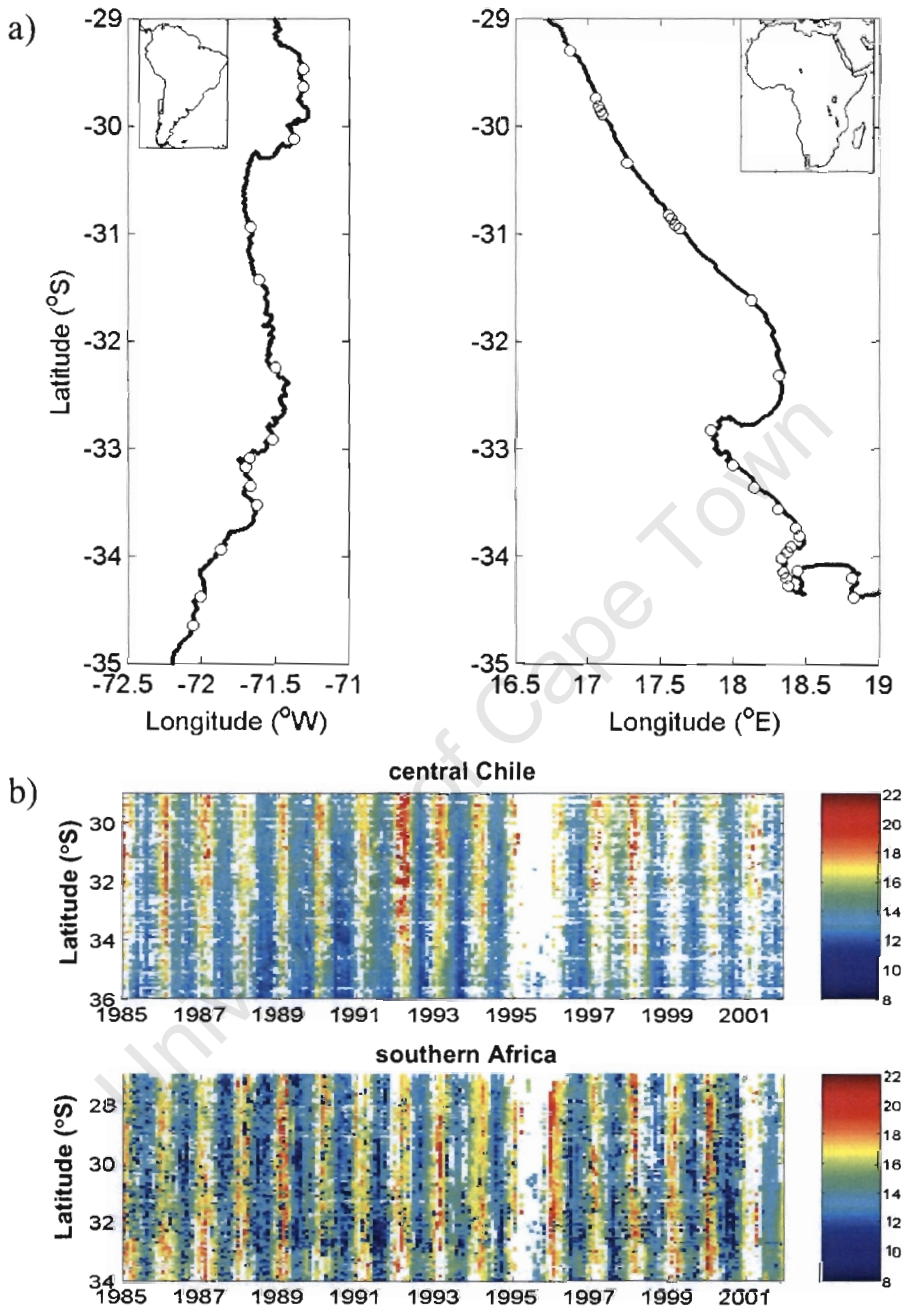


Fig. 2.1. a) Location of study sites (circles) on wave-exposed, rocky intertidal shores spread across mid-latitude regions of central Chile (left) and South Africa (right). b) 16-yr time-series of satellite-measured (AVHRR, Advanced Very High Resolution Radar) nearshore sea surface temperature across the study regions. White = missing data.

conversions of cover to mass and length/mass regressions for sessile and mobile species, respectively (see Chapter 1). Species abundances were pooled into functional groups to allow direct comparisons between Chile and South Africa, as the two systems have different species but possess comparable functional groups. The functional groups were defined according to (a) morphological/anatomical characteristics associated with productivity potential and susceptibility/resistance to herbivory (algae) or (b) trophic position and foraging strategy (invertebrates) (see Table 1.1 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, I used principal component analyses (PCA) with biomass of each of the functional groups as the variables (see below).

Variability in Sea Surface Temperature (SST)

I used SST as a representative variable that summarizes temporal and spatial variation in a number of oceanographic/climatological processes. Across each study region, characterization of spatial and temporal dynamics of nearshore hydrographic conditions, as evaluated through SST, was based upon a 16-year time series (1987-2003) of SST derived from 4-km resolution Advanced Very High Resolution Radiometer (AVHRR) thermal imagery (Fig. 2.1b). The data represent nearshore temperatures approximately 5-10 km offshore, as estimates are based on averages of the first two cross-shelf pixels closest to the coastline. Cross-shelf averaging was necessary in order to improve temporal

coverage, which was often compromised nearshore due to missing data and variation in coastline position (Broitman et al. 2005).

Long-term (16-year) mean, minima, and maxima of SST were calculated from time-series of monthly averages for each alongshore pixel. To examine temporal (weekly, monthly, intra-seasonal, annual, and long-term) variability in SST at each site, time-series of 7-day composite images were used. First, to evaluate the relative importance of temperature fluctuations of the dominant cycles (time scales), I used two different techniques that are robust to the temporal uncertainty inherent in satellite-measured data. I estimated the percentage of total temporal variability that is explained by the annual, semi-annual, and intra-seasonal cycles. To this end, I performed a least-squares harmonic regression analysis to estimate the amplitude and phases of the dominant annual, semi-annual, and intra-seasonal components of SST. The predicted harmonic means for the different time scales were then removed from the time series and I calculated the variance over the residuals. Comparison of these variances against the total variance in the original time series allowed me to estimate the percentage of variation explained by each cycle. Second, to examine variation in weekly to monthly time scales, I performed autocorrelation analyses of site-specific time series after removing the annual and semi-annual trends. Estimates of autocorrelation functions for the entire regions of Chile and South Africa were obtained by simply averaging the de-trended time series for each site and then conducting the autocorrelation on the average time series. Autocorrelation functions represent dissimilarity between observations at increasing time lags. The decorrelation scale is the elapsed time necessary to achieve independence between observations in serially correlated data. Autocorrelation at lag-1 (in this case, 7 days) is an indicator of linear dependence between successive observations in a time series (Buishand & Beersma 1993). Therefore, I

used the autocorrelation at lag-1 as an indication of weekly changes in oceanographic conditions.

The variables (scales) of temporal variation in SST act simultaneously and are correlated to varying degrees across regions and systems. Because of this, I used principal component analyses with six variables (mean, long-term variance, % annual, % semi-annual, % intra-seasonal, and lag-1 autocorrelation) to reduce the dimensionality of data and describe the prominent spatial structure of temporal variability. Reducing the data through PCA also allowed me to discriminate between groups composed of 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 meaning of the different components. As a first step to describe and compare the dynamic regimes of these two coastal upwelling systems, analyses were first carried out on pooled data for South Africa and Chile. To then gain further insight into environmental variability between and within each system, separate analyses were performed for South Africa and Chile.

Bio-physical coupling

To distinguish spatial correlations resulting from regional or latitudinal trends from those due to among-sites (meso-scale) variation, the spatial variation in SST components and functional group biomass was decomposed into its regional trend (i.e. variation common to several sites adjusted throughout the region) and the residual variation (local variation not accounted for by the larger, regional trend). A cubic polynomial was fitted to the spatial pattern in SST and biomass ($\log n + 1$) as a function of distance from the northernmost study site in each region. Visual inspection of the residuals plotted against

predicted values revealed variances were homogeneous, and normality was tested using Shapiro-Wilks W test. For each polynomial regression, the predicted values for each focal point (Ys) and the local residuals were retained, which provided three descriptors of each variable: 1) the fitted polynomial values (hereafter, regional trends), 2) the local residuals (hereafter, meso-scale variation) and 3) the observed means at each site (hereafter, raw data). See Lagos et al. (2005) and Navarrete et al. (2005) for similar applications.

As a first step to discern whether the biomass of functional groups responded to the differences in temporal dynamics of thermal regimes that occur between and/or within South Africa and Chile, I calculated r-Pearson correlations between (1) the raw estimates of functional group biomass and individual SST variables (between-system) and (2) the residual, meso-scale variation in biomass of functional groups and the de-trended, anomalous SST variables (within-system). I also estimated correlation coefficients between the spatial series of the first three principal components of SST and (a) raw functional group biomass and (b) the first three principal components of community biomass.

2.3. **Results**

Oceanographic Conditions

The patterns of long-term mean SST presented clear and opposing latitudinal trends between coasts, with temperature declining poleward in Chile but increasing poleward in South Africa (Fig. 2.2a). Although data represent the same latitudinal range in both systems, the South African coast is about 20% longer than that of central Chile due to differences in coastline topography and orientation. In general, South Africa is overall

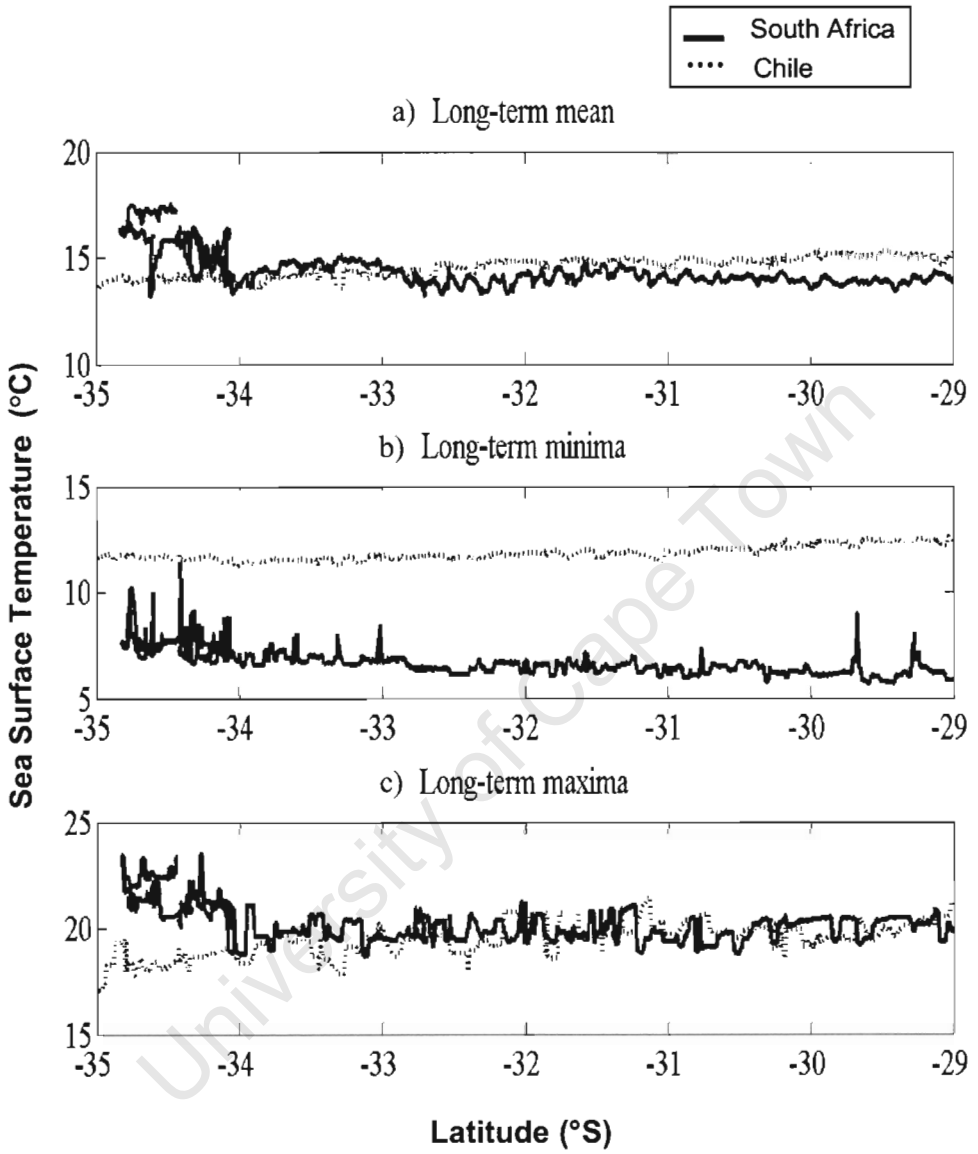


Fig. 2.2. Alongshore variation in long-term a) mean, b) minima and c) maxima SST in South Africa and Chile.

colder north of about 33°S (Fig. 2.2a), and experiences more extreme thermal conditions, with much lower historic minima across the entire coast (Fig. 2.2b) and higher historic maxima south of 32°S (Fig. 2.2c). Moreover, South Africa is characterized by greater spatial variability in SST (compare fluctuations of lines in Fig. 2.2).

The temporal dynamics of nearshore thermal conditions were also strikingly different between the two systems (Fig. 2.3). Across South Africa, clear spatial structure in the relative strength of different temporal variables was observed, with a strong discontinuity at about 32° S (approx. 600 km in Fig. 2.3) that partitioned the coast into two distinct regions. The northern region was dominated by strong annual signals in SST, which explained up to 79% of local variation (Fig. 2.3b). In contrast, relatively weaker annual signals that varied among sites were observed to the south. Moreover, the semi-annual cycle, which was positively correlated with summer/autumn mean temperatures (Pearson $r = 0.70$, $p = 0.01$), played an increasingly more important role in temperature variation poleward, culminating at the southern end of the Cape Peninsula (Fig.2.3c). Likewise, the progression of variation within seasons was relatively stronger, yet variable among sites, south of 32°S (Fig. 2.3d). In comparison, Chile was characterized by greater long-term stability in thermal conditions (Fig. 2.3a), and among-site changes in variance were overall smaller than that observed along South Africa. A trend of increasing stability to the south was, however, apparent. Similar to South Africa, the strength of the annual signal was greatest in the north, peaking towards the center of the study region (~32°S; Fig. 2.3b). However, the semi-annual and intra-seasonal cycles were slightly stronger at the northern and southern extremes, respectively (Figs. 2.3c,d). In general, the contrast between north and south so evident in South Africa was less apparent in Chile.

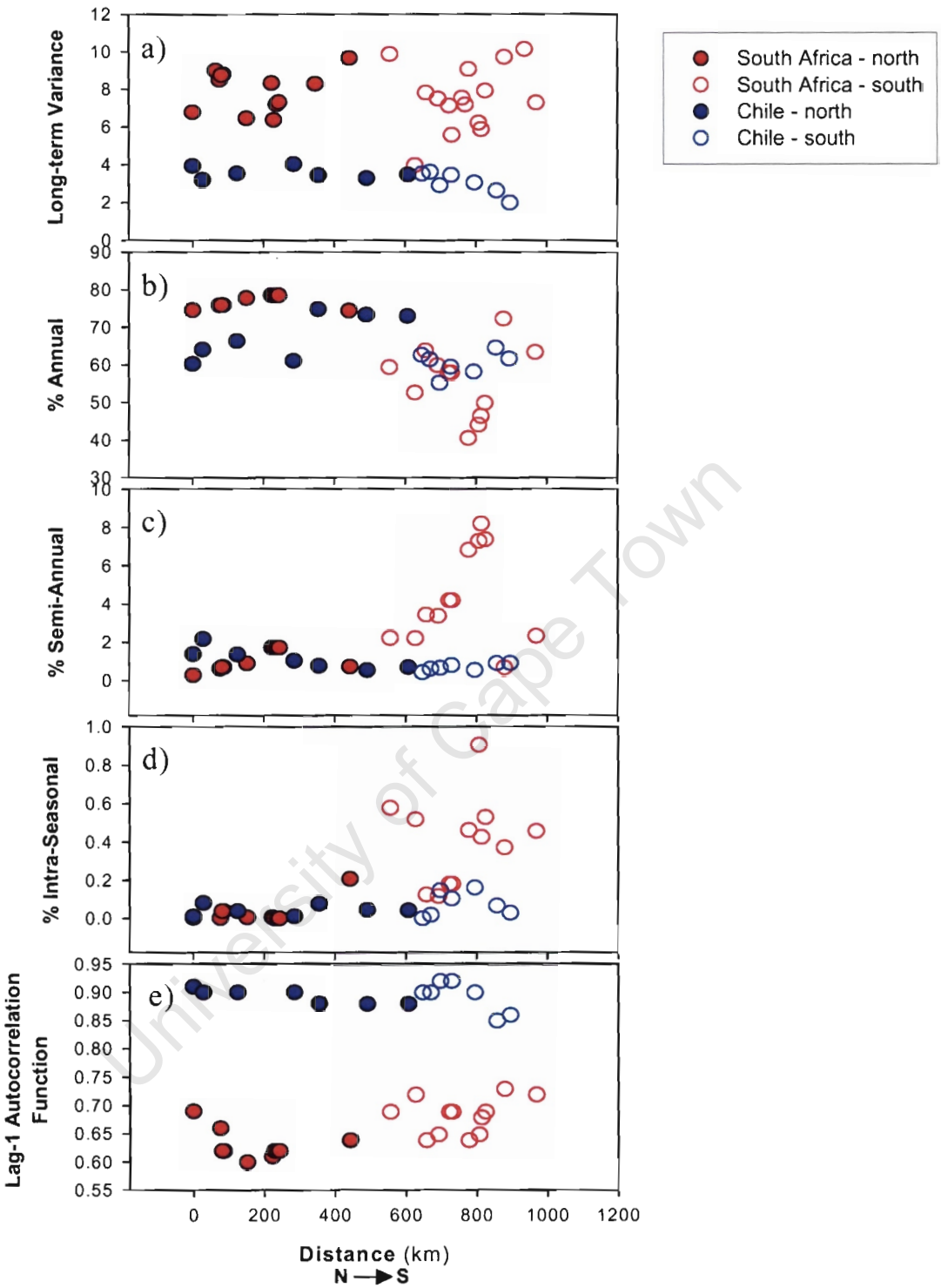


Fig. 2.3. Alongshore variation in temporal components of SST for South Africa (red) and Chile (blue). Solid circles are sites north of 32°S, open circles are sites south of that. Distance is north to south.

After removal of long-term signals, background SST dynamics across South Africa appeared to be dominated by greater "high frequency" variability (Figs. 2.3e, 2.4), and the alongshore patterns in short-term temporal dynamics revealed that all sites in Chile were less variable than those in South Africa (Fig. 2.3e). 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 stability of SST 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, I ran correlations on the residuals after removing the large-scale, regional trends. Week-to-week stability characterized anomalously warm sites in South Africa (Pearson $r = 0.70$, $p = 0.0003$), but anomalously cold sites in Chile (Pearson $r = -0.71$, $p = 0.0044$). Across the entire regions of Chile and South Africa, striking differences in the decay of correlation coefficients with increasing time lags were observed (compare slopes of lines in Fig. 2.4), with de-correlation time scales of approximately 35 days in South Africa and 95 days in Chile.

The multivariate characterization of dominant SST variability detected clear structure in relationships between SST components, with striking differences between Chile and South Africa (Fig. 2.5a). First, the spread of points (sites) was greater in South Africa than in Chile. Second, differences between regions north and south of 32°S were apparent within each system. 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. 2.5a highlight similarities and differences in local nearshore SST regimes, with groups separated primarily on component 1 and, secondarily, on component 2. The first three

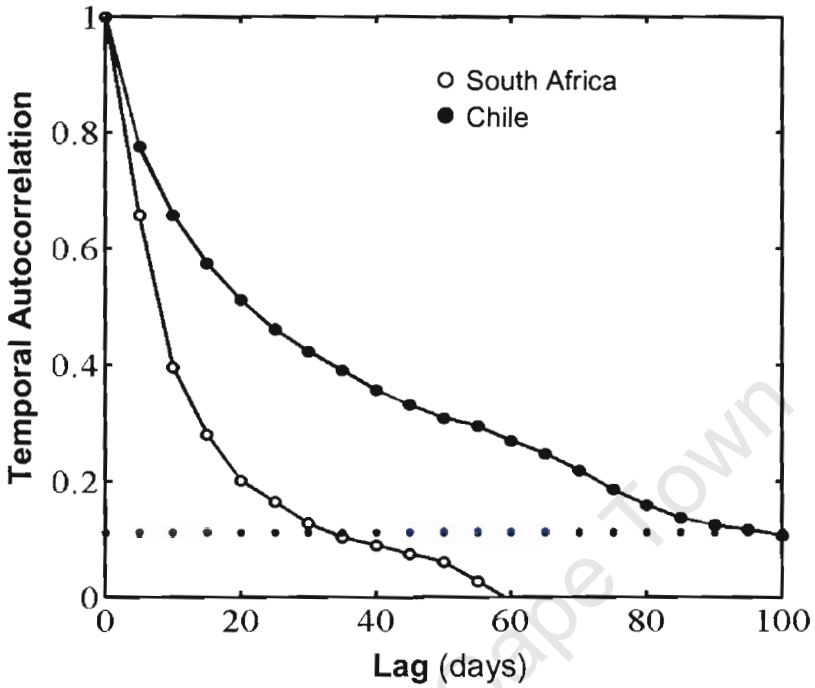


Fig. 2.4. Temporal autocorrelation functions of sea surface temperature (SST) for average of time series at South Africa (open circles) and Chile (solid circles).

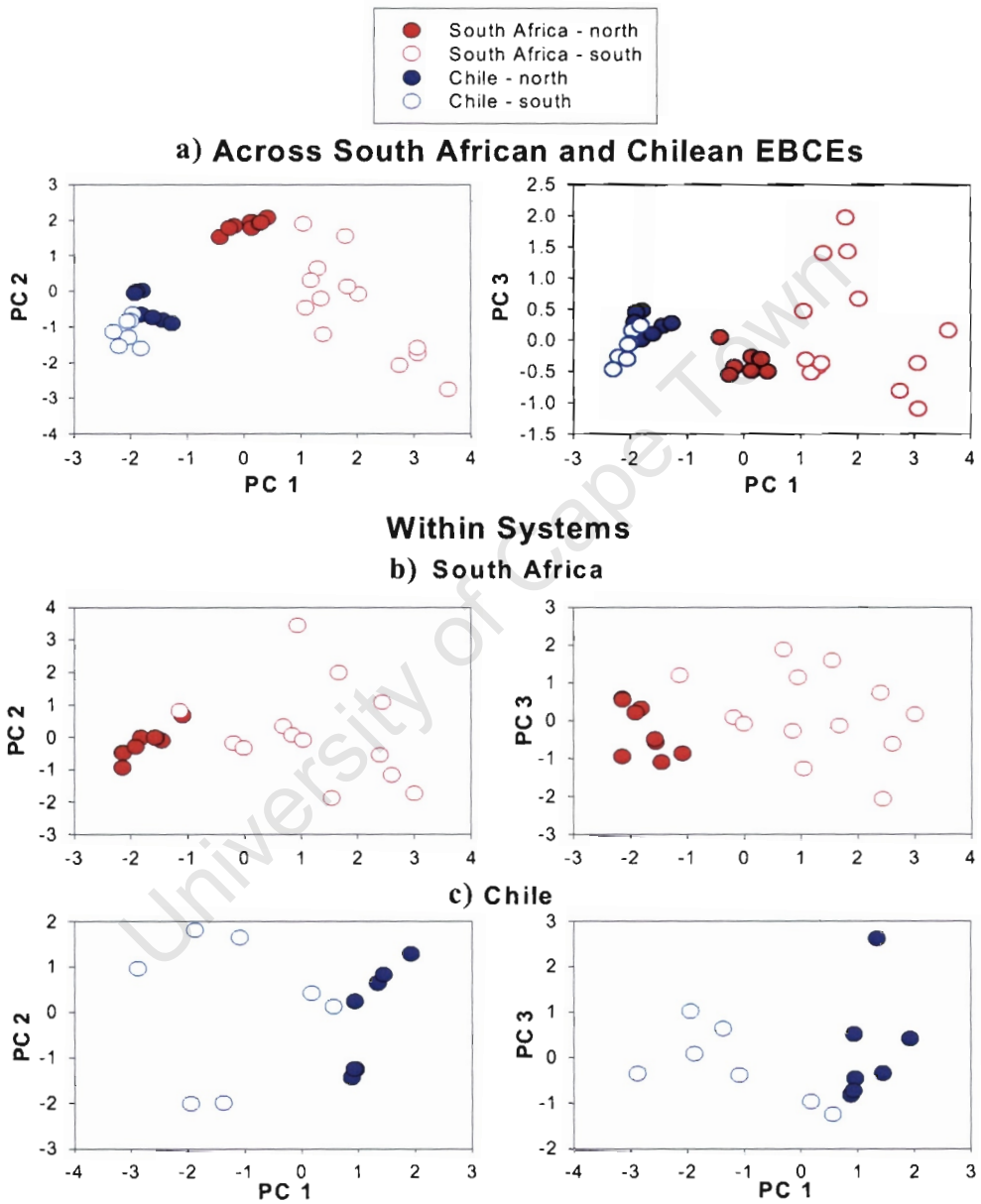


Fig. 2.5. a) Relationships for the first three principal components obtained from principal component analysis (PCA) of sea surface temperature a) across both South Africa (red) and Chile (blue), b) within South Africa and c) within Chile. Solid circles are sites north of 32°S, whereas open circles are sites to the south.

principal components (PC1, PC2, and PC3) cumulatively accounted for 52%, 85%, and 92% of the observed variability. In general, these systems were largely characterized by environments in which the temporal dynamics were evenly weighted by short-term and long-term temperature pulsing (Table 2.1a). Weights were similarly high for all temporal descriptors except the annual cycle for PC1, while PC2 was most strongly weighted by the strength of the annual cycle. Weights for mean SST and the annual cycle were weak for PC3.

Since South Africa and Chile were characterized by rather different relationships between the terms driving SST variability, principal component analyses were also carried out within each system to obtain further insight into dominant nearshore conditions of each EBCE (Figs. 2.5b,c). Similar between-region differences in the grouping and spread of sites were apparent. Most of the observed variation in South Africa was explained by PC1 (52%), while PC1 and PC2 were similarly important in Chile (38% and 29% variation explained, respectively). Moreover, the principal components represented different dynamics in the two systems (Table 2.1c,e). Whereas long-term mean and variance dominated PC1 in Chile, they were weakly weighted in PC1 for South Africa, where "high frequency" (weekly) stability played a more prominent role (0.40 compared to 0.08). The lag-1 autocorrelation function dominated PC2 in Chile. In contrast, PC2 in South Africa was most heavily weighted by the long-term mean, the lag-1 autocorrelation function and the semi-annual cycle. PC3 accounted for similar magnitudes of variability (16-17%) in both systems, but represented long-term fluctuations in South Africa and the semi-annual cycle in Chile.

Patterns of Functional Group Biomass

In general, the rocky shores of Chile supported consistently higher biomass than South Africa in the low intertidal zone ($F_{1, 38} = 101.44$, 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, $p = 0.023$). Clear between-system differences in the abundances of functional groups were also observed (Fig. 2.6). While Chile was characterized by relatively higher biomass of kelp, mid-shore algae, and low-shore predators/scavengers, South Africa was characterized by higher biomass of filter feeders and herbivores, particularly towards the north in the case of low-zone herbivores. Regardless of these differences in mean abundances, the degree of site-to-site variation in local, residual biomass of most functional groups was generally greater in South Africa, particularly for algae (Fig. 2.7). Only predator biomass had consistently higher coefficients of variation across Chile than across South Africa.

Clear structure was also observed in across-system multivariate characterization of community biomass in terms of the first three components of PCA (Fig. 2.8). Striking separation was observed between South Africa and Chile. Moreover, important (albeit weaker) separation was additionally observed between regions north and south of 32°S within each system. In general, strong separation among groups was observed across low intertidal shores, which were primarily separated on component 1. Relatively weaker separation occurred for mid shores. 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 2.1b). On low shores, PC1 was strongly weighted by consumers, while on mid shores macroalgae dominated PC1 and consumers dominated PC2. Kelp and filter feeders were prominent components of PC2 in

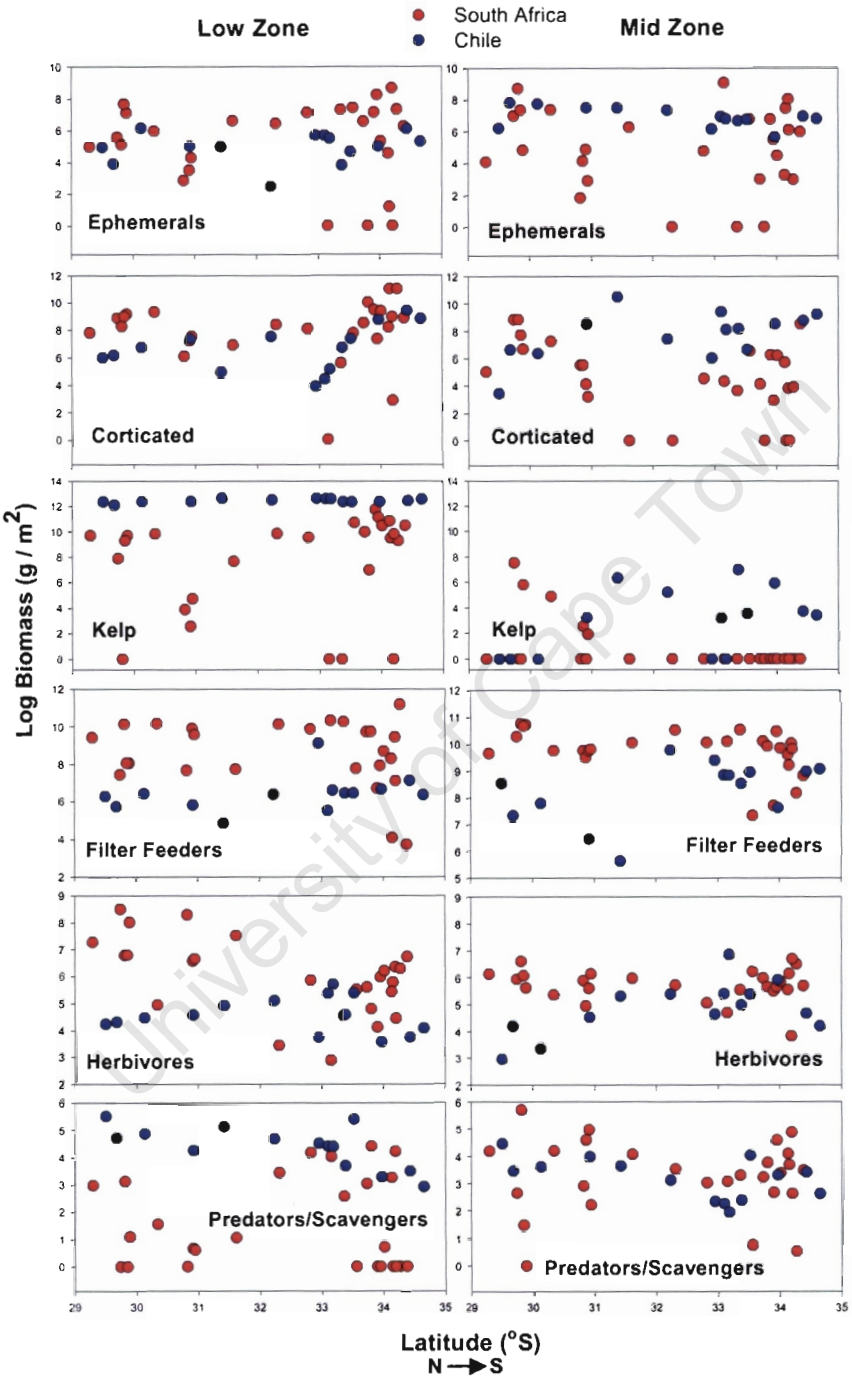


Fig. 2.6. Mean biomass of functional groups occupying wave-exposed rocky intertidal shores along the coast of South Africa (red circles) and Chile (blue circles).

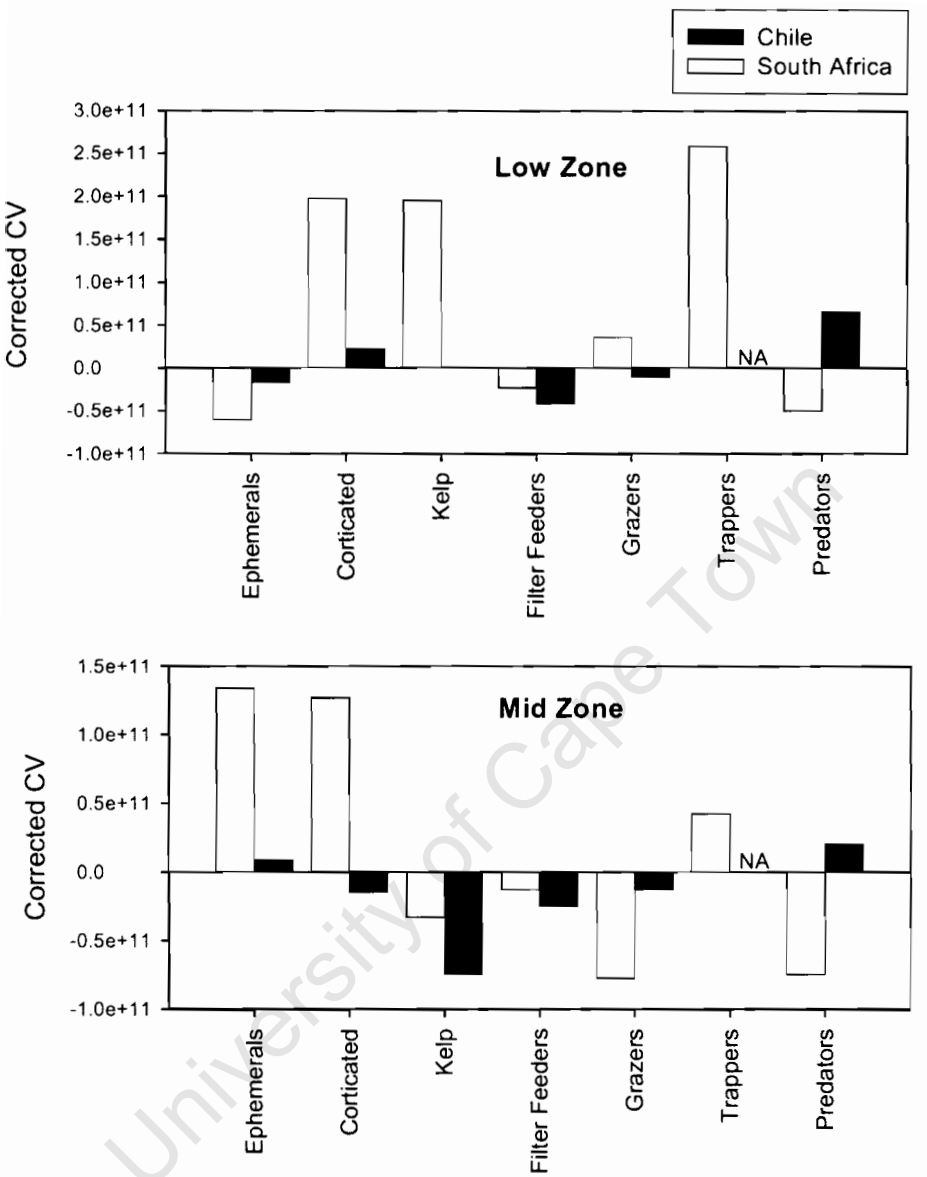


Fig. 2.7. Corrected coefficient of variation of local, residual biomass (spatially detrended) of functional groups across the coasts of South Africa (white bars) and Chile (black bars). Specialized kelp-trapping limpets (Trap) do not occur in Chile.

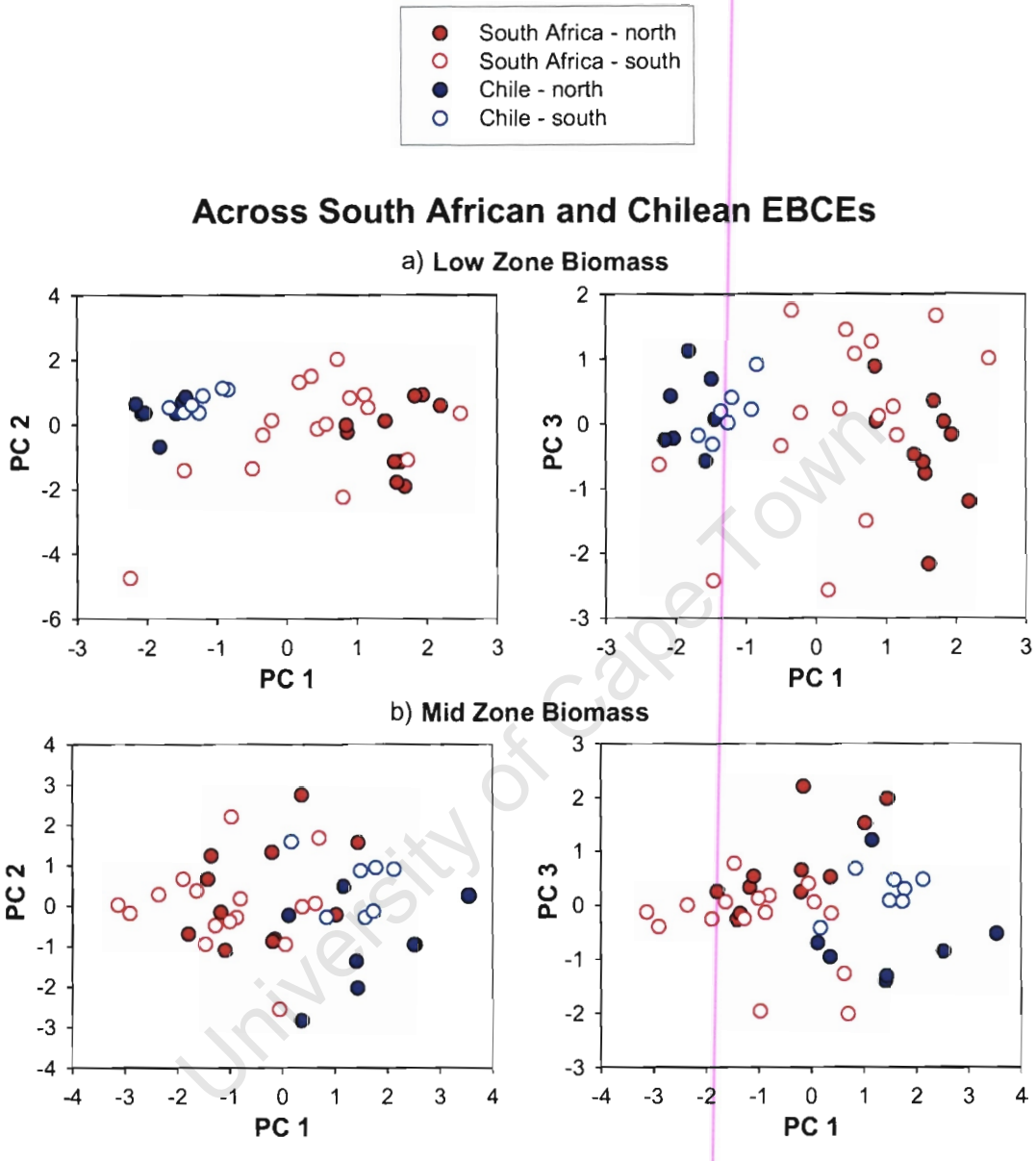


Fig. 2.8. Relationships for the first three principal components obtained from principal component analysis (PCA) of community biomass across both South Africa (red) and Chile (blue) for a) low and b) mid intertidal zones. Solid circles are sites north of 32°S, whereas open circles are sites to the south.

the low zone. PC3 mostly reflected a combination of filter feeders and predators/scavengers, as well as ephemerals (low zone) and kelp (mid zone).

Principal component analyses were also carried out within each system (Table 2.1d,f). In general, observed variation on low and mid South African shores were similarly partitioned among the principal components (Table 2.1d). For PC1, both low and mid shores similarly reflected strong and even-weighted combination of corticated algae, kelp, and kelp-trapping limpets. Biomass of ephemeral macroalgae and filter feeders dominated PC2 on low shores, while grazers and filter feeders dominated PC2 on mid shores. However, filter feeders played an important, secondary role in PC2 for both tidal heights. Low-shore PC3 mainly reflected grazers (0.71) and kelp-trapping limpets (0.53), whereas ephemeral algae, filter feeders, and predators/scavengers were all relatively highly weighted (0.44-0.57) in PC3 on mid shores.

Across low and mid shores of Chile, similar percentages of observed biomass variation were accounted for by the different principal components (Table 2.1f). Moreover, most of the functional groups dominating each of the principal components on mid and low shores were commonly shared. Differences were largely due to tidal-height zonation of kelp and filter feeders. While weights of all groups but ephemeral algae and filter feeders (or kelp) were high for PC1, PC2 was dominated by filter feeders (or kelp) and ephemerals. Kelp, predators, and filter feeders (or ephemerals) played prominent roles in PC3 of each zone.

Between EBCEs

Individual Variables. Between-system differences in biomass of functional groups were largely unassociated with that of long-term mean SST (Pearson $r < 0.25$, $p > 0.1$ for all functional groups). However, strong spatial linkages were observed between biomass and the individual variables of temporal dynamics in SST (Fig. 2.9). Responses to long-term variance (inter-annual fluctuations) and weekly stability were the most consistently important, as all groups showed significant association to these scales of temporal variability. Kelp, mid-shore algal groups, as well as low-shore predators all responded similarly, with greatest biomass significantly associated with more stable conditions. Filter feeders, mid-shore grazers and total herbivores showed the opposite pattern.

Multivariate Descriptors. The described differences in multivariate nearshore thermal regimes between South Africa and Chile explained much of the observed variation in biomass of individual functional groups (Fig. 2.10). All groups were coupled to one or both of the first two principal components of SST variability, but the strength and direction of preference sometimes differed between the low and mid intertidal zones. However, similar responses between tidal heights were observed for kelp, filter feeders, and total herbivores. Filter feeders and herbivores were both positively correlated with PC1 and PC2, whereas biomasses of all macroalgal functional groups occupying the mid shore were consistently negatively associated with these same components. Corticated algae did show an opposite response to PC1 of SST in the low shore, as well as a strong negative relationship with PC3. Kelp and predators both responded negatively to PC1.

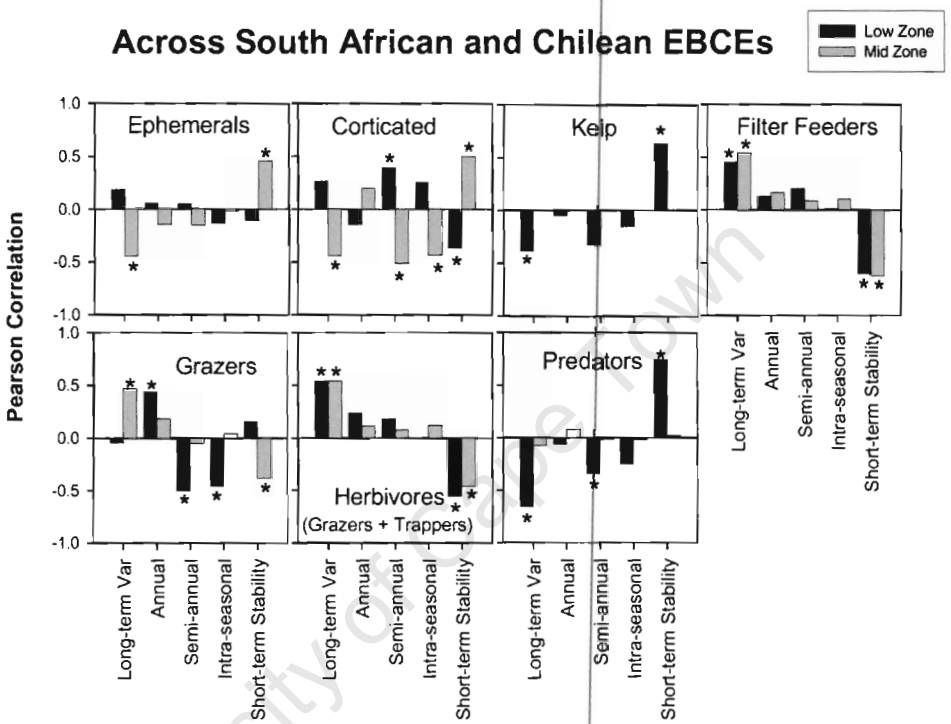


Fig. 2.9. Correlation coefficients between individual variables of SST dynamics and biomass of individual functional groups on low (black bars) and mid (grey bars) shores across both South Africa and Chile. Stars indicate significant correlations ($p<0.05$). Functional groups were omitted if they lacked significant correlations.

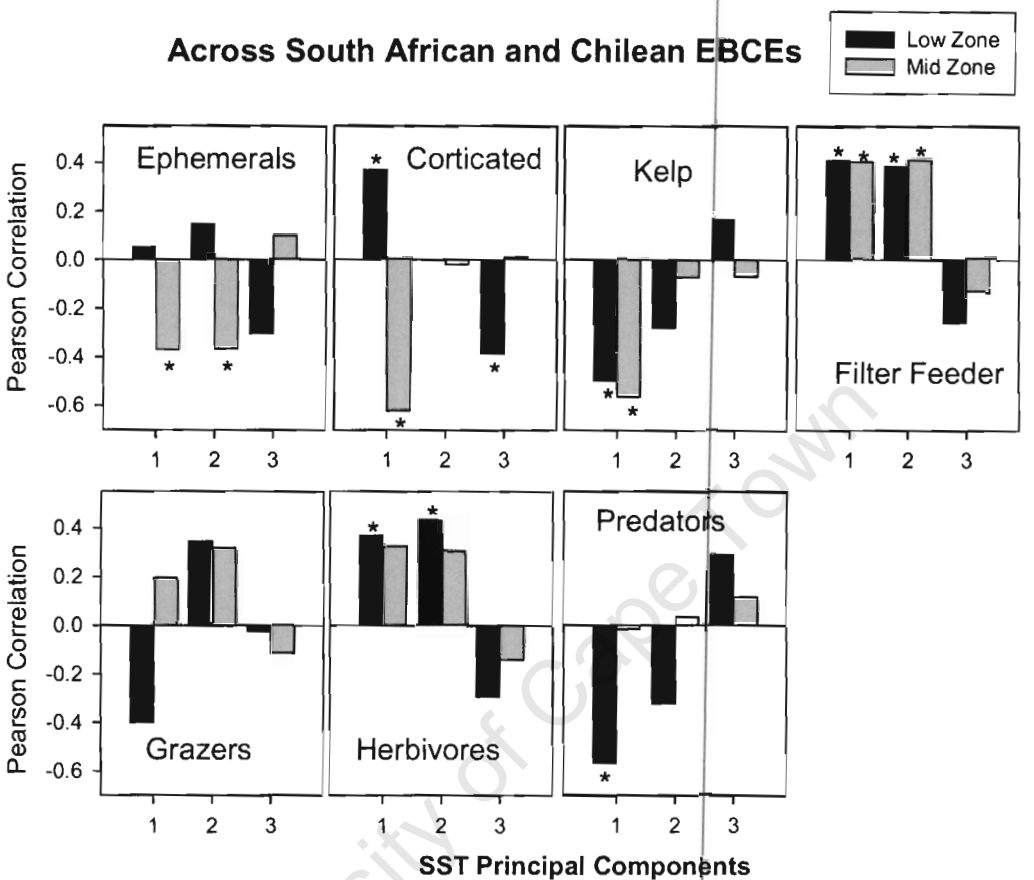


Fig. 2.10. Correlation coefficients between the first three principal components of SST and biomass of individual functional groups, on low shores (black bars) and mid shores (grey bars), across both South Africa and Chile. Stars indicate significant correlations ($p<0.05$). Functional groups were omitted if they lacked significant correlations.

The first three principal components of SST variability also explained most of the structure and between-system differences observed in the multivariate characterization of low and mid intertidal communities (Fig. 2.11). In general, PC1 of community biomass was strongly associated with PC1 of temperature dynamics: positively across low shores and negatively across mid shores. In addition, PC1 of biomass on low shores was significantly coupled to PC2 and PC3 of SST variability, though relationships were of opposing directions. Interpretation of relationships with PC3 requires caution due to the low degree of overall temperature variability explained by this component. Again, the greater spread of data for South Africa and the distinction between areas north and south of 32°S were obvious.

In general, the striking consistencies among relationships suggest that filter feeders and herbivores benefit from increased variability in SST, while macroalgae (except corticated in the low zone) and predators benefit from more stable thermal conditions.

Within EBCEs

Individual Variables. Within each EBCE, site-to-site variation in local, residual biomass of most functional groups was significantly correlated with meso-scale spatial variation in individual temporal components of SST dynamics (Fig. 2.12). However, associations often varied with tidal height. Moreover, different functional groups responded to different temporal scales of SST dynamics. Similar responses were observed for kelp and grazers in South Africa (Fig. 2.12a), both appearing to benefit from long-term, inter-annual variation. In addition, some functional groups responded either negatively or positively to the local pattern of high frequency (weekly) temporal variation in SST, which explained much of the meso-scale variation in low-shore biomass of corticated algae,

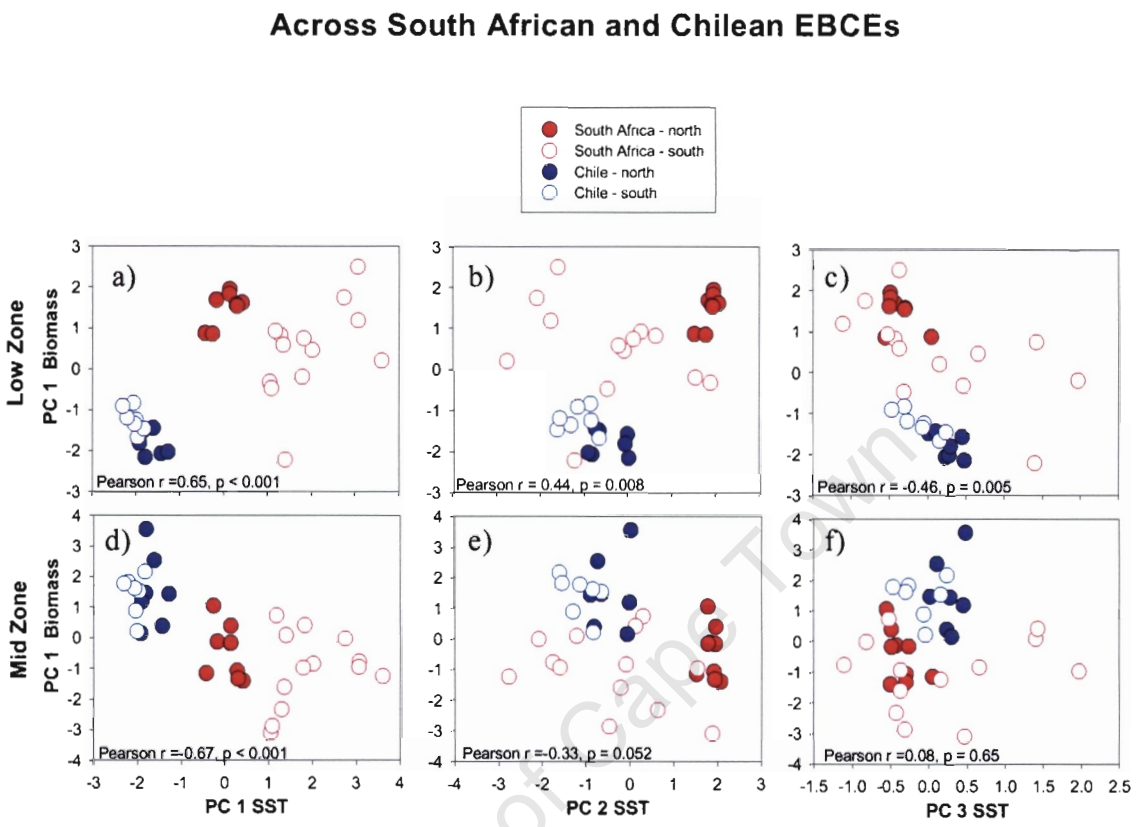


Fig. 2.11. Relationships between the first three principal components of SST variability and the first principal component of community biomass variability, on low and mid shores, across both South Africa (red) and Chile (blue). Solid circles are sites north of 32°S, open circles are sites south of that.

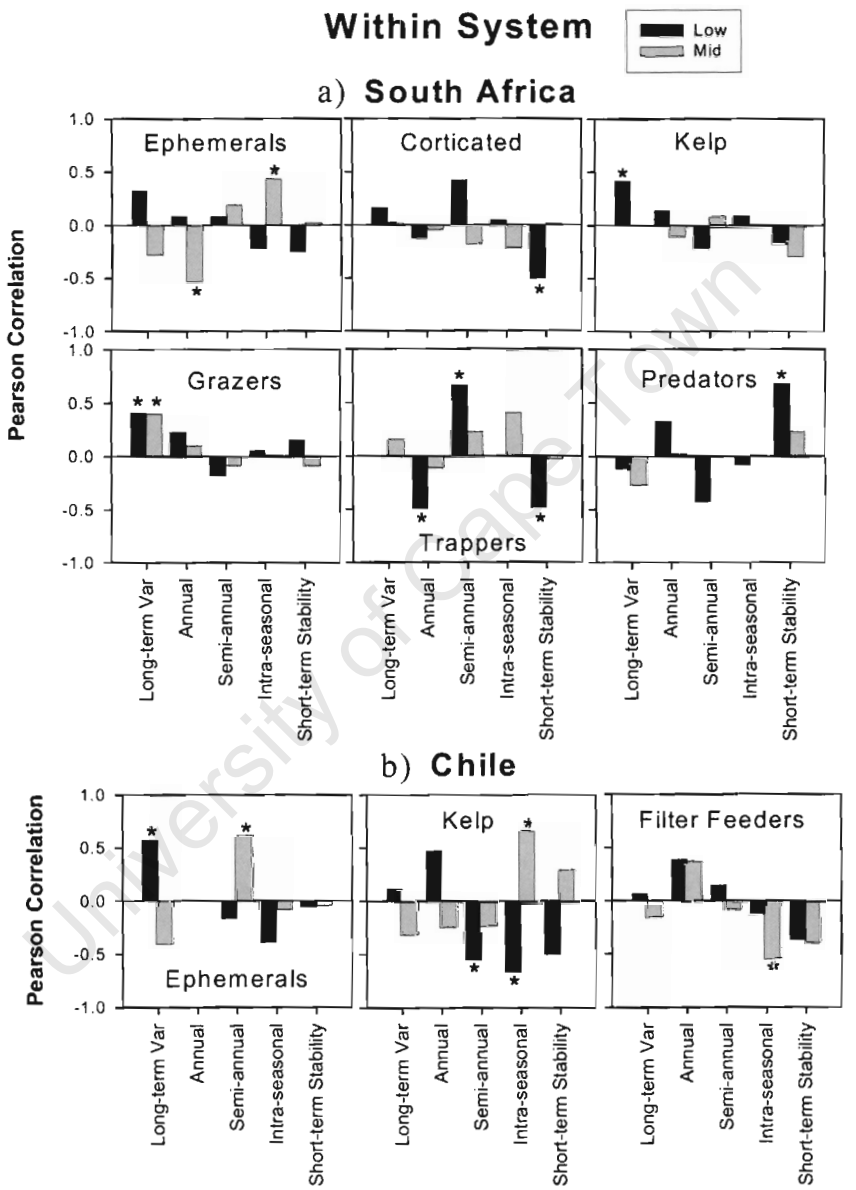


Fig. 2.12. Correlation coefficients between individual variables of SST dynamics and biomass of individual functional groups on low (black bars) and mid (grey bars) shores within a) South Africa and b) Chile. Stars indicate significant correlations ($p<0.05$). Functional groups were omitted if they lacked significant correlations.

predators, and kelp-trapping limpets in South Africa. More stable conditions seemed to favor predators, but disfavored kelp-trapping limpets and corticated macroalgae. Mid-shore ephemeral algae and low-shore trappers were both strongly, negatively correlated with the annual cycle, and positively associated with either intra-seasonal or semi-annual cycles.

Across Chile, site-to-site variation in biomass was more strongly linked to intra-seasonal and semi-annual temperature modifications (Fig. 2.12b). Kelp and filter feeders were significantly correlated with intra-seasonal cycles in SST, but the strength and/or direction of relationships differed between low and mid shores. Ephemeral biomass, on the other hand, appeared to be enhanced where long-term variability was strong (low zone) or semi-annual fluctuations were relatively important (mid zone).

Multivariate Descriptors. After separate characterization of SST regimes within each of the coastal upwelling systems, I analyzed how these multivariate descriptors were spatially coupled to alongshore variation in biomass of (1) individual functional groups (Fig. 2.13) and (2) the EBCE-specific multivariate characterization of relationships between functional groups (Figs. 2.14, 2.15). In general, individual functional groups were clearly favored by one of the components of SST variation. However, there were no instances where biomasses on both low and mid shores were highly and significantly correlated to the same factor.

Along the coast of South Africa, responses of individual functional groups to temporal variability in SST were relatively consistent among groups (Fig. 2.13a). Across the low intertidal zone, all algal groups (ephemeral, corticated, and kelp) were positively correlated with PC3. In contrast, grazers and predators/scavengers showed significant and negative relationships with PC1 and PC2, respectively. On the mid shore, only one strong

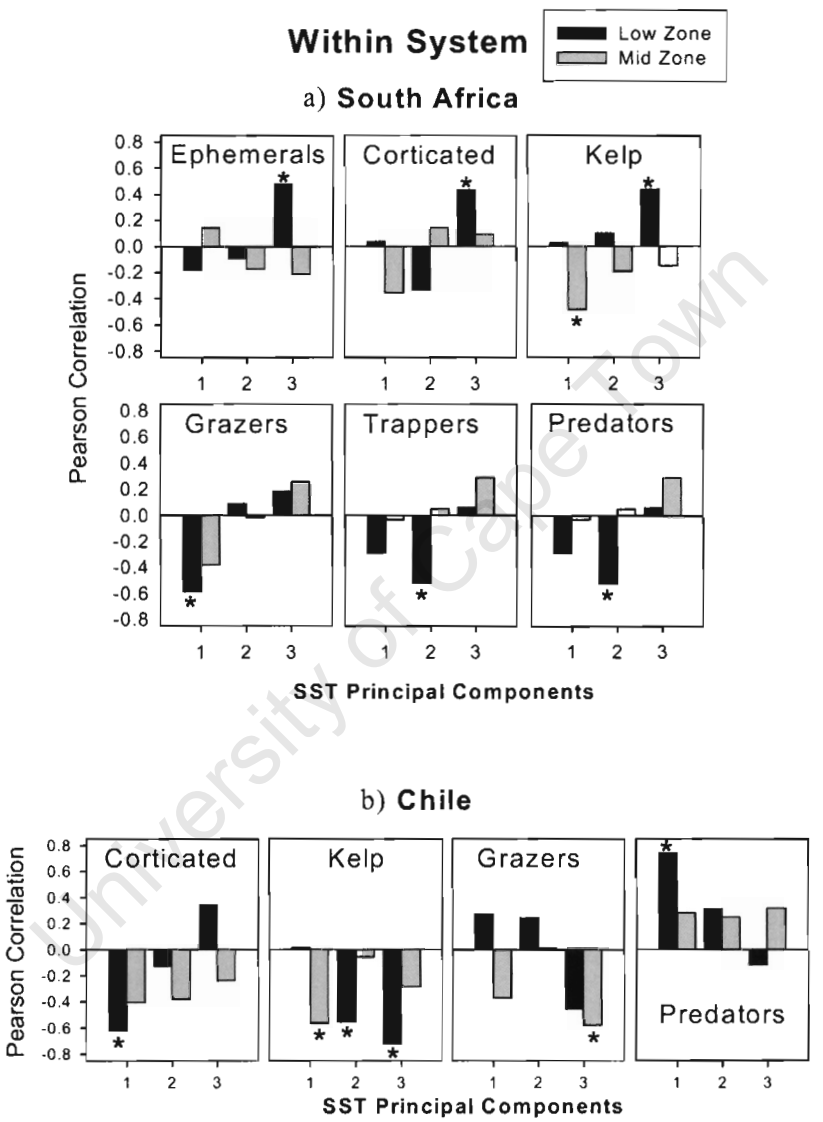
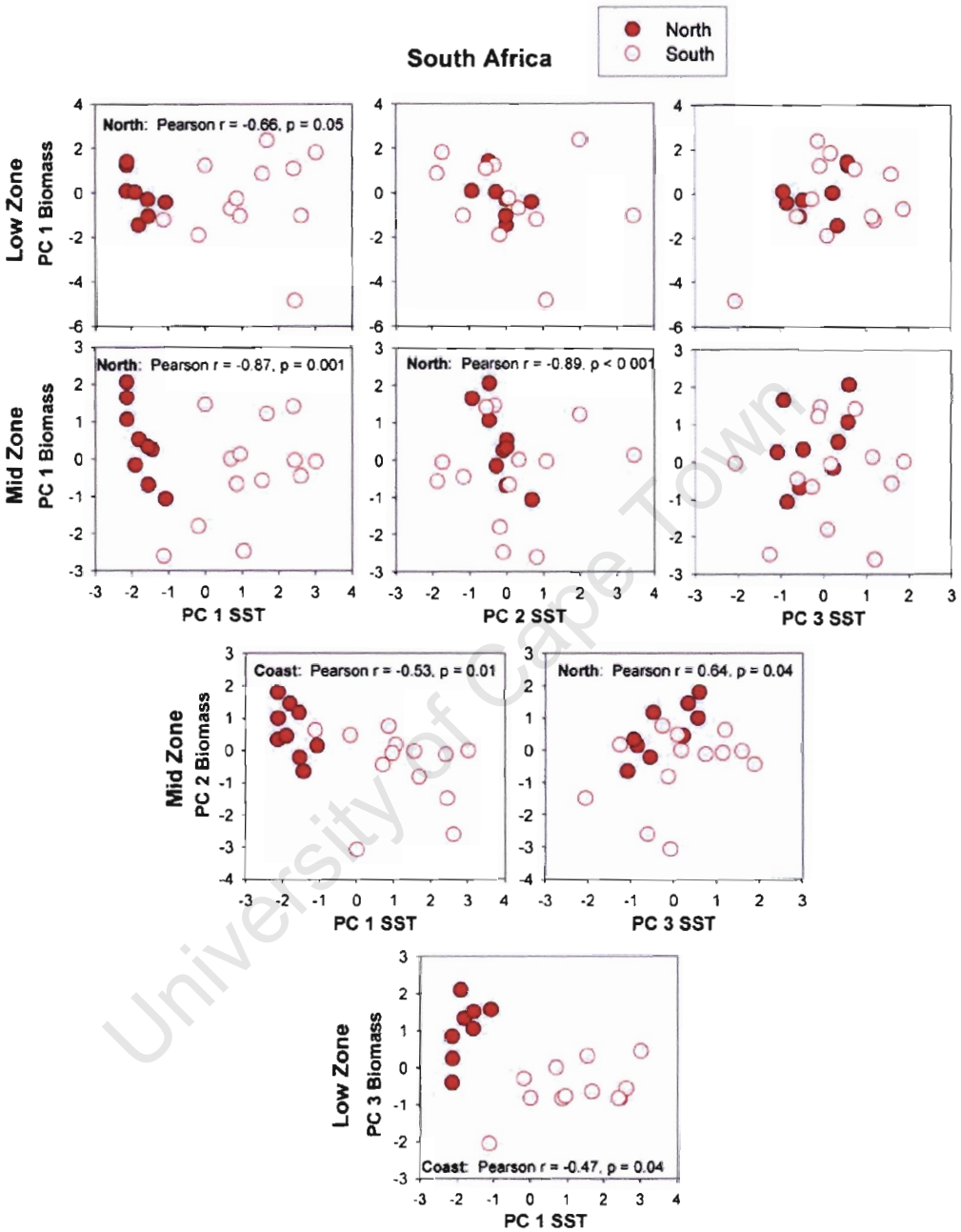


Fig. 2.13. Correlation coefficients between the first 3 principal components of SST dynamics and biomass of individual functional groups on low (black bars) and mid (grey bars) shores within a) South Africa and b) Chile. Stars indicate significant correlations ($p<0.05$). Functional groups were omitted if they lacked significant correlations.

Fig. 2.14. Relationships within South Africa (red) between the first three principal



components of SST variability and the first three principal components of community biomass variability, for low and mid shores. Solid circles are sites north of 32°S, open circles are sites south of that. Coast refers to both north and south regions.

relationship was observed between functional group biomass and components of SST variability: kelp was negatively associated with PC1.

In Chile, the primary SST dynamics driving biomass differed among individual functional groups (Fig. 2.13b). While increasing strength of PC1 disfavored low zone corticated macroalgae, predator biomass was enhanced. Low-shore kelp biomass was negatively associated to both PC2 and PC3, while mid-shore kelp was negatively associated with PC1. Biomass of grazers was negatively correlated with PC3.

When considering dominant components of the multivariate descriptors of intertidal community biomass across South Africa (Fig. 2.14), PC1 of SST variability was significantly and negatively associated with PC2 and PC3 of biomass variability on the mid and low shore, respectively. No other significant relationships were observed when considering variation across the entire coast. However, striking differences in the responses of biomass to dominant SST components were observed within regions north versus south of 32°S (filled or empty circles). In the northern region, strong and significant negative correlations were observed between PC1 of biomass variability and the first one (low shore) or two (mid shore) principal components of SST variability. In addition, PC2 of biomass on mid shores was positively associated with PC3 of SST variability.

On low and mid shores of central Chile, significant, yet opposing, relationships were observed between the first principal components of SST and community biomass variability (Fig. 2.15). Moreover, as in South Africa, some components of biomass variability showed important differences in their response to SST dynamics, depending upon whether north or south of 32°S.

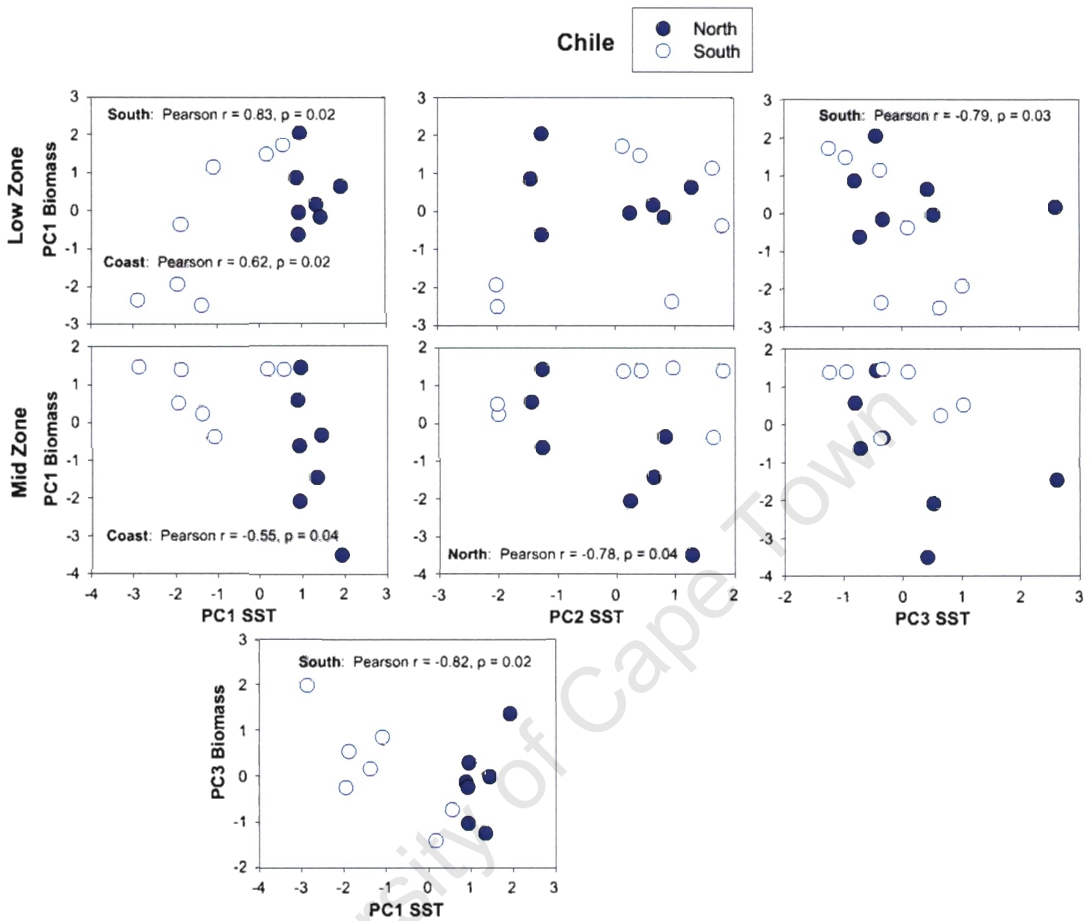


Fig. 2.15. Relationships within Chile (blue) between the first three principal components of SST variability and the first three principal components of community biomass variability, for low and mid shores. Solid circles are sites north of 32°S, open circles are sites south of that.

North and South of 32°S

Individual Variables. To further explore potential differences in bio-physical links between regions north and south of 32°S within each EBCE, I ran separate correlations between local, residual functional group biomass and the residuals of individual variables of SST dynamics for each region (Figs. 2.16, 2.17). While several groups did show consistent and significant patterns of biomass responses to the different temperature signals, there were numerous cases in which the responses depended upon whether sites fell into the regions north or south of 32°S. On low shores of South Africa (Fig. 2.16a), kelp and grazer biomass benefited from long-term (inter-annual) temperature fluctuations in the southern region, while increased importance of intra-seasonal pulsing across the northern region strongly disfavored grazers but benefited ephemeral algae. Patterns of responses by specialized kelp-trapping limpets and predators generally opposed one another, regardless of whether in the north and south. In the mid intertidal zone, significant relationships with SST variables were only observed in the northern region (Fig. 2.16b). Here, ephemeral and corticated biomass appeared to be restricted by a strong annual cycle, which was characteristic of sites with anomalously colder average autumn (Pearson = -0.63, $p = 0.02$) and summer (Pearson = -0.71, $p = 0.007$) temperatures. Corticated algae seemed to respond positively to the semi-annual cycle in temperature, such that biomass was greatest where such variation was relatively more important. Filter feeders, on the other hand, seemed to benefit from greater long-term variation and intra-seasonal temperature fluctuations.

In Chile, the relative importance of the intra-seasonal cycle to alongshore variation in local biomass seemed to outweigh most other temporal scales of SST variation, both on low (Fig. 2.17a) and mid (Fig. 2.17b) shores. Higher biomass of corticated algae,

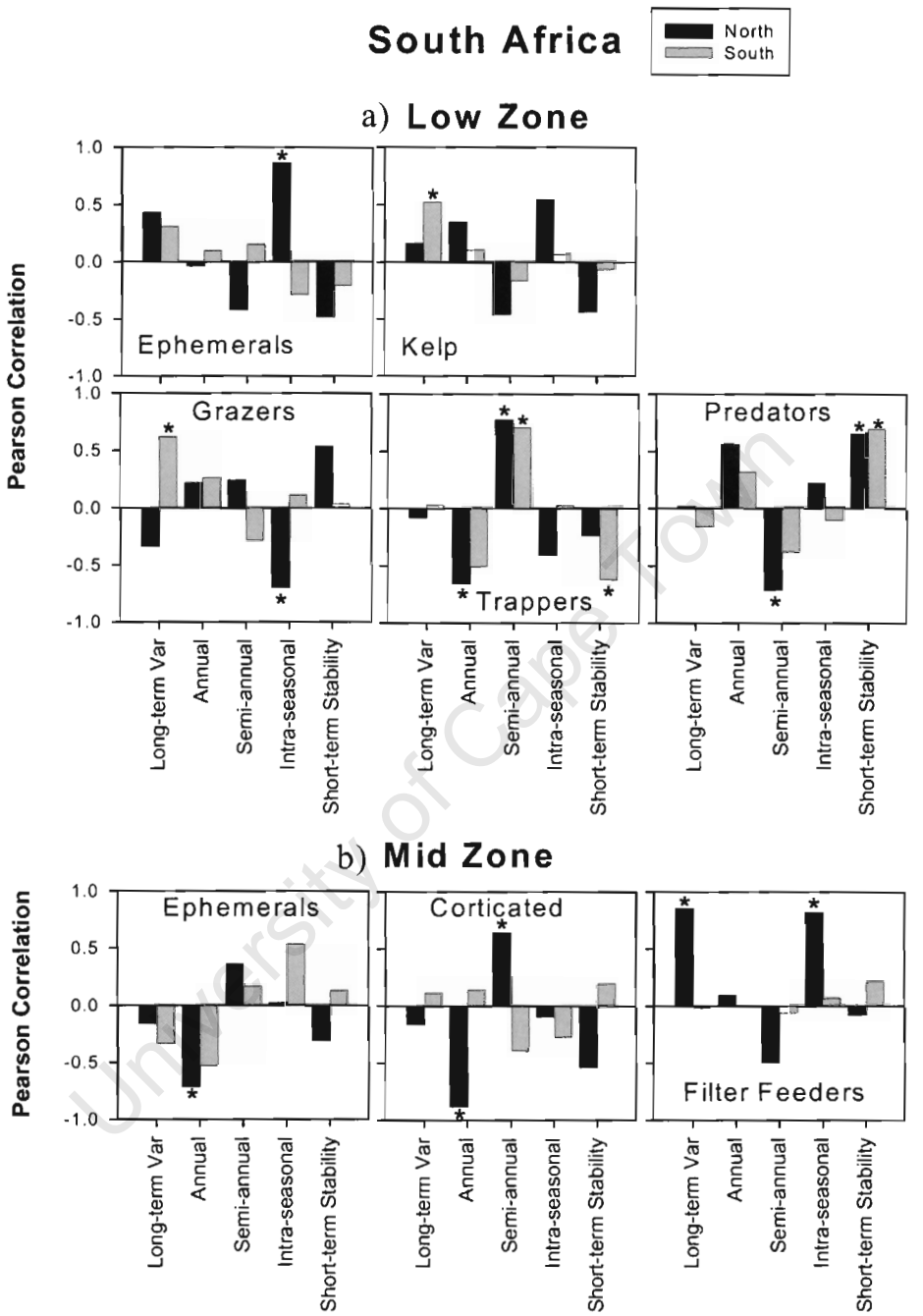


Fig. 2.16. Correlation coefficients between individual variables of SST dynamics and biomass of individual functional groups, north (black bars) and south (grey bars) of 32°S, on a) low and b) mid shores of South Africa. Stars indicate significant correlations ($p<0.05$). Functional groups were omitted if they lacked significant correlations.

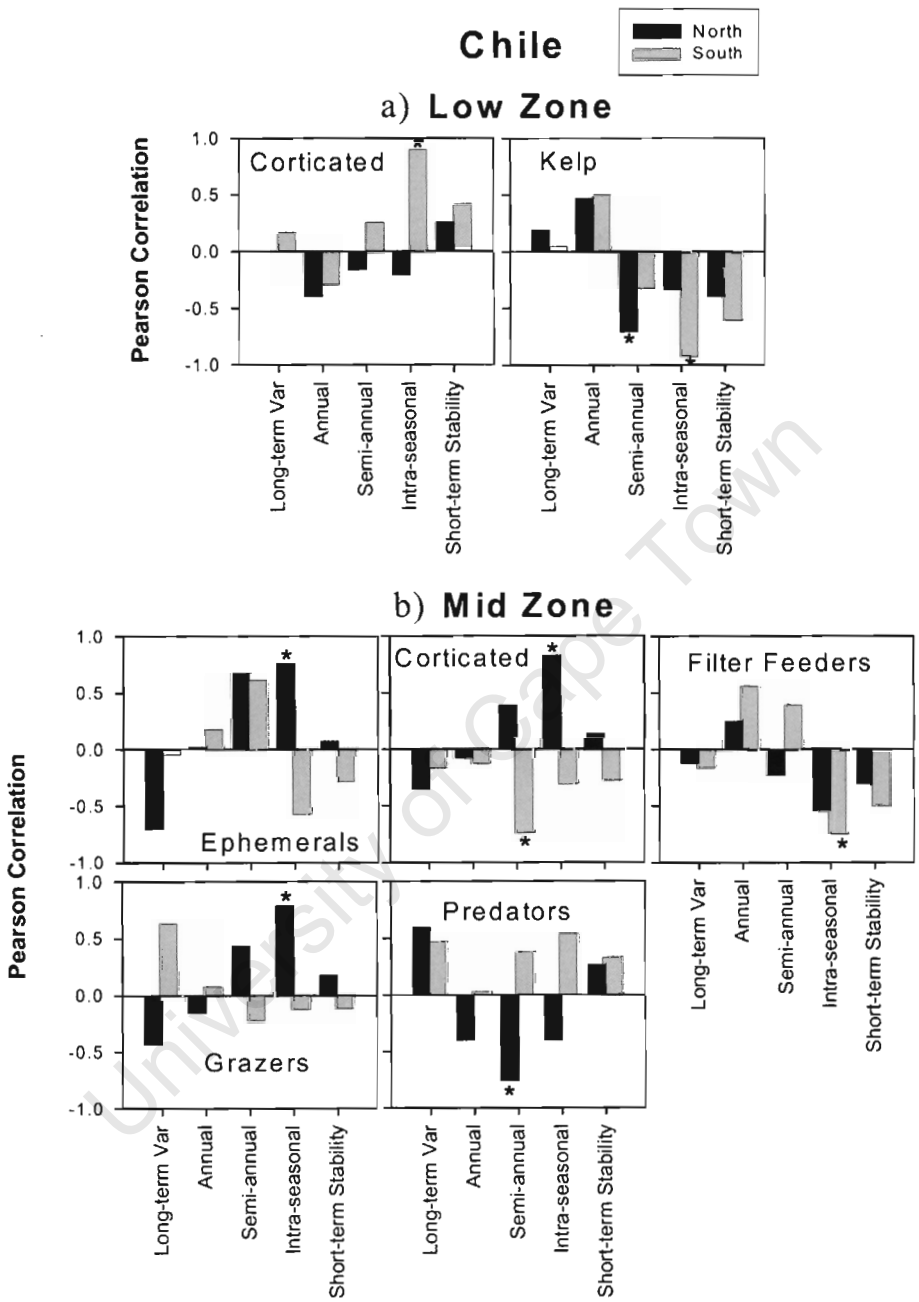


Fig. 2.17. Correlation coefficients between individual variables of SST dynamics and biomass of individual functional groups, north (black bars) and south (grey bars) of 32°S, on a) low and b) mid shores of Chile. Stars indicate significant correlations ($p<0.05$). Functional groups were omitted if they lacked significant correlations.

ephemeral algae, and grazers were observed at sites of increasing intra-seasonal SST pulsing, particularly north of 32°S. In the southern region, intra-seasonal oscillations appear to restrain biomass of filter feeders and kelp, which dominated the mid and low shores, respectively. Negative effects of the semi-annual cycle on kelp, as well as on mid-shore predators and corticated algae, were also significant. Similar to most other associations for both EBC systems, these negative relationships were observed across only part of the coast, with a discontinuity at 32°S.

2.4. **Discussion**

The physical forcing of upwelling along the Benguela and Humboldt EBCEs encompasses a broad range of time scales. The intensity, timing and duration of pulsed upwelling events (days) are modulated by inter-annual variability, as well as by cyclic, low-frequency annual (seasonal), semi-annual, and intra-seasonal oscillations that strongly interact to set the stage for biological productivity and shape biomass patterns. My results show that the intensity and relative importance of these different modulating fluctuations differ between the west coasts of South Africa and central Chile to produce unique thermal regimes. However, shifts in temporal variables of SST within each system create coincident discontinuities at ~32°S. Differences between regions north and south of this are most pronounced in South Africa but are also evident in Chile. In general, the spatial structure of thermal regimes was strongly coupled with patterns in the biomass of rocky intertidal communities, implying that nearshore hydrographic processes are important drivers of inter-EBCE and regional patterns of community structure. However, the dominant components of SST dynamics driving biomass varied greatly among functional

groups, and the strength and/or direction of responses to local conditions was often context-dependent. This suggests that local SST regimes may reflect very different mechanisms for nutrient replenishment, primary productivity, physiological stress, and/or particle transport.

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 (Figs. 2.2, 2.3). Third, Chile is characterized by relatively warmer, more stable dynamics, mainly influenced by fluctuations of relatively longer time-scales (in the order of several months). Several studies have shown that the coastal oceanography of Chile is dominated by large-scale circulation that produces important low-frequency variability that can strongly modify upwelling (e.g. Pizarro 1991, Shaffer et al. 1997, Hormazabal et al. 2001, Hormazabal et al. 2002, Carr & Kearns 2003). In contrast, South Africa is generally colder in the north and experiences greater extremes in thermal conditions that are more strongly pulsed over shorter time scales. These results are in agreement with previous studies showing that local forcing plays a more prominent role in South Africa, particularly in the southern Benguela (Enfield & Allen 1980, Shannon 1985, Carr & Kearns 2003, Hardman-Mountford et al. 2003).

Across the whole of the west coast, South Africa is also characterized by relatively stronger inter-annual variability, as observed by greater long-term variance in SST (Fig. 2.3a). This suggests that the large-scale episodic warm-cold extreme events caused by the "Benguela Niño" (sensu Shannon et al. 1986) and/or changes in the Agulhas retroflection,

or shedding of rings (Lutjeharms & Stockton 1987), may produce relatively greater thermal disturbances than the Pacific ENSO events that dominate inter-annual variability in Chile (Wyrtki 1975). In the period covered by the time series of this study, three Benguela Niño events (1984, 1995, and 1999) and two Agulhas interactions (1986 and summer of 1997-1998) are known to have influenced the Benguela upwelling system (Shannon 1985, Roy et al. 2001, Risien et al. 2004). Nelson and Hutchings (1983b) showed that inter-annual changes can double the wind effect from one year to the next.

Shared Discontinuity in Spatial Structure

Within both the South African and central Chilean EBCEs, shifts in the relative strength of annual and intra-seasonal cycles create latitudinal discontinuities, with regions north and south of ~32°S showing distinctive SST regimes. Regional differences in thermal dynamics were clearly identified in the principal component analyses (Figs. 2.5a). These results reflect the differing seasonal cycles of macro-scale wind-forcing driven by shifts in the high-pressure systems, the South Atlantic and Pacific Anticyclones (Shannon 1985). Indeed, winds and Offshore Ekman Transport in both systems are persistently upwelling-favorable throughout the year north of 32°S, whereas poleward they are typically downwelling-favorable during austral winter (Shannon 1985, Lutjeharms & Meeuwis 1987, Thomas 1999, Navarrete et al. 2005 and see Chapter 1).

Differences between regions north and south of 32°S are most pronounced in South Africa, where the southern region is characterized by important low-frequency signals, large among-site variability, and a broader range of thermal dynamics. These patterns likely reflect the impact of the diverse, transient, meso-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 (Gill 1977, Reason & Jury 1990, Risien et al. 2004). Warm-water tongues or advected eddies and rings from Agulhas origin can also modulate temperature in time scales from days to several months, but seldom penetrate north of 33°S. In addition, Risien et al. (2004) observed intra-seasonal variability (centered at around 40 days) in mid-latitude wind stress of the southern Benguela that they suggest is forced by wind events originating over eastern South America and propagating eastward across the Atlantic. It is notable that the mean de-correlation scale of SST observed in my study was around 35-40 days (Fig. 2.4).

Intra-seasonal oscillations along the coast of Chile appear to be mostly associated with free, coastal-trapped waves of equatorial origin propagating poleward (e.g. Shaffer et al. 1997). These occur at times scales of 50-120 days, which matches well the relatively longer de-correlation scales observed across Chile in my study (Fig. 2.4). The sharp change in the importance of low-frequency signals south of 32°S is likely related to the westward initiation of Rossby waves documented to occur around 33°S (e.g. Hormazabal et al. 2004). As Kelvin waves impinge upon the coast at the equator, they also cause local wind disturbances that propagate towards the south, generally on scales of about a month. The relative contribution of atmospheric or oceanic tele-connections along the central coast is still unclear.

Further inspection of the structure of the first principal component of SST variability reveals underlying differences in the dynamics distinguishing regions in the two EBCEs. The directional separation of southern regions relative to their northern pairs in PC1 are converse (Fig. 2.5a), largely due to opposing trends in mean SST (Fig. 2.2). The

southern region of South Africa is unique in that it is bounded by a warm current at relatively low latitude due to the termination of the continent. Shannon (1966) 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.

In short, a range of processes operating at different time scales contribute to the opposite latitudinal mean temperature gradients in South Africa and Chile and to the contrasts in conditions north and south of 32°S in both systems.

Biomass Responses to SST dynamics across EBCEs

Wave-exposed rocky intertidal communities of South Africa and Chile showed distinctly different biomass characteristics (Figs. 2.6 - 2.8). In addition, both EBCEs showed coincident, sharp divergence in community biomass at ~ 32°S. Individual functional groups, as well as multivariate descriptors of biomass variability, were consistently and highly correlated to principal components of SST dynamics across the EBCEs (Figs. 2.10, 2.11), suggesting that the regional and inter-EBCE differences in nearshore oceanographic processes are important drivers of observed biomass patterns. In general, the controlling component was most often related to intensification of the relative importance of short-scale (e.g. intra-seasonal, weekly) temporal fluctuations, as well as the large differences in inter-annual variation. However, whether such variability was

beneficial or disadvantageous to biomass accumulation depended upon the functional group considered (Figs. 2.10).

Amplification of pulse frequency and duration of SST and upwelling can have important implications for nutrient replenishment, as well as influencing larval supply to the shore (e.g. Shanks 1995, Shanks et al. 2000, Worm & Sommer 2000, Botsford 2001, Connolly et al. 2001, Navarrete et al. 2005). As observed in both EBCEs, variability at time frequencies below those typical for local wind forcing (e.g. intra-seasonal variability caused by free, coastal trapped waves) interact to change the average depth of the thermo/nutricline, modulating the effectiveness of nutrient pumping into the euphotic zone during local upwelling events (Shannon 1985, Shaffer et al. 1997, Hormazabal et al. 2001, Hormazabal et al. 2002, Hormazabal et al. 2004). The fact that increased weekly and low-frequency SST pulsing consistently disfavored macroalgae (see Fig. 2.9 and PC1 in Fig. 2.13) could be a result of nutrient re-supply. Persistent, year-round upwelling with little modification by remote or local pulsing mechanisms may provide more reliable, repeated replenishment of nutrients, such that nutrient limitation of primary production is rarely attained. Indeed, long exposure of macroalgae to elevated nutrients is necessary to raise internal levels to a critical point to be beneficial for growth (Fujita et al. 1989, Pedersen et al. 1995, Pedersen & Borum 1996, Worm et al. 2000) and more consistent enrichment can favor the intensity and duration of algal growth and production (e.g. Neckles et al. 1993, Worm et al. 2000). In contrast, greater temporal variability in nutrient supply over weeks to months can restrict algal growth responses (e.g. Rosenberg et al. 1984, Worm & Sommer 2000).

Increased pulsing frequency of temperature and/or nutrients across EBCEs and regions are also likely to interact with light to influence algal performance (e.g. Richardson

et al. 1983, Beardall et al. 1998, Lotze & Worm 2002, Thompson et al. 2004). According to Carr & Kearns (2003), South Africa is characterized by generally higher satellite-measured photosynthetically available radiation during most of the year and therefore may experience higher UV radiation stress. UV radiation can directly alter nutrient uptake, pigment composition and photosynthetic performance in plants (e.g. Franklin & Forester 1997), particularly under changing nutrient and/or temperature conditions. Therefore, the more variable SST conditions along the South African coast may additionally cause plants to be more susceptible to limitation by physiological stresses.

The differential responses of low-shore algal functional groups to changes in thermal regimes (Figs. 2.9, 2.10; black bars) may be related to differences in competitive abilities in the face of nutrient enrichment. Changes in nutrient pulsing regimes are expected to affect algal functional groups differentially, since they differ in morphology, tissue chemistry and ability to store nutrients (Worm et al. 2000). Indeed, several experimental studies have found that the direct impacts of enhanced nutrients depend upon the functional group considered (Nielsen 1998, Worm et al. 2000, Nielsen 2003). Thus, small modifications of upwelling may disproportionately enhance growth and/or reproduction of some algae, which then exclude or limit the performance of others in competitive situations, or enhance their performance if the relationship is facilitative. Such indirect controlling mechanisms are particularly likely to constrain corticated macroalgae, as well as mid-shore ephemerals, since responses of these groups strongly opposed those of their dominant space competitors, namely kelp in the low zone and invertebrate filter feeders on mid shores (Figs. 2.10). Competitive interactions between these groups have been experimentally demonstrated at several sites along the coast of Chile (Ojeda & Santelices 1984, Camus 1994).

The consistently strong and opposing responses of herbivores and kelp to SST dynamics (Figs. 2.9, 2.10) suggest prevailing top-down grazing effects may limit kelp biomass between EBCEs. Indeed, in South Africa much of herbivore biomass on low shores reflects the presence of specialized limpets that trap live kelp fronds through "mushrooming" behavior (Branch & Branch 1981, Bustamante et al. 1995a). However, similar results were observed when considering grazers alone. Temperature directly affects metabolic rates of consumers, which can drive changes in feeding rates (Newell & Branch 1980, Stickle et al. 1985). Recently, Sanford (1999, 2002b) found that variation in the frequency and intensity of upwelling along the Oregon coast alters foraging rates by a key consumer, with community-wide consequences. However, the relative importance of such interspecific interactions driving biomass shifts in kelps and their herbivores across South Africa and Chile are difficult to evaluate due to between-system differences in the habitat requirements of species. In Chile, kelp biomass is dominated by *Lessonia nigrescens*, a true intertidal kelp. In contrast, kelps found intertidally in South Africa are individuals at the edge of their vertical range, as the bulk of the populations of these species (mainly *Ecklonia maxima* and *Laminaria pallida*) form large subtidal forests. Thus, it is unlikely the differences in kelp biomass between systems are due to top-down control by grazers.

Enhanced pulsing of SST and upwelling can also strongly influence larval transport onshore (Shanks et al. 2000, Botsford 2001). Navarrete et al. (2005) found clear, persistent differences in recruitment of intertidal mussels and barnacles between regions north and south of 32°S along central Chile, which they attribute to abrupt changes in upwelling regimes. Larvae of many invertebrates can be entrained in offshore-moving, newly-upwelled waters, so that their delivery and settlement onshore occurs when upwelling relaxes (Small & Menzies 1981, Farrell et al. 1991, Wing et al. 1995b, Shanks et al. 2000).

Indeed, under consistent and year-round upwelling, with little low-frequency modification, fewer opportunities for onshore transport exist (Navarrete et al. 2005). This mechanism may also account for differences observed between EBCEs, as filter feeders (predominantly mussels and barnacles) were most abundant where weekly, short-term variability was greatest (i.e. low short-term stability, Fig. 2.9; PC1 and PC2, Fig. 2.10). Moreover, maximum Ekman transport (during spring) appears to be higher off Chile (Carr & Kearns 2003), whereas the broader continental shelf off South Africa may enhance coastal water retention. Indeed, onshore daily recruitment rates of mussels, which were estimated using the same artificial substrates as part of complementary on-going studies, are on average higher across sites in the southern region of South Africa than that of Chile (mean ± SE; South Africa = 3.85 ± 1.36, Chile = 0.82 ± 0.27; M. Pfaff and S. A. Navarrete, unpublished data). However, differences in recruitment rates may also reflect differences in reproductive output or larval survival over these scales. Phytoplankton (chlorophyll-a) concentrations are reported to be consistently higher off South Africa (Shannon & Field 1985, Brown 1992, Ware 1992, Thomas et al. 2001b, Carr 2002) and therefore could translate into increased food that enhances reproductive output or larval condition. Recent studies of mussel growth rates across subsets of these same study sites suggest that spring-summer growth is relatively higher in southern regions of South Africa than Chile (Navarrete et al. in prep, Xavier et al. in prep.). Whatever the mechanisms, greater temporal variability seems to favor filter feeders.

Changes in productivity rates may also interact with predation intensity to produce the observed pattern of filter feeder biomass. Indeed, filter feeders and predators showed strongly opposing responses to the same descriptors of environmental variation (Fig. 2.9, 2.10). Numerous studies have demonstrated the strong influence of key predators (e.g.

Concholepas concholepas and *Heliaster helianthus*) on mussel abundance across central Chile (Castilla & Duran 1985, Castilla et al. 1985, Paine et al. 1985, Castilla & Paine 1987, Navarrete & Castilla 2003, Navarrete et al. 2005), whereas predators appear to have a relatively weak impact in controlling mussels on South African shores (reviewed by Branch & Griffiths 1988).

Variation in larval retention and/or transport is not a likely cause of the negative association of predator biomass with different SST regimes. The main predators in South Africa are predatory whelks (i.e. *Nucella* and *Burnupena*), which are direct developers with crawl-away larvae that are born and live in the same habitat as adults (Bokenham & Neugebauer 1938). In contrast, the diverse suite of rocky shore predators along central Chile have pelagic larvae with long-distance dispersal.

Biomass Responses to SST dynamics within EBCEs

Nested within the basin-wide differences described above, large variation in SST regimes and community biomass also occurs alongshore within each EBCE. Consistent relationships between the local temporal dynamics of SST and biomass were observed. In South Africa, all low-shore algae appeared to benefit from more stable thermal conditions dominated by strong inter-annual variation, whereas grazers appeared constrained by higher-frequency fluctuations (Fig. 2.13). Kelp-trapping limpets and predators both responded to yet a different component of SST variability (Fig. 2.13a). These results suggest that local changes in hydrographic conditions set the stage for trophic dynamics on the low shore and may have important consequences for species interactions.

Across Chile, filter feeder biomass on mid shores was linked to increased modification of upwelling, with higher biomass observed where intra-seasonal variation was strongest. This was likely due to increased recruitment rates of mussels where upwelling relaxation events occur more frequently (Navarrete et al. 2005). This can have important indirect effects on the community, since mussels are the dominant competitors for space on the mid shore. Indeed, competition may constrain the local abundance of kelp on the mid shore, as I suggested by the opposite patterns of response observed by these groups (Fig. 2.12b).

Biomass Responses to SST dynamics north and south of 32°S

My results also highlighted sharp discontinuities in SST regimes (Figs. 2.5) and community biomass (Figs. 2.8) within each EBCE, which coincided at around 32°S. Perhaps even more striking, functional groups occupying northern and southern regions showed marked differences in their responses to alongshore variation in local SST dynamic regimes (Fig, 2.14 - 2.17). In South Africa, structure of multivariate descriptors of intertidal community biomass on low shores appeared more tightly coupled to changes in environmental conditions across the northern region than the southern region (Fig. 2.14). Indeed, all functional groups, with the exception of kelp, were spatially correlated with variables of SST dynamics across the north (Fig. 2.16). The strong and opposing responses of ephemeral macroalgae and grazers to similar scales of temporal variability suggests that pulsing of SST at intra-seasonal scales has important implications for the responses of primary producers and their consumers. Predators and kelp-trapping limpets also showed consistently opposite patterns in their response to SST variability. Given the large size and

aggressive behavior that these limpets invoke in response to potential predators, lifting up their shells and slamming down to crush them (Branch 1979), it is unlikely that tight bottom-up/top-down effects are driving these patterns. Across northern mid shores, ephemeral and corticated algae reacted similarly, with strong negative relationships with increased importance of the annual cycle. Here, where upwelling is largely persistent year-round, increasing seasonality in upwelling may cause marked changes in the consistent supply of nutrients (see above).

Similar between-region differences were observed across Chile, suggesting the causes may be general to EBCEs. While local biomass of filter feeders and low-zone corticated algae showed significant links to SST variation in the south, ephemerals, grazers and predators were more tightly linked to the local thermal regimes in the north. As stated earlier, Navarrete et al. (2005) documented a sharp discontinuity in upwelling regimes at 32°S that produces abrupt and persistent breaks in benthic community dynamics, such that top-down control by predators regulates communities to the south, but northern communities appear recruitment-limited and predators play little role. My results suggest that the regional change in SST regimes may further frame algal-herbivore interactions. The strong and similar responses of mid-shore ephemeral and corticated macroalgae, as well as grazers, to local SST variability suggests that bottom-up effects may be important in determining local, among-site variation in biomass in the north, but not the south (Fig. 2.17). This hypothesis is amenable to experimentation.

2.5. **Conclusions**

In general, my results suggest that differences in SST regimes observed across basin-wide, regional, and meso-scales reflect very different mechanisms for nutrient replenishment, primary productivity, physiological stress, and particle transport, with important consequences for benthic-pelagic links. These may then modify species interactions and community regulation, setting bounds to community structure (Navarrete et al. 2005). This is the focus of my next chapter, in which I examine the effects of upwelling intensity on the morphology of a specific algal turf, and the influence of this and predation on mussel recruitment.

Table 2.1. Weights and statistics of principal components for SST regimes and community biomass structure across a-b) both EBCEs, c-d) within the South African coast, and e-f) within the central Chilean coast.

SST Regimes

a)

Across EBCEs	PC1	PC2	PC3
Eigenvalue	3.13	1.98	0.40
Percent	52.17	33.06	6.60
Cum Percent	52.17	85.23	91.83
Lag-1 Autocorrelation	-0.43	-0.38	0.43
% intra-seasonal	0.43	-0.35	0.47
% semi-annual	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

c)

South Africa	PC1	PC2	PC3
Eigenvalue	3.15	1.33	0.94
Percent	52.50	22.14	15.74
Cum Percent	52.50	74.62	90.35
Lag-1 Autocorrelation	0.40	0.52	-0.04
% intra-seasonal	0.50	-0.04	0.27
% semi-annual	0.44	-0.48	0.07
% annual	-0.51	0.30	-0.11
Long-term variance	-0.18	0.15	0.95
Mean sst	0.33	0.62	-0.08

e)

Chile	PC1	PC2	PC3
Eigenvalue	2.31	1.77	0.99
Percent	38.48	29.45	16.60
Cum Percent	38.48	67.93	84.54
Lag-1 Autocorrelation	0.08	0.72	-0.13
% intra-seasonal	-0.44	0.24	0.15
% semi-annual	0.29	0.13	0.87
% annual	0.33	-0.52	-0.17
Long-term variance	0.48	0.006	0.12
Mean sst	0.62	0.37	-0.40

Community Biomass Structure

b) Low Zone

Across EBCEs	PC1	PC2	PC3
Eigenvalue	2.10	1.56	1.00
Percent	34.92	25.94	16.68
Cum Percent	34.92	60.86	77.54
Ephemerals	0.30	0.35	0.66
Corticated	0.39	0.44	0.16
Kelp	-0.34	0.63	0.04
Filter Feeders	0.32	-0.51	0.48
Predators	-0.50	-0.11	0.44
Herbivores	0.54	0.09	-0.33

d)

South Africa	PC1	PC2	PC3
Eigenvalue	2.44	1.54	1.29
Percent	34.84	22.03	18.49
Cum Percent	34.84	56.87	75.36
Ephemerals	0.27	0.61	-0.33
Corticated	0.47	0.40	-0.01
Kelp	0.43	-0.12	-0.29
Filter Feeders	-0.40	0.50	-0.04
Grazers	-0.09	0.17	0.71
Trappers	0.37	0.22	0.53
Predators	-0.47	0.36	-0.15

f)

Chile	PC1	PC2	PC3
Eigenvalue	2.15	1.63	0.94
Percent	35.91	27.17	15.64
Cum Percent	35.91	63.07	78.71
Ephemerals	-0.15	0.55	0.10
Corticated	-0.49	-0.38	0.32
Kelp	0.16	0.59	0.48
Filter Feeders	-0.31	0.44	-0.52
Predators	0.53	-0.05	-0.51
Herbivores	0.58	-0.06	0.35

Mid Zone

Across EBCEs	PC1	PC2	PC3
Eigenvalue	2.29	1.36	0.80
Percent	38.13	22.71	13.27
Cum Percent	38.13	60.83	74.10
Ephemerals	0.47	-0.20	0.14
Corticated	0.56	0.18	0.20
Kelp	0.44	0.30	0.48
Filter Feeders	-0.44	0.05	0.68
Predators	-0.07	-0.69	0.45
Herbivores	-0.27	0.59	0.21

South Africa	PC1	PC2	PC3
Eigenvalue	2.02	1.40	1.32
Percent	28.79	20.03	18.81
Cum Percent	28.79	48.82	67.62
Ephemerals	0.36	-0.22	0.44
Corticated	0.54	0.01	0.28
Kelp	0.42	0.36	0.23
Filter Feeders	-0.25	0.55	0.48
Grazers	-0.14	0.66	-0.21
Trappers	0.46	0.29	-0.27
Predators	-0.33	-0.05	0.57

Chile	PC1	PC2	PC3
Eigenvalue	2.31	1.80	0.93
Percent	38.45	30.06	15.54
Cum Percent	38.45	68.51	84.05
Ephemerals	-0.08	0.49	-0.68
Corticated	0.56	0.30	-0.13
Kelp	0.45	0.24	0.53
Filter Feeders	-0.01	-0.65	-0.07
Predators	-0.41	0.41	0.48
Herbivores	0.55	-0.14	-0.05

Chapter 3

Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores

3.1. Introduction

Direct positive interactions that result from biotic habitat modification have recently received renewed attention (Stachowicz 2001, Bruno et al. 2003), revitalizing facilitation as a critical force structuring many communities and increasing diversity. The physical presence of facilitators assists other species in a wide variety of ways, including enhancement of population size, growth rate, distributional range, or individual fitness (see Bruno & Bertness 2001, Stachowicz 2001 for review). However, complex combinations of positive and negative interactions often operate between species, and their net outcome (positive, neutral or negative) can vary over space and time (Callaway & Walker 1997, Holmgren et al. 1997, Jones et al. 1997). Factors that shift the balance from positive to negative are poorly understood, but it is expected they will ultimately be intertwined with environmental conditions (Bronstein 1994).

Population or individual traits of a facilitator can also affect whether (or how much) it modifies the environment, determining the degree to which other species benefit. For example, increased density and architectural complexity of plants often increases abundance and diversity of associated organisms, whether in the sea (Gee & Warwick 1994, Levin & Hay 1996, but see Kelaher 2003a for negative relationships), in freshwater systems (Jeffries 1993) or on land (Callaway & Walker 1997). Therefore, factors

controlling such traits can ultimately determine the relative balance of costs and benefits of interactions between species. Yet, in most systems we still know little about the spatial and temporal scales of variability in such traits, and even less about the processes causing such variation. Despite this scarcity of information, Bruno & Bertness (2001) have speculated that trait-dependent facilitation may be driving a number of landscape patterns in marine communities.

A common positive interaction on rocky shores is facilitation generated by the physical habitat created by turf-forming algae. Algal turfs are important components of intertidal and subtidal communities worldwide, sometimes dominating extensive areas of the shore (Stephenson & Stephenson 1972, Santelices 1989, 1991, Boaventura et al. 2002). Turf-forming species show considerable morphological plasticity, and the physical structure of these biogenic habitats can alter turbulence and flow velocity (Eckman 1983), sediment and particle trapping (Kelaher 2003b, Prathep et al. 2003), and moisture retention (Hay 1981, Taylor & Hay 1984). Therefore, morphological traits can change the environment and have a major influence on associated assemblages by providing substrate for settlement and recruitment of invertebrates (Eckman 1983), refuge from predators (Moreno 1995), shelter from desiccation (Hay 1981) and protection from wave forces (Whorff et al. 1995).

Along the rocky, wave-exposed shores of central Chile, algal turfs, composed largely of *Gelidium chilense* (hereafter *Gelidium*), form distinct and often extensive bands in the low intertidal zone (Santelices 1989). Previous studies have revealed that *Gelidium* turf facilitates recruitment of mussels, including the competitively dominant mussel *Perumytilus purpuratus* (E. Wieters, S. Navarrete, B. Broitman, unpublished data). Because mussels cannot settle on smooth rock surfaces (Navarrete & Castilla 1990a), the

presence of some complex substrate that facilitates recruitment is critical for their successful colonization (Navarrete & Castilla 2003). Moreover, since mussels are the competitive dominants of the mid and low intertidal zones (Castilla & Duran 1985, Navarrete & Castilla 2003), such facilitation can have important consequences for community regulation. However, the height and morphology of turf vary greatly among sites along the coast (Santelices 1989, personal observations), which could influence the magnitude or nature of turf-mussel interactions.

Although diverse processes can affect macroalgal morphology, temperature and nutrient-induced changes in size and biomass have been highlighted in experimental and correlational studies in several coastal systems (Bosman et al. 1986, Bustamante & Branch 1996b, Nielsen 2001, Blanchette et al. 2002). Temperature and nutrient supply in marine systems are driven by nearshore oceanographic conditions, and along the coast of central and northern Chile the main process is seasonally-variable, wind-driven upwelling that draws cold, nutrient-rich waters to the surface (Strub et al. 1998, Poulin et al. 2002a, Poulin et al. 2002b, Narváez et al. 2004). However, considerable alongshore variation in surface temperature and nutrient availability over scales of few to tens of kilometers is characteristic of such coastal systems (Shannon 1985, Strub et al. 1998), with upwelling intensity varying according to topography and coastline orientation (Jury 1985, Kelly 1985, Figueroa & Moffat 2000). In central Chile, Broitman *et al.* (2001) have shown that this meso-scale spatial variation in upwelling can influence patterns of abundance (cover) of some algal functional groups. Nielsen & Navarrete (2004) showed that growth rates of the red alga *Mazzaella laminarioides* is faster at upwelling centers than elsewhere.

In this study, I explored: (1) whether the turf-forming alga *Gelidium chilense* varies in size (height) over a geographic region of ~900 km in central Chile; (2) whether the

growth rate and height of these turfs can be related to local differences in environmental conditions linked to upwelling focal points; (3) if height of the algae influences their effects on mussel recruitment. To my knowledge, this is the first set of data that documents the physical factors generating environmental conditions that control trait-dependent habitat modification and facilitation over geographic scales in benthic marine communities.

3.2. **Methods**

The System and Sites

Studies were conducted along the open, high-energy coast of central Chile, which is characterized by large meso-scale variation (10s-100s km) in sea surface temperature, particularly during spring and summer (Strub et al. 1998, Wieters et al. 2003, Narváez et al. 2004). The localized nature of upwelling along central Chile is easily observed in thermal imagery (AVHRR) and onshore temperature measurements (Broitman et al. 2001, Poulin et al. 2002b, Wieters et al. 2003, Narváez et al. 2004, Nielsen & Navarrete 2004). Areas of cold water nearshore correspond to localized upwelling centers, where clear, nutrient-rich waters are forced to the surface and rapidly advected away from shore. In contrast, areas downstream from such cells are characterized by warmer water that has been near-surface for a few days. This aged surface water is depleted of nutrients by photosynthetic activity, but supports higher chlorophyll-a concentrations (Wieters et al. 2003). The main upwelling centers within this region (Fig. 3.1) include Punta Roncura-Toro (Pichilemu, Bucalemu), Punta Curaumilla (Curaumilla, Quintay), and Punta Lengua de Vaca (Talca), which have all been previously identified and described in the literature (Johnson et al. 1980, Fonseca & Farías 1987, Paolini & Barría 1999, Bello 2001). Warmer downstream areas correspond to Las Cruces (ECIM), Tunquen, Montemar, Guanaqueros, and Temblador (Broitman et al.

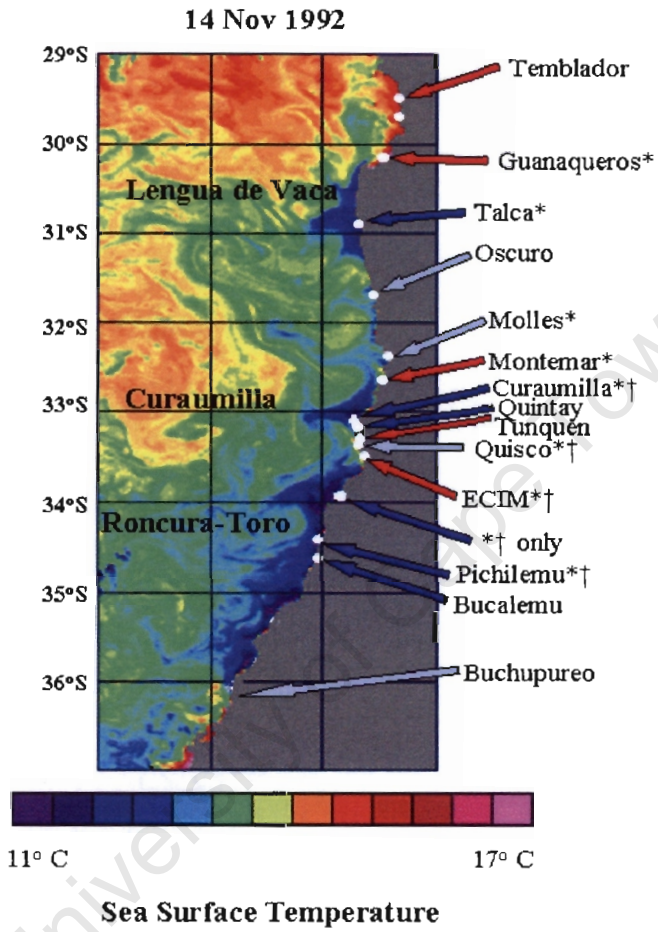


Fig. 3.1. AVHRR (Advanced Very High Resolution Radiometer) satellite image of sea surface temperature, also showing locations of field sites. Alongshore variation in temperature reflects the existence of cold upwelling centers with warm downstream areas in between. Asterisks indicate sites with *in situ* temperature loggers. Crosses indicate sites where nutrient samples were collected. Dark blue arrows = upwelling centers, light blue arrows = intermediate upwelling, red arrows = downstream sites.

2001, Poulin et al. 2002a, Poulin et al. 2002b, Wieters et al. 2003, Narváez et al. 2004, Nielsen & Navarrete 2004). Buchupureo, Quisco, Molles and Oscuro are areas of intermediate upwelling intensity, as upwelling only occurs there during persistent, strong southerly winds (e.g. Poulin et al. 2002a, Narváez et al. 2004).

My studies were conducted in the low intertidal zone of rocky outcrops with approximately similar slope (20-30°) and high wave exposure. In general, extensive areas (65-80%) of the low intertidal zone at all sites were covered by a patchy mosaic of *Gelidium* turf and fleshy crustose algae (largely *Hildenbrandia* sp.), particularly in situations not directly exposed to strong wave action. Only Pichilemu and Bucalemu supported a more diverse macroalgal assemblage in the low zone (E. Wieters, unpublished data), but large monocultures of *Gelidium chilense* were still predominant there (~ 30% cover).

Sea Surface Temperature and Nutrient Concentrations

To characterize the physical environment and shed light on potential mechanisms driving variation in growth and/or morphology of *Gelidium* turf, I recorded onshore sea surface temperature (SST) at eight sites along the coast (noted with asterisk in Fig. 3.1) that were expected to vary in upwelling intensity. Throughout the study, surface water temperature was recorded at 20-min intervals with Optic Stowaway® (Onset Computer Corp., Fourne, MA, USA, ± 0.1° precision) submersible temperature loggers placed at approximately 1-m depth below the lowest low tide at sites indicated with asterisks in Fig. 3.1.

Sea surface temperature is often used as a proxy for nutrient (nitrate) concentrations. To validate the relationship between SST and nitrate concentrations in onshore waters within the region, shore-based water samples were simultaneously collected at five sites (noted with † in Fig. 3.1) on four dates. On each sampling date, three water samples were taken from each of three benches (separated by 10s of meters) at each site, and this sampling scheme was repeated two times on each sampling date. Water samples were taken from 20-40 cm depths using 3 x 250 ml acid-washed plastic (high density polyethylene) dark bottles. Immediately after collection, 100 ml from each sample was filtered through a combusted GF/F Whatman glass fiber filter using a syringe and inline filter holder, and the filtrate was packed in ice and transported to the laboratory, where it was frozen until later analysis of nitrate and nitrite using a Traacs autoanalyzer (Bran+Luebbe Inc., Norderstedt, Germany).

Geographic Variation in Turf Height

To characterize meso-scale spatial variation in algal height, I surveyed 14 sites separated by 10s to 100s of kilometers and stretching across 7° of latitude (see Fig. 3.1). Sites were chosen according to their proximity to major upwelling centers: five sites at known upwelling centers (Bucalemu, Pichilemu, Quintay, Curaumilla, Talca), five at "downstream" locations not directly affected by upwelling (ECIM, Tunquen, Montemar, Guanaqueros, Temblador), and four in intermediate conditions (Buchupureo, Quisco, Molles, Oscuro).

"Divet" samples were taken from the natural turf at each site during spring/summer of 2002-2003. Within the low intertidal zone, 8-10 samples of approximately 16-25 cm^2 turf were haphazardly collected across two rock benches at each site. Divets were taken

from areas with 100% *Gelidium* cover and all turf was removed, including holdfasts. In the laboratory, 10 intact fronds (with holdfasts) were randomly chosen from each sample and their maximum lengths measured to the nearest 0.1 mm. Mean frond length was calculated for each divet and analyzed using ANOVA. Upwelling condition was considered a fixed factor, whereas site was considered a random factor (replicates) nested within upwelling condition. Visual inspection of the residuals plotted against predicted values revealed variances were homogeneous, and normality was tested using Shapiro-Wilk W test.

Turf Growth Rates

To determine differences in growth rates among sites with different turf height, I conducted transplant experiments on four different occasions, covering the four seasons in 2002, at two sites, Pichilemu (an upwelling center) and ECIM (a downstream site). To then assess whether turf growth rates varied predictably along the coast, depending on proximity to upwelling centers, I conducted two further transplant experiments in the austral winter and spring, 2003 that included nine sites stretched across a broad geographic region (Fig. 3.1): four sites at known upwelling centers (Bucalemu, Pichilemu, Curaumilla, Talca), three sites at "downstream" locations not directly affected by upwelling (ECIM, Montemar, Guanaqueros), and two sites of intermediate upwelling (Quisco, Molles).

By transplanting turf originating from a single location, I was able to avoid potential confounding effects of spatial and temporal differences in turf morphology, physiology (e.g. nutrient reserves) and reproductive status. From a site lying between ECIM and Quisco, I collected large (7–10 cm) keyhole limpets, genus *Fissurella*, whose shells were naturally covered (80-100 %) with short (5-10 mm), non-reproductive *Gelidium chilense*. Flesh was removed from the shells and the inner cavity of each shell was filled with marine

epoxy to reduce breakage. Shells were then numbered and transplanted into the low intertidal zone, fixing them to the rock surface with a stainless steel screw that fit through the "keyhole" of the shell. To reduce possible effects of herbivory, shells were placed atop a tube 1.5 cm in diameter and 3 cm tall. Ten shells were randomly placed in natural patches of turf at each site.

Growth in the genus *Gelidium* results from activity of apical cells. However, individual plants are difficult to identify, and growth often occurs via regeneration of erect fronds from creeping axes. Differences in growth might therefore be expressed as changes in frond length, frond density, or spatial extension. Therefore, I measured frond elongation rates, as well as changes in biomass. Before transplant, and again at the end of each growth trial, each shell was photographed and two small (1-3 cm^2) samples of turf were removed from a) the center and b) edges of each limpet shell. The two areas of the shell were sampled to determine if there was any spatial variation in turf growth at a scale of centimeters. In each case, the area sampled was measured and the turf was blotted dry and weighed. Ten intact fronds (with holdfasts) were randomly chosen from each sample and measured to the nearest 0.1 mm. There are no data available for Quisco during spring 2003, as all transplanted turf were lost, presumably due to human interference.

Data Analysis: Since in each trial new shells were transplanted to new positions at each site, the different trials were independent and considered as a fixed factor ('season') in ANOVA. In all trials, there were no significant differences in growth rates between samples from center and edge of shells ($P > 0.62$ in all occasions), which were then averaged and considered as subsamples within each shell. Results for turf transplant experiments at Pichilemu and ECIM during 2002-2003 were analyzed using a two-way ANOVA with site and season considered as fixed effects. Results for transplants across the

larger geographic region were analyzed considering trial ('season') and upwelling condition as fixed factors and site as the replicates (random factor) nested within upwelling condition. In all cases, results for changes in frond length and biomass were equivalent; therefore, for simplicity, I present only frond elongation rates.

Effect of turf height on mussel recruitment

To test whether between-site differences in turf height (tall vs. short) modify its facilitative augmentation of mussel recruitment, I conducted a replicated, reciprocal transplant experiment between ECIM and Pichilemu during the austral summer (January-March), 2003. Rock pieces (~150-200 cm^2) covered with 80-100% *Gelidium chilense* were collected from sites that had either tall turf (~ 4cm, Pichilemu) or short turf (< 1 cm, ECIM). Rocks were then transplanted into the low intertidal zone by gluing them to the surface using a non-toxic submarine epoxy (Super As®, Santiago, Chile). Turf transplants were placed within natural turf beds, where I carefully scraped and chipped the surface in order to embed each transplant flush with the natural rock surface. Treatments included turf from (a) Pichilemu or (b) ECIM re-planted in their original sites to control for disturbance effects, (c) turf from Pichilemu transplanted to ECIM and (d) vice versa. Field observations suggested small mussel recruits dominate the diet of the predatory seastar *Heliaster helianthus* in the low zone, which may influence mussel colonization. Therefore, to determine potential interactive effects of turf height and predators on mussel recruitment, I combined transplants of tall/short algal turf with manipulations that controlled predator access to the plots. Predators were either (a) allowed free access to otherwise undisturbed transplants or (b) excluded by installing a 30 x 30 cm domed, plastic mesh cage. Potential

effects of the cage itself were evaluated by installing a two-sided mesh dome that provided similar shading and flow alteration as cages, while still allowing access to predators. Five replicates of all treatments were assigned in a completely randomized design. All treatments at both sites were installed within the same low tide series; thus, temporal effects were not counfounded. Percentage cover of all sessile species within the transplant was monitored each month, but duration of the experiment was limited to 3 months because turf height responded quickly to local environments, nullifying the intended treatments after this time. Translocating turfs to multiple sites (in addition to ECIM and Pichilemu) simultaneously proved to be logistically impossible, largely due to the rapid morphological changes of the turf to their new environment and the amount of time required to extract, transport, and install turf transplants. Likewise, attempts to shorten existing tall plants dramatically changed turf morphology, rendering them distinct from naturally short turf, and resulted in replacement by other species.

Data Analysis: In some treatment combinations with tall turf, the effects were so strong that there were no mussels in any replicate at the end of the experiment (see Results), which precluded statistical analyses of the complete experiment. Therefore, I restricted statistical analysis to short turf treatments. Mussel cover after 3 months was analyzed with a two-way ANOVA, with site and predator access considered fixed factors. Data were transformed (ln (x+1)) to meet model assumptions, which were checked by visual inspection of the residuals plotted against predicted values and the Shapiro-Wilk W test for normality.

3.3. **Results**

Sea Surface Temperature and Nutrient Concentrations

Onshore nitrate concentrations were strongly, inversely related to SST (Fig. 3.2 and see Fig. 1b in Nielsen & Navarrete 2004). Strikingly, 81% of the variation in onshore nitrate concentrations along the central Chilean coast was explained by a simple measure of SST.

Consistent among-sites differences in onshore daily mean sea surface temperature (SST) were repeated alongshore, following spatial patterns of upwelling intensity along the coast (Fig. 3.3). ECIM had consistently warmer temperatures than the colder conditions at Pichilemu (Fig. 3.3a), Montemar was consistently warmer than Curaumilla (Fig. 3.3b) and Guanaqueros consistently warmer than Talca (Fig. 3.3c). Temperatures at Quisco and Molles (squares in Fig. 3.3) were intermediate to their proximate upwelling centers and downstream sites. During the first growth trials in 2002, the differences in SST between ECIM and Pichilemu persisted (Fig. 3.4a) and were similar to differences observed among other sites along the coast. Differences among sites were most pronounced during spring, when downstream sites (ECIM, Montemar, Guanaqueros) showed marked seasonal warming in contrast to the overall colder temperatures that resulted from more frequent and prolonged temperature drops at upwelling centers (Pichilemu, Curaumilla, and Talca; Figs. 3.3 and 3.4a). Likewise, cooling events at the downstream sites of Montemar and Guanaqueros were smaller in magnitude, brief, and lagged behind those at the corresponding upwelling sites at Curaumilla and Talca, respectively. These patterns of alongshore variability in upwelling frequency and intensity were also apparent in AVHRR satellite images (e.g. see Fig. 3.1).

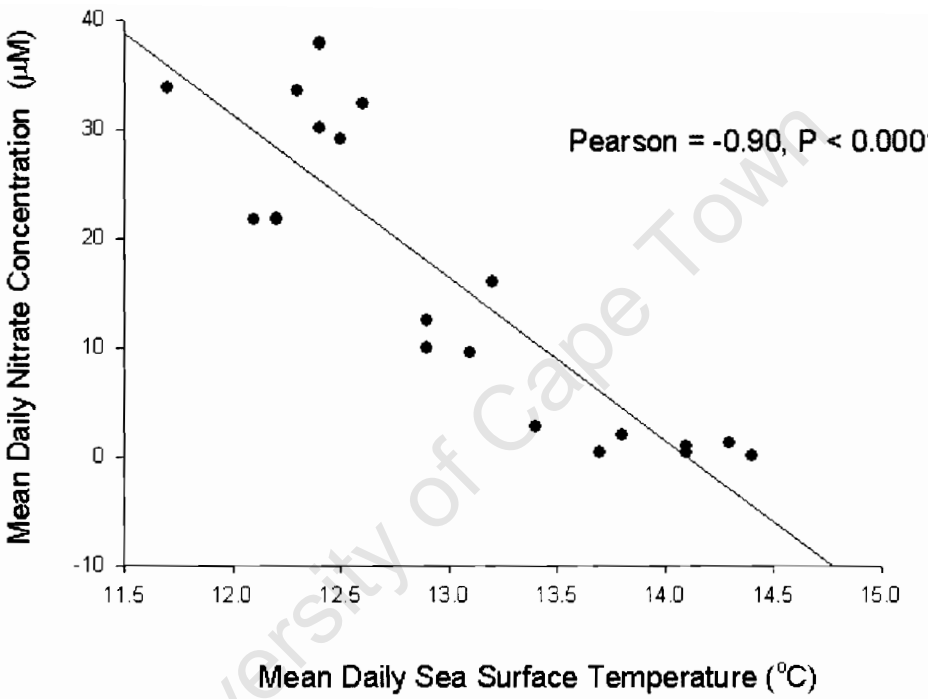


Fig. 3.2. Relationship between onshore mean daily *in situ* water temperature and nitrate concentration. Pearson correlation coefficient was statistically significant at P = 0.05. Data were generously provided by S.A. Navarrete.

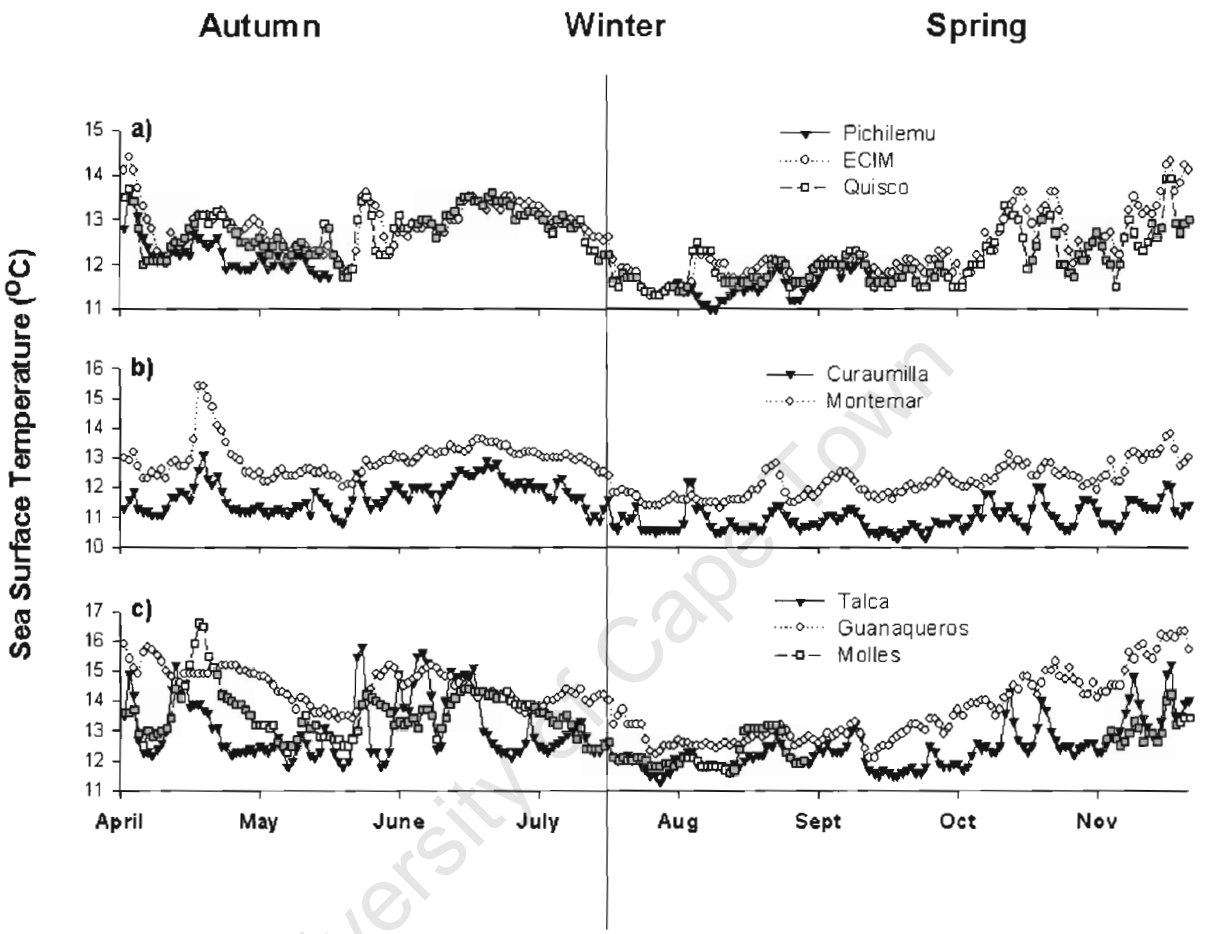


Fig. 3.3. Mean daily *in situ* sea surface temperatures in 2003 from onshore loggers at all growth-trial sites except Bucalemu. The vertical line indicates end of winter trials and the start of spring growth trials. Triangles = upwelling centers, squares = intermediate upwelling, circles = downstream sites. There were no data for Pichilemu for certain periods due to logger failure or loss.

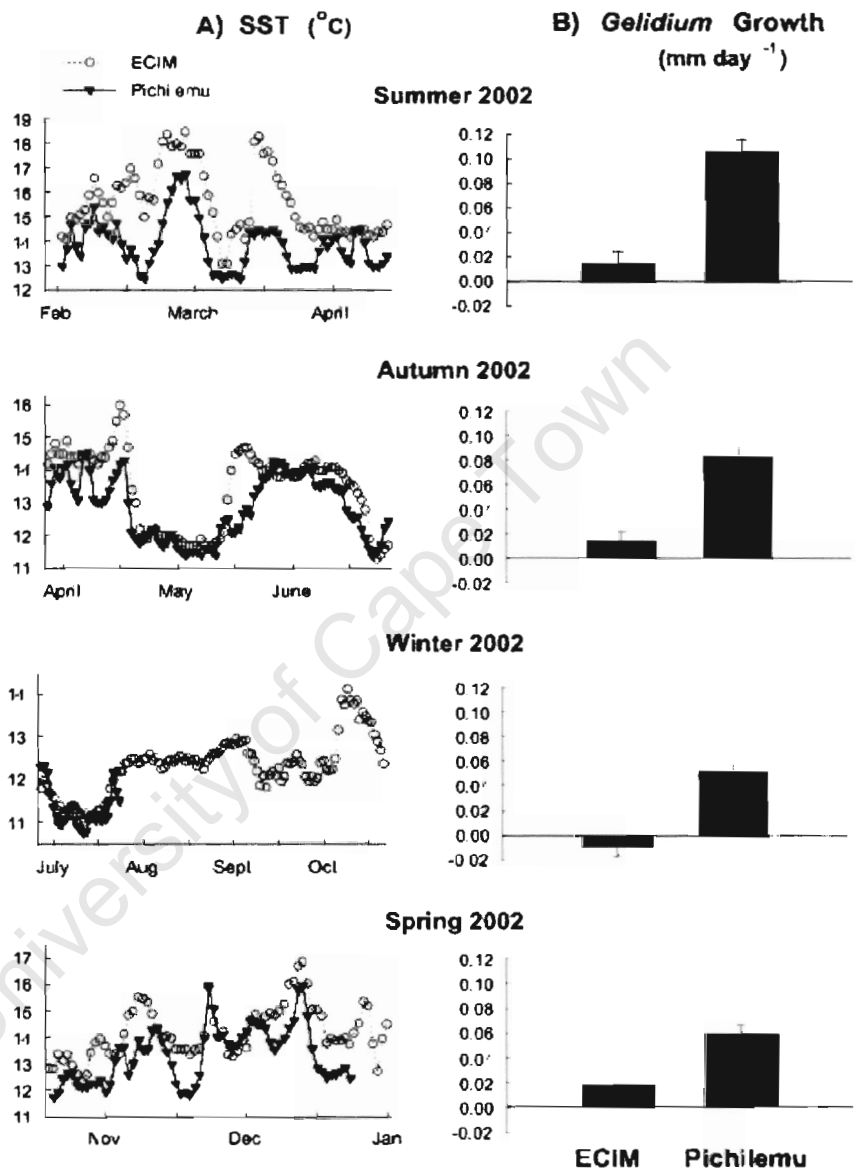


Fig. 3.4. A) Mean daily *in situ* sea surface temperature during growth trials run during 2002 at ECIM and Pichilemu. Triangles = Pichilemu, circles = ECIM. There were no data for Pichilemu between August and October. B) Mean daily growth rate (+ SE) of algal turf.

Geographic Variation in Turf Height

The geographic pattern of mean frond length remarkably matched the alongshore pattern in relative intensity of upwelling (Fig. 3.5, upwelling effect: $F_{2,11} = 6.73$, MS = 4707.21, P = 0.011). The longest turfs were present at upwelling centers (mean frond length ± SE = 34.7 mm ± 1.9), while turfs at downstream sites were shortest (9.0 ± 1.1). Sites of intermediate intensity and frequency of upwelling had intermediate turf heights (14.6 ± 3.1). However, turf size also varied significantly among sites within upwelling categories (site {upwelling} effect: $F_{11,122} = 29.02$, MS = 965.34, P < 0.0001), and a general trend of decreasing turf height to the north was observed for upwelling centers (black bars in Fig. 3.5).

Turf Growth Rates

Distinct and persistent differences in algal turf growth rates were evident between sites during 2002 (Fig. 3.4b, site effect: $F_{1,43} = 135.1$, MS = 0.043, P < 0.0001). *Gelidium* at Pichilemu grew 3-6 times faster than turf at ECIM. Moreover, Pichilemu exhibited positive growth rates throughout the year and even the slowest growth rates there (winter and spring) were still faster than any ever observed at ECIM. In contrast, growth at ECIM was persistently slow, and in winter, plants had negative growth rates, suggesting that energy expenditure and tissue loss due to necrosis of frond tips exceeded photosynthetic rate. Therefore, the magnitude of seasonal (between trials) differences between sites changed (Season x Site effect: $F_{3,43} = 6.44$, MS = 0.002, P = 0.001). Negative growth rates at ECIM were again observed during the following winter (see Fig. 3.6), which suggests that negative growth and pruning of turf is a regular occurrence at this site during winter months.

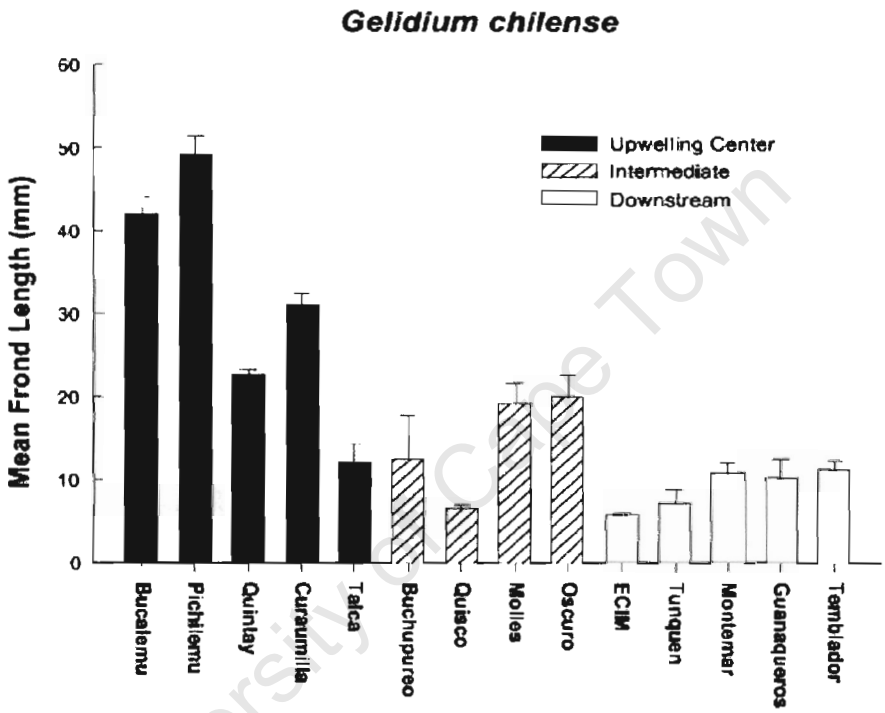


Fig. 3.5. Mean turf size (+ SE) in the low intertidal zone at 14 sites along the coast (29° – 36°S). Solid black bars = upwelling centers, open bars = downstream, hatched bars = intermediate upwelling. Within each upwelling condition, sites are ordered from south to north.

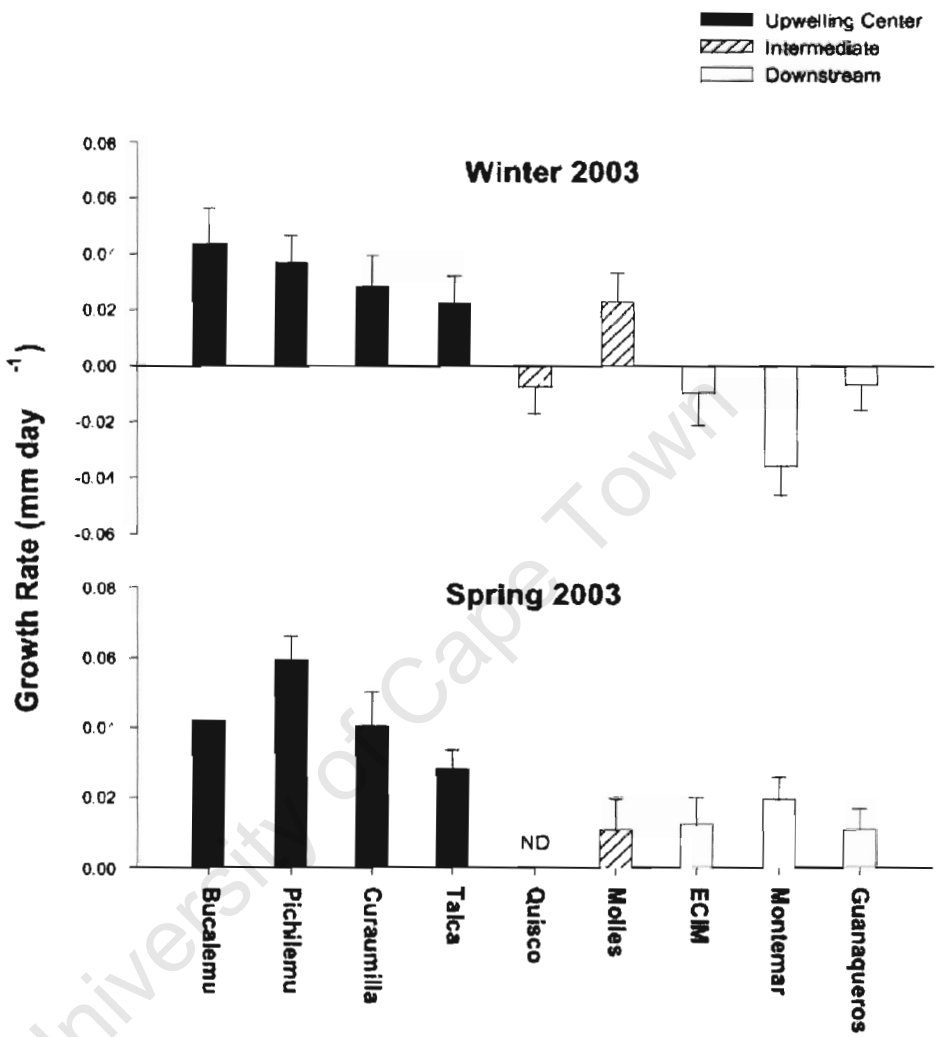


Fig. 3.6. Mean daily growth rate (+ SE) of algal turf during winter and spring 2003 at nine sites along the coast (29° – 36° S). Black bars = upwelling centers, hatched bars = intermediate upwelling, white bars = downstream sites. Within each upwelling condition, sites are ordered from south to north.

During 2003 there were striking, persistent alongshore differences in growth rates of transplanted turf, which varied predictably according to upwelling intensity (Fig. 3.6; upwelling effect: $F_{2,10} = 8.15$, MS = 0.0117, P = 0.007). The fastest growth rates were observed at upwelling centers (mean growth rate (mm d^{-1}) ± SE = 0.034 ± 0.005), while downstream sites exhibited the slowest algal growth rates (-0.001 ± 0.006). Sites of intermediate upwelling had intermediate rates of growth (0.012 ± 0.01). These differences were similar between seasons (Season x Upwelling effect: $F_{2,10} = 1.13$, MS = 0.0016, P = 0.366), but were most pronounced during autumn-winter, when all downstream sites exhibited negative growth (Fig. 3.6). During spring, growth rates at downstream sites increased, achieving positive, albeit low, values similar to those at sites with intermediate upwelling. Turf growth rates also varied significantly among sites within upwelling categories (Site {Upwelling, Trial} effect: $F_{10,84} = 2.78$, MS = 0.0014, P = 0.0051), and a general trend of decreasing growth rates to the north was observed for upwelling centers (black bars in Fig. 3.6).

Most of the variation in natural turf height along the central coast of Chile was explained by turf growth rates, resulting in a striking positive correlation between growth rates and overall turf height (Pearson = 0.89, P = 0.0032, n = 8).

Effect of turf height on mussel recruitment

Height of the turf (tall vs. short) had a large effect on mussel colonization at both sites, regardless of the origin of the plants. Virtually no mussels colonized and grew enough in the long turf at either site to be able to register a change in mussel cover, regardless of the presence or absence of predators (Fig. 3.7). Short turf strongly facilitated mussel colonization, and the effect of predator access to short turf was highly significant

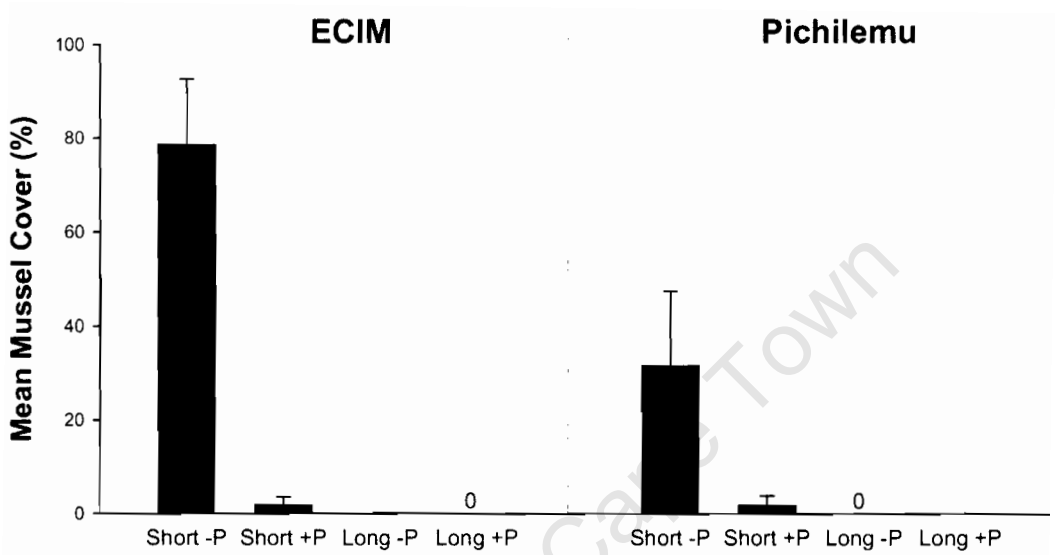


Fig. 3.7. Effects of algal turf height (short vs. tall) and predators (+P or –P) on mean mussel cover (+ SE) at ECIM and Pichilemu.

and consistent between sites (predator effect for short turf: $F_{2,23} = 26.88$, MS = 29.43, $P < 0.0001$; site x predator interaction for short turf: $F_{2,23} = 1.95$, MS = 2.13, $P = 0.16$). Predators prevented mussel recruits from establishing the short turf. Contrasts revealed that mussel covers were similarly low in controls and two-sided domes ($F_{1,23} = 0.51$, MS = 0.56, $P = 0.48$), making it unlikely that cage artifacts contributed to the predator effects. Both controls and two-sided domes differed from areas where predators had been excluded ($F_{1,23} = 50.82$, MS = 55.65, $P = 2.92\ e^{-7}$). Where predators were excluded from the short turf, mussels quickly colonized (within ~2 months) and began to overgrow the short turf. The magnitude of the positive effect of the short turf on mussel cover did not significantly differ between sites (site effect: $F_{1,23} = 3.37$, MS = 3.69, $P = 0.08$).

3.4. **Discussion**

The concept of facilitation is well established in the literature, and empirical and theoretical studies have shown the important consequences that positive interactions can have for population and community dynamics (Stachowicz 2001). The extent to which facilitation is dependent on the traits of the participating species has, however, seldom been investigated under natural conditions. My results demonstrate a case of conditional facilitation of recruitment of a dominant mussel competitor by an algal turf, in which oceanographically-determined changes in the traits of the facilitator, occurring over meso-scales of tens to hundreds of kilometers, ultimately determine the strength of the positive interaction and the effects on local community regulation.

As evidenced by satellite imagery and verified by *in situ* temperature data, there are persistent differences in upwelling intensity along the coast of central Chile. Mimicking

this pattern, field surveys showed that fronds of the turf-forming corticated alga *Gelidium chilense* were longer ("taller") in regions of intense and frequent upwelling than at sites downstream from such upwelling centers. Seaweeds exhibit a great range of morphology and size, as they quickly acclimate to local habitat conditions (Norton et al. 1982). The large differences in turf height that I observed among sites along the coast are indicative of the plastic nature of *Gelidium chilense* and the differences in the conditions experienced by the turf. Indeed, transplant experiments to sites with contrasting upwelling regimes demonstrated that morphological differences in height are not due to genetically determined variation among local populations, but due to environmentally-determined differences in growth rates. The negative growth rates observed during winters of 2002 and 2003 at some sites are central to understanding why turfs remained short at these sites, since spring-summer gains can be overcome by losses during winter, preventing growth accumulation over time. Further studies spanning multiple years are necessary to determine the temporal generality of these seasonal trends.

The mechanism by which upwelling controls turf height and growth is likely to be tightly linked to nutrients. Onshore nutrient concentrations along central Chile are higher at areas of more intense coastal upwelling and colder temperatures (Nielsen & Navarrete 2004), and my data also revealed high correlation between nutrient concentration and SST. Increased growth and changes in morphology appear to be a common response of *Gelidium* species to increased nutrient loadings, whether nutrient supplies are driven by upwelling, fertilization of commercialized crops, or domestic pollution (Santelices 1991). Working in the mid intertidal zone at four sites within the same study region, Nielsen & Navarrete (2004) observed similar among-site differences in growth rates of a different corticated alga, *Mazaella laminarioides*. They also found highest growth rates of *Mazzaella*

associated with upwelling centers, which matched well with the meso-scale pattern of abundance of this alga across the region (Broitman et al. 2001). Thus, the positive correlation between upwelling intensity and growth rates could be a general characteristic of corticated algae in this eastern boundary ecosystem.

Growth of *Gelidium* is controlled by complex interactions among light, temperature, nutrients and water movement (Santelices 1991). Therefore, observed differences in net turf growth and final height might result from direct or indirect effects of nutrients. For example, short-term stresses associated with extreme light, desiccation and/or heat during spring-summer low tide periods may interact with nutrients to differentially constrain growth and frond length. Bleaching of *Gelidium* turf, followed by necrosis, is common along the central coast after days of high solar radiation (Santelices 1991, personal observations), although these events appear to vary among years and sites. Laboratory studies with *Gelidium* and related genera suggest that sensitivity to such stressful events can be modulated by nutrients, especially nitrate (Santelices 1991). Therefore, higher nutrient concentrations at upwelling centers may not only act to increase production, but may also buffer the turf from abiotic stresses such as solar radiation.

Besides the differences in nutrient inputs among sites, the differences in SST could directly affect growth of algae. Laboratory studies have shown that *Gelidium* growth increases with increasing temperature, at least up to about 15°C, after which growth remains unchanged with increasing temperature (Santelices 1991). However, I observed the opposite pattern in the field: highest growth rates occurred at the coldest sites and slowest at warmest sites, strongly suggesting that temperature is not the primary controlling factor.

Likewise, water movement or turbulence could potentially co-vary with natural, meso-scale variation in upwelling and nutrient supply since upwelling centers are fixed in place by coastal topography. However, local study benches were specifically chosen to be of similar slope, orientation, and wave exposure in attempt to standardize effects of water movement and immersion, and field observations suggest these were not likely causative factors of variation in turf growth and morphology. Moreover, independent measurements of wave forces and flow rates at exactly these same study sites have shown that no significant differences occur among sites (S. Navarrete & G. Finke, unpublished data).

Differential grazing was also unlikely to have generated the observed patterns in turf growth and height. The most common grazers in the low zone are keyhole limpets and chitons, but their densities do not vary consistently with upwelling (E. Wieters, unpublished data and see Fig. 3.4 of Broitman et al. 2001) as has been reported for small patellid limpets that graze on ephemeral algae in the mid zone at a subset of these sites (Nielsen & Navarrete 2004). Moreover, neither benthic herbivores nor scrape/bite marks were encountered on experimental turf during monthly observations of transplants. Grazers seem to have little direct effect on established turf, but can indirectly influence turf abundance by foraging on less resistant competitors (Ojeda & Santelices 1984, Santelices 1990, Ojeda & Muñoz 1999).

The microhabitat provided by short algal turf from ECIM strongly facilitated mussel recruitment, a phenomenon observed in many other mussel species (Bayne 1964, Suchanek 1978). Since the competitively dominant *Perumytilus purpuratus* cannot settle onto smooth surfaces (Bayne 1964, Navarrete & Castilla 1990a, 2003), the presence of recruitment mediators is critical for mussel colonization. In contrast, tall turf from Pichilemu simply did not augment mussel recruitment/colonization. Results from a

separate set of experiments conducted across multiple sites and years advocate that these observed differences in mussel recruitment are best explained by turf morphology, rather than site-specific effects or differences in algal genetic structure. Across the central coast, mussel colonization in the absence of predators was similarly dependent on the height of turf naturally inhabiting sites: mussels quickly colonized sites characterized by short turf, but did not colonize where the turf was tall (E. Wieters, B. Broitman, and S. Navarrete, unpublished data). It is still unclear why mussels do not do well in tall turf, but it may inhibit mussels in a variety of ways. Tall turf likely modifies local flow velocity and turbulence differently from short turf, which may negatively influence larval contact with the substrate (Eckman 1983) and explain why relatively few mussel settlers are found in tall turf (mean individuals $(100\ cm^2)^{-1} \pm SE = 77 \pm 12.7$) as compared to densities in short turf (310 ± 127) or in a matrix of conspecific mussels (421 ± 81) (B. Kelaher & E. Wieters, unpublished data). Alternatively, increased "whiplash" (Hawkins 1983, Jenkins et al. 1999) and/or sediment deposition (Kelaher 2003b and personal observations) may be more associated with tall turf, leading to increased physical disturbance of mussel settlers. Tall turf may also diminish food supply for mussel recruits, limiting growth and/or survival. In addition, other aspects of the physical architecture of turf (e.g. surface area, frond density) often covary with height and may play a role in differentially attracting or inhibiting mussel recruits. Whatever the mechanisms, results are consistent with the hypothesis that turf morphology dictates the relative importance of facilitation, and that the interaction may switch from facilitation to inhibition when long *Gelidium* turf overgrows other recruitment mediators.

Critical examination of the influence of bottom-up processes on the regulation of marine communities is a relatively new endeavor among benthic marine ecologists (Menge

2000b). On rocky shores, bottom-up factors are represented by (1) plankton and particulate matter which influence the growth of sessile filter feeders, which in turn are consumed by carnivores, or (2) nutrients that influence algal productivity. Nielsen & Navarrete (2004) recently described clear upwelling influences on plant-herbivore interactions in the mid intertidal zone of central Chile. Stronger upwelling led to increased growth rates of a common corticated alga, *Mazzaella laminarioides*, but this increased productivity did not propagate up to the herbivore trophic level because this alga is unpalatable to small grazing mollusks. My results reveal a new, previously unforeseen "path" by which variation in nutrients driven by upwelling can penetrate the benthic food web through the algal turf, eventually determining the input of recruits of a dominant filter-feeding species, *Perumytilus purpuratus*, and potentially propagating up to higher trophic levels when these mussels are consumed by carnivores. Recruitment is probably the most important determinant of sessile invertebrate prey production, as variation is often orders of magnitude greater than that of growth, and can drive the intensity of competition for space and the supply of food for predators (Underwood 1978, Sutherland & Ortega 1986, Navarrete & Castilla 1990b). Cage experiments showed that carnivores readily consume all the mussels that continuously settle into the short turf and, therefore, increased mussel colonization increases food supply and may lead to increased carnivore biomass and stronger top-down interactions. In any case, my results introduce a new mechanism by which upwelling can regulate rocky shore communities: through modifying the strength of a positive interaction between algae and mussels. Interestingly, since upwelling centers are generally locked into position by coastal topography, the locations and spatial extent over which facilitation is likely to be important are predictable and can lead to repetitive, alternating patterns in variation of mussel recruitment rates.

The consequences of trait-dependent facilitation for community structure ultimately depend upon its relative importance compared to other processes (Menge 2000a, Bruno & Bertness 2001). In this case, since carnivores are able to remove all mussels that colonize the short turf in the low intertidal zone, and since mussels do not colonize the long turf, there are no apparent differences in terms of abundance (cover) of mussel beds or algal turfs between upwelling centers and areas downstream from upwelling, leading to remarkably consistent patterns of low-intertidal community structure along central Chile (Broitman et al. 2001). However, this similarity in structure results from contrasting regulatory processes (cf. Robles 1997). In my case, tall turf inhibits establishment of mussels at upwelling centers, whereas predators prevent colonization of mussel recruits in short turf at downstream sites. Thus, facilitation interacts with trophic dynamics to modify the relative importance of predators. Predators are critical to maintain the short turf by preventing it from becoming overgrown by mussels, but seem to play a non-significant role where the turf is tall.

3.5. **Conclusions**

The role of upwelling in community regulation now appears more complex, and multi-faceted, than originally perceived (Menge 2000b). By regulating landscape patterns in facilitator traits (turf height) that determine differences in mussel recruitment over meso-scales (10s of km), upwelling controls bottom-up propagation of prey supply to higher trophic levels in the low intertidal zone along central Chile. At upwelling centers, turf-forming algae grow faster, attain taller heights that repress facilitation of mussel recruitment, and predators play a minor role. At warmer downstream locations, algal turf remains short because it grows slower and is pruned-back in winter. This short turf

enhances mussel recruitment; but predators prevent mussels from establishing and are critical to maintain the turf. In contrast to direct trophic pathways, these results (1) describe a new "path", via habitat modification and facilitation, by which the affects of upwelling penetrate the food web to link bottom-up and top-down processes and (2) highlight how local, ecological processes can be modulated by those acting over larger scales.

Synthesis

The structure and dynamics of communities are influenced by a diverse array of ecological and physical processes that interact over varying temporal and spatial scales (Levin 1992, Pascual & Ellner 2000). Despite the important insights gained into the nature of species interactions through rigorous field experiments, ecologists have experienced major roadblocks in extrapolating results to scales relevant to conservation and management. Recent spatially-extensive and long-term studies are beginning to shed light onto the map, providing orientation to the limits and types of conditions that cause large-scale variation in coastal ecosystems. Although appropriate data are only now starting to mount, some of the more prevalent regularities identified so far include the effects of nearshore oceanographic processes on benthic communities. Processes that occur in the water column can determine the supply of nutrients, particulate food, and larval delivery to coastal habitats (Farrell et al. 1991, Roughgarden et al. 1991, Botsford 2001). Interest in the effects of variability in the intensity of coastal upwelling along eastern boundary current ecosystems has flourished, partly due to the highly advective nature and disproportionately high productivity observed in these systems. In this thesis, I explored spatial coupling between rocky intertidal community structure and dynamics and nearshore oceanographic variability in mid-latitudes of the two southern-hemisphere eastern-boundary current ecosystems, the Benguela and Humboldt. A combination of correlational, comparative, and experimental approaches were used. Results of the different approaches revealed important meso-scale, regional, and basin-wide variation in nearshore hydrographic conditions that were associated with alongshore patterns of community structure, suggesting strong

benthic-pelagic linkages. Here, I highlight the most prominent links in order of scale and emphasize the main hypotheses that could guide future research.

Clear alongshore, meso-scale variation in upwelling intensity occurs along the South West Cape of South Africa, producing alternating localized centers of coastal upwelling interspersed by downstream warm-water areas not directly influenced by upwelling. The intensification of wind-driven upwelling at fixed centers associated with capes is well known (reviewed by Shannon 1985). In Chapter 1, I showed that such variation in the intensity of upwelling produced predictable changes in the biomass of key functional groups: macroalgae and specialized gardening and kelp-trapping herbivores were more abundant at upwelling centers, while filter feeders and their predators and scavengers had higher biomass at relatively warm downstream sites. Although the descriptive study along South Africa does not answer the question of which processes give rise to the differential patterns of association with upwelling, observed patterns largely follow predictions of nutrient/productivity and upwelling-relaxation models (Wroblewski 1977, Oksanen et al. 1981, Fretwell 1987, Alexander & Roughgarden 1996, Menge et al. 2004). However, different processes can lead to similar resultant community patterns (e.g. Robles 1997). Thus, a main product of this work is the generation of a variety of testable hypotheses. Although evidence is limited, different sources of inputs (particulate food, larvae) for benthic intertidal communities are thought to be decoupled across meso-scales in South Africa, apparently due to the subsidizing role of subtidal kelp (Bustamante et al. 1995a, Bustamante & Branch 1996a, Xavier et al. in prep.), which differs from that documented across other eastern boundary current systems (Menge et al. 1997a, Menge 2000b, Broitman et al. 2001, Connolly et al. 2001, Menge et al. 2002b, Menge et al. 2003, Menge et al. 2004, Broitman et al. 2005, Navarrete et al. 2005, Blanchette et al. in press).

Meso-scale variation in upwelling intensity is expected to alter onshore nutrient availability. In some systems, this bottom-up factor propagates up the food web to indirectly control patterns of abundance at higher trophic levels, the effects of which can then cascade down the food web (e.g. Carpenter et al. 2001, Nielsen 2001, Schmitz & Sokol-Hessner 2002, Urabe et al. 2002, Worm et al. 2002, Nielsen 2003). Across central Chile, Nielsen and Navarrete (2004) found that upwelling impacts on mid intertidal communities could not be easily predicted from simple food-chain models of community regulation due to differential competitive abilities of algae in the face of herbivory. In Chapter 3, I documented an altogether new 'path', via habitat modification and facilitation, by which the effects of nutrients penetrate the food web to link bottom-up and top-down processes. Meso-scale variation in upwelling intensity regulated landscape patterns in facilitator traits (turf height), which determined differences in mussel recruitment, controlling bottom-up propagation of prey supply to higher trophic levels in the low intertidal of central Chile. These results highlight how processes acting over large scales can modify local, ecological processes and produce regular spatial variation in interaction webs along the coast. Whether such mechanisms are general to eastern boundary ecosystems remains for future studies, but the question is feasibly tackled by designing similar experiments in other systems. The comparative experimental approach is the most powerful means to determine how natural variation in large-scale processes influence community dynamics.

Multiple large-scale processes that are impossible to manipulate interact to drive regional patterns and relationships. Therefore, comparative studies utilizing more than one system may be the only means to begin to discriminate between factors and reveal the underlying environmental processes controlling large-scale benthic-pelagic linkages. One

of the more striking and consistent findings in Chapter 1 and 2 was a sharp, regional-scale shift in nearshore thermal regimes and upwelling at about 32°S. In South Africa, this shift in hydrographic conditions coincided with dramatic breaks in 1) the abundance of several species, 2) the magnitude of meso-scale, residual variability in biomass, 3) functional group relationships with components of SST variability, and 4) multivariate community biomass characteristics. Using the same methods to obtain comparable data across central Chile revealed a similar biological break (Chapter 2, and see Broitman et al. 2001, Navarrete et al. 2005), despite the large system-specific differences in community composition and physical forcing associated with large-scale circulation. Thus, the shared regional discontinuities in oceanographic conditions that modulate the timing, frequency, and duration of pulsating upwelling events appear to control major breaks in benthic community structure and may be general to eastern boundary current ecosystems. However, functional groups appear to be tuned to different local components of SST dynamics in South African and Chilean systems. Likewise, the strength and/or direction of responses to local, within-system regimes were often context-dependent. These results suggest that local SST regimes may reflect very different mechanisms for nutrient replenishment, primary productivity, physiological stress, and/or particle transport. An important attribute of comparisons is the increased ability to differentiate the significance of common patterns of variability from that of the "noise" due to vagaries of individual ecosystems.

The rather abrupt and differential relationships of functional groups, as well as whole-community descriptors, to SST in regions north and south of 32°S may indicate either 1) the existence of multiple ecotypes, such that these similar assemblages are differentially acclimated to different thermal regimes, 2) thermal regimes that reflect

different mechanisms of nutrient replenishment/depletion and physiological stress, or 3) a combination of both. These are testable hypotheses that could have important consequences for our understanding of benthic-pelagic links and the potential mediatory role of physiology. Acclimation-induced variation in tolerances and rates of physiological processes is probably an important, yet poorly understood cause of spatial heterogeneity in most ecosystems.

Comparisons across systems also provide the opportunity to describe biological-physical links occurring on a global scale. For example, Carr and Kearns (2003) observed a strong and positive relationship between average phytoplankton biomass and offshore temperature difference across all four major eastern boundary current ecosystems, suggesting that differential productivity of these systems is related to a global gradient in upwelling intensity. In Chapter 2, I found strong and significant relationships between biomass of rocky intertidal communities and basin-wide differences in thermal regimes across South Africa and central Chile. These results support the idea that global gradients in hydrographic regimes drive between-system differences in biomass on rocky shores. Interestingly, stresses related to tidal height appear to consistently interact with these oceanographic regimes in a regular way. Across these systems, highly modulated temperature pulsing appeared beneficial for low-shore communities, whereas increased stability and regularity of upwelling events benefited biomass on mid shores. Incorporating comparable data from other major eastern boundary current ecosystems could help evaluate the robustness of these results. Since ecosystem structure is closely coupled to variation in atmospheric physical forcing, this may imply greater sensitivity to the alterations in currents and frequency of particular pulsing events (e.g. El Niño events) that are predicted to occur with increasing climate change. Among-system regularities in biological-physical

coupling suggests the effects of climate change may be uneven, yet potentially predictable. This is of critical importance to management and economies.

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