Progress in Oceanography xxx (2009) xxx–xxx

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand

C.A. Blanchette [a,*], E.A. Wieters [b,1], B.R. Broitman [c], B.P. Kinlan [a], D.R. Schiel [d]

[a] Marine Science Institute, University of California, Santa Barbara, CA 93106-6150, USA
[b] Marine Biology Research Centre, Zoology Department, University of Cape Town, Private Bag, Rondebosch 7701, South Africa
[c] Ctr Estud Avanzados Zonas Áridas, Univ Católica Norte, Fac Ciencias Mar, Larrondo 1281, Coquimbo, Chile
[d] Univ. Canterbury, Sch. Biol. Sci., Marine Ecol. Res. Grp., Private Bag 4800, Christchurch 1, New Zealand

ARTICLE INFO

Article history:
Received 18 July 2008
Received in revised form 21 March 2009
Accepted 16 July 2009
Available online xxxx

ABSTRACT

The Benguela, California, and Humboldt represent three of the major eastern boundary upwelling ecosystems in the world. Upwelling ecosystems are highly productive, and this productivity forms the base of the food chain, potentially leading to ecosystems similar in trophic structure and diversity among upwelling regions. Here we compare the biological and trophic structure of rocky intertidal communities in each of these major upwelling regions. Our comparison includes a fourth region, New Zealand, which spans a similar latitudinal range, and experiences intermittent upwelling. The influence of oceanographic conditions on these communities was evaluated by using the long-term mean and standard deviation of satellite-based sea surface temperature (SST). Large differences emerged in the taxonomic richness in each of these systems, with California as the most and the Humboldt as the least taxonomically rich. Across all regions, richness tended to decrease progressively from lower trophic levels (macrophytes) to higher trophic levels (carnivores), and richness was inversely correlated with the proportion of variance in SST contained in the seasonal cycle, suggesting that strongly seasonal, predictable environments are relatively low in diversity. The functional and trophic structures were remarkably similar across these four regions of the world. Macrophytes were slightly dominant over filter-feeders in terms of space occupancy in all regions except the Benguela. Densities of herbivorous grazers were greatest in California and Benguela and far outnumbered carnivore densities in all regions. Despite some similarities, the overall structure of the communities from these regions differed significantly supporting the hypothesis that the biological and ecological consequences of similar physical forcing mechanisms (e.g. upwelling) are likely to be context-dependent.

1. Introduction

The regions associated with the Atlantic and Pacific equatorward-flowing eastern boundary currents (EBC) have long been recognized for their physical vigor and high productivity (Barber and Smith, 1981). Although their area makes up a small fraction of the world ocean (<1%), they account for 5% of global marine primary production and 17% of global fish catch (Carr, 2002; Pauly and Christensen, 1995). High biological productivity is fueled by coastal wind-driven upwelling of cold, nutrient-rich subsurface waters (Strub et al., 1998). Shared environmental dynamics across these systems have prompted comparative research aimed at understanding the extent to which these systems are similar in their ecological and functional structure and diversity. Comparisons of estimated productivity among the major EBC regions have found a clear hierarchy, with maximum values in the Benguela, followed by the Canary, the Humboldt (primarily due to high productivity in northern Peru) and with lowest values in the California Current (Carr, 2002; Cushing, 1969). The high productivity fueling extensive fisheries in all these systems has inspired various research efforts to understand the trophic and functional structure of these ecosystems. In all cases, the pelagic food webs share similar characteristics. Most systems typically contain a large number of species at the lower (e.g. planktonic) trophic levels. They also contain a substantial number of predatory fish, seabirds, or marine mammals that feed at the upper apex and near-apex trophic levels. However, across all of these highly productive ecosystems, there tends to be a crucial intermediate

---

[*] Corresponding author. Tel.: +1 805 893 5144; fax: +1 805 893 8062.
E-mail addresses: blanchette@msi.ucsb.edu, blanchet@lifesci.ucsb.edu (C.A. Blanchette).

[1] Present address: Pontificia Univ. Católica Chile, Estac Costera Invest Marinas, Casilla 114-D, Santiago 6513677, CP, Chile.

0079-6611/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.pocean.2009.07.038

trophic level occupied by small, plankton-feeding pelagic fish that is typically dominated by only one, or at most a few, species (Bakun, 1996). They are most abundant in upwelling areas and exploited stocks of these species are prone to large interannual and interdecadal variation of abundance as well as to collapse (Freon et al., 2005). These trophic intermediates exert a major control on the trophic dynamics of upwelling ecosystems and the trophic diversity of these systems has been termed “wasp-waist” due to the low diversity in these mid-trophic levels (Cury et al., 2000). In addition to these broad similarities, comparisons of the four marine upwelling systems (the Benguela, California, Humboldt, and Canary) utilizing ecopath models have shown that the models cluster together by system rather than by species dominance (Jarre-Teichmann, 1998; Jarre-Teichmann et al., 1998), suggesting that quantitative indicators for fisheries management that aim to track fishing impacts might be confounded by inter-system differences. This begs the question of whether or not there are generalities in the processes influencing the ecological structure and function across these types of ecosystems that are discernible beyond the level of individual taxa.

The shared characteristics and dynamics of coastal upwelling interact strongly with numerous other physical forcing processes that contribute to variability of the physical environment. Thus, sensible among-system comparisons require quantification of variability in environmental conditions. Recent efforts to describe and compare the multi-variate temporal dynamic regimes of coastal oceanographic variability along parts of the Benguela and Humboldt revealed striking differences between systems, with the Benguela characterized by an overall more variable nearshore environment (Wieters et al., 2009). These changes in the pattern of fluctuation may be critical to biological composition since increased temporal and spatial variability in the environment is expected to promote coexistence of species and lead to increased diversity (Chesson, 2000). Indeed, small-scale controlled experiments have documented more species and even more communities when grown under pulsed regimes of limiting resources (e.g. Sommer, 1984). Whether the complex, fluctuating oceanographic conditions that occur over large, basin-wide scales are linked to variation in diversity of natural, multi-species communities has not been explored.

Here we take the first steps to describe and quantitatively compare the biological and ecological structure of coastal rocky-shore communities across three of the major EBC ecosystems (Benguela, Humboldt and California). To provide further insight into context-dependency and the degree to which interpretation should be limited to EBC ecosystems, our comparison also includes a fourth region, New Zealand, which is not an EBC, but is a temperate system spanning a similar latitudinal range that is affected by intermittent upwelling along parts of the coastline. Our focus on rocky intertidal ecosystems addresses the issue of whether, or to what degree, the high productivity of offshore waters is reflected in intertidal habitats. Rocky intertidal systems are ideal for this type of comparison due to their high diversity and the great depth of knowledge about their structure and function within each of these regions. Over the past several decades, research in these systems has led to the recognition of these coasts as among the best studied marine systems of the world (Schiel, 2004), and recently available spatially-extensive information make them ripe for comparison. Our focus is on broad-scale patterns and comparisons among, rather than within, regions. Because global richness has been shown to be related to climate (Francis and Currie, 2003; Sanders, 1968) we expected climatically similar regions to have similar taxonomic richness. We also expected differences in productivity among regions to influence trophic and functional structure and to scale with diversity (Connell and Orias, 1964).

2. Study regions

2.1. Benguela

The Benguela Current forms the eastern boundary of the South Atlantic subtropical gyre. Its sources include Indian and South Atlantic subtropical thermocline water, saline, low-oxygen tropical Atlantic water, and cooler, fresher deep water (Field and Shillington, 2006; Shannon, 1985; Shannon and Nelson, 1986). The Benguela ecosystem can be divided into Northern (Angola and Namibia) and Southern sub-systems (South Africa), separated by the permanent upwelling cell off Luderitz, which is the strongest in the world. Here we focus on the Southern Benguela system along the west coast of South Africa, from approximately 29–34° south latitude (see Fig. 1a).

The intertidal flora and fauna of the west coast of South Africa are biogeographically distinct from South Africa’s south and east coast species (Bustamante and Branch, 1996; Sink et al., 2005). Emanuel et al. (1992) divided the West Coast of southern Africa into two separate cool-temperate provinces, the Namaqua and Namib provinces, with a division near Luderitz. On the basis of seaweed flora, a third division is recognized on the southern portion of the Western Cape which is also reflected in the invertebrate fauna (Emanuel et al., 1992). Recently, Wieters (2006) documented a sharp discontinuity in patterns of intertidal functional group biomass at about 31–32°S latitude. This break is consistent for wave-exposed and sheltered environments and is not easily explained by changes in species composition. On local scales, the main patterns of zonation and processes regulating community structure are summarized in the review by Branch and Griffiths (1988).

2.2. California

The California Current System (CCS) is the eastern boundary current of the North Pacific. Its northern extent is marked by the southward branch of the bifurcating North Pacific Current off Washington, USA, and it extends south to Baja California, Mexico. Detailed reviews of the circulation in the CCS can be found in Hickey and Banas (2003) and Huyer (1983). Prevailing winds during summer are equatorward throughout the region (Huyer, 1983), resulting in offshore Ekman transport and upwelling along the coast. During winter, the wind forcing is strongly downwelling-favorable in the northern region (Bakun and Nelson, 1991; Huyer, 1983), particularly off Oregon and Washington, but as far south as 35°N during storms (Castelao et al., 2006). Here we focus on the southern portion of the California current from approximately 29–42°N latitude (Fig. 1b) which is the region of most intense upwelling activity.

The biogeographic patterns of intertidal species across this region have been recently well characterized (Blanchette et al., 2008; Schoch et al., 2005) and highlight a major discontinuity in community structure near Point Conception, CA (at approximately 34°N latitude). This biogeographic break is coincident with a major oceanographic discontinuity across Point Conception, with strong upwelling to the north, and weak, seasonal upwelling to the south.

2.3. Humboldt

The Humboldt Current flows along the west coast of South America from northern Peru to the southern tip of Chile. The waters of the Humboldt Current system can extend 1000 km offshore. A summary of the main oceanographic features has been presented by Strub et al. (1998). The northern, equatorward flowing branch of the West Wind Drift, which reaches the South

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

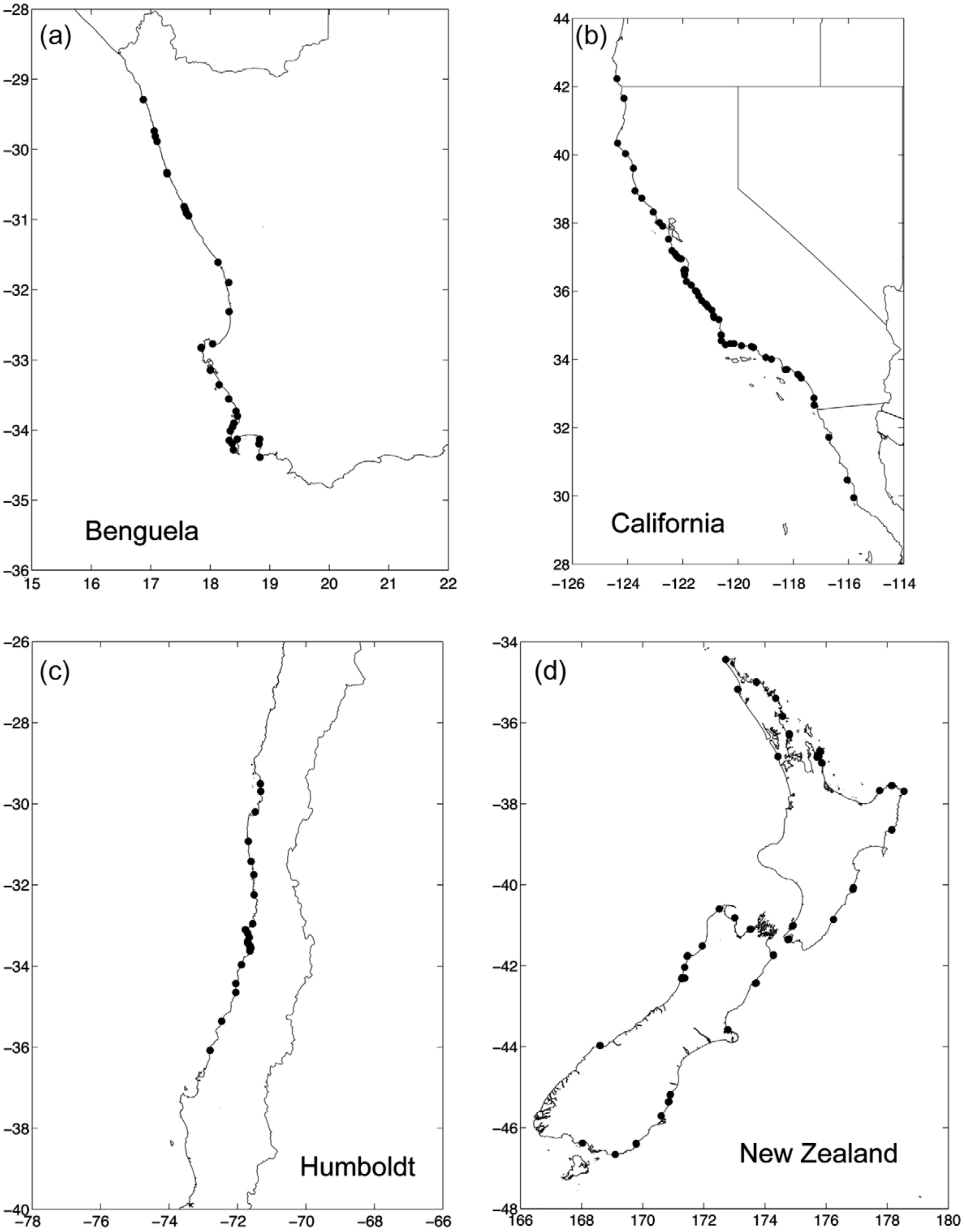

Fig. 1. Maps of each of the study sites (black dots) within each of the main study regions; (a) Benguela, along the coast of South Africa, (b) California along the coast of North America, (c) Humboldt, along the coast of Chile, and (d) New Zealand. Detailed site names and locations are in Supplementary Table 1. Vertical axes show latitude (north positive) and horizontal axes show longitude (east positive).

American continent around 40°S and a complex group of coastal currents comprise what is called the Humboldt or Chile–Peru Current system. To date, most studies of this system have emphasized offshore oceanography. Because of the geomorphological characteristics of the coastline and the scant attention that nearshore oceanography has received, it is difficult to assess coastal circulation patterns (i.e., from the coast to a few miles from shore). Here we focus on the portion of the Humboldt region along the central coast of Chile from approximately 29–36°S latitude (Fig. 1c).

Wave-exposed rocky intertidal areas are common habitats all along the Chilean coastline. The central coast is characterized by a narrow continental shelf and an almost linear coastline, most of which is directly exposed to prevailing South Western weather systems, with few protected bays or coves. Biogeographic provinces based on compositional affinities appear to differ for benthic invertebrates and macroalgae (Fernandez et al., 2000). The central coast region is described as a diffuse 'transition zone' between the major Peru–Chile and Magellanic zoogeographic provinces. An

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

abrupt break in abundance and recruitment of competitively dominant mussels occurs near 32–33°S latitude (Broitman et al., 2001; Navarrete et al., 2005) which produces sharp, persistent variation in the strength of species interactions that defines regions of contrasting benthic community dynamics (Navarrete et al., 2005).

2.4. New Zealand

New Zealand is surrounded by several distinct water masses, and the major currents are the subtropical East Australian Current in the north, the Westland Current in the southwest, and the Southland Current that flows from the south-western end of the South Island and northwards up the east coast (Chiswell and Schiel, 2001; Heath, 1985; Vincent and Howard-Williams, 1991). Around the middle of the South Island, a mixture of water from the Southland Current is deflected eastwards along the continental shelf, but some northward flow is evident intermittently through a submarine saddle (Shaw and Vennell, 2000). Upwelling occurs intermittently from at least the central west coast of the South Island northwards to Cook Strait (separating the two main islands) (Stanton, 1976; Vincent and Howard-Williams, 1991) and also along the northeast coast of the North Island. There is some debate about how frequently upwelling occurs along the west coast. There is considerably higher rainfall on the west coast than the east coast and there are two large rivers that may have caused the cold-water plumes seen in some studies. Vincent and Howard-Williams (1991) found cold-water plumes extending offshore from the coast in the vicinity of river mouths but argued they were unlikely to be a direct effect of cold riverine input because of dilution and because differences between seawater and river temperatures were not large at the time of their study. Productivity along the west coast of NZ, therefore, may not be due to upwelling alone but to freshwater input of nutrient-rich water, a ‘‘benthic-terrestrial’’ rather than a ‘‘benthic–pelagic’’ coupling (Schiel, 2004).

The sites in New Zealand spanned wave-exposed rocky habitats along all shores (Fig. 1d). The nearshore environment around New Zealand is complex, but most of the west coast is considered very wave-exposed. However, the coastline is topographically complex with numerous headlands, bays and inlets. The east coast is mostly semi-protected north of East Cape but more exposed on outer coasts sites to the south. Most east southern coast sites are composed of softer sedimentary rocks, except for headlands such as Banks Peninsula, which are harder volcanic or metamorphic rock, while west coast reefs are composed mostly of hard metamorphic rock. Sites north of East Cape (North Island) are mostly hard rock. The broad relationship between rock types and exposure may affect community structure; few mussels are found on the softer sedimentary rocks, mostly because they do not attach well. Reefs composed of softer rocks rarely occur where wave-exposure is great, and are usually dominated by fucoid seaweeds. Cook Strait is considered to be a region of biogeographic discontinuity (Goldstien et al., 2006).

3. Methods

3.1. Sea surface temperature (SST)

SST estimates were derived from 21 years (1985–2005) of 5-day (pentad) composites of 4-km spatial resolution AVHRR satellite data processed using the Pathfinder algorithm (version 5.0, available at: http://www.nodc.noaa.gov/sog/pathfinder4 km). A pentad climatology was calculated for each sampling site as the 21-year average of SST in the closest usable pixel to the site location for each of the 73 pentads in a 365-day year (ignoring the extra day in leap years). Residual SST was calculated by subtracting the climatological pentad means from the observed value in each pentad. The fraction of variance in the seasonal cycle was then calculated for each site's time series: Fraction of Variance in Seasonal Cycle = 1 -[Variance(Residual SST) /Variance(Raw SST)].

3.2. Field methods

We did intensive quantitative surveys of rocky intertidal community composition and structure across our four main study regions (Benguela – 39 sites, Humboldt – 26 sites, California – 60 sites and New Zealand – 73 sites; see Supplementary Table 1 and Fig. 1). In each of the regions, sites were sampled by teams of marine scientists with expertise in the taxonomy of the flora and fauna of each region (team leaders: Benguela – E. Wieters, Humboldt – B. Broitman, California – C. Blanchette, and New Zealand – D. Schiel). Although not every organism could be identified to the species level in these surveys, we feel that the dataset compiled here represents the best available state of the knowledge of these systems across this spatial scale and is unprecedented in quality and scope.

Sites were sampled across a ten-year period between 1995 and 2005. For sites that were sampled multiple times, we used a temporal average of taxon abundance. Within each system, sites and rocky benches sampled were selected to be representative of the intertidal biota of that section of coast and were chosen to be as similar as possible in terms of geomorphology, bench slope and orientation, wave exposure, and habitat type, however access limited sampling of some sections of coast. In all cases, data from sites considered not to be representative of at least a moderately exposed shoreline within a given system were excluded from these analyses.

To quantify broad compositional patterns of intertidal assemblages across the regions, we examined species' abundances pooled into functional groups, which is necessary and important because almost no species, very few genera and few families are common across all four regions. Functional groups or guilds have increasingly been used as means of understanding the trophic structure of marine communities (McQuaid and Branch, 1985; Menge and Sutherland, 1987). Although members of a functional group can vary considerably in localized ecological interactions (Schiel, 2004), the advantage of using such groups (sometimes called 'ecological equivalents' (Schoener, 1988)) is that they provide a common ecological base for comparing sets of taxonomically unrelated species (e.g. barnacles and mussels are both filter-feeders and are both functionally similar in being sessile). Functional groups that use resources in a similar way may respond similarly to variation in the processes that control those resources (Underwood and Petraitis, 1993). The classification that we employed assumes the resource use strategies of the taxonomic entities in each functional group broadly captures (or serves as a proxy for) the ecosystem function the groups perform (Padilla and Allen, 2000). To examine trophic structure of these systems we grouped taxa into five main categories: carnivores (e.g. seastars and whelks), herbivores (e.g. limpets, snails, chitons), filter-feeders (e.g. barnacles and mussels), macrophytes (all seaweeds and seagrasses) and omnivores (a numerically scarce, but diverse group ranging from crabs to worms). In this way, our functional classifications are an attempt to synthesize the taxa that dominated the surveyed assemblages in terms of abundance and represent the central focus of the analyses presented below.

To characterize patterns of rocky intertidal community structure, all surveys extended from the highest to lowest intertidal zones, otherwise known as the supralittoral fringe to infralittoral fringe in the universal zonation terminology of Stephenson and Stephenson (1949).The abundance of sessile taxa (e.g. macroalgae, barnacles, mussels) was quantified using both stratified point-intercept sampling and standard transect-quadrat sampling

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

methods (Blanchette et al., 2008; Broitman et al., 2001; Wieters, 2005). Although there were slight differences in sampling design within and among the four systems, we feel that the results presented here are robust to differences in methodology as extensive sampling effort was involved in data acquisition across all regions and locations. For the purposes of our analyses, data are summarized as the mean percentage cover of each functional group at the level of "site". Across all systems, percentage 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%. Mobile invertebrate taxa (e.g. limpets, snails, whelks) were scored by direct counts within quadrats stratified by tidal zone at each site, so data are summarized as the mean density (number of individuals per m^2) at each site.

3.3. Data analysis

To facilitate comparisons of taxon richness among regions containing different numbers of sites, we calculated jackknifed estimates of richness (Magurran, 1988). To compare herbivore densities and community patterns among regions we excluded all snails in the genera *Littorina* and *Nodlittorina* from our analyses. Most littorinid snails encountered in our surveys were much smaller than most other herbivores (usually only several mm) and their ecological importance in these systems is not well understood (Norton et al., 1990). Snails of those taxa were common to all regions and were the only taxa with extreme outliers in abundances (commonly several thousand snails per m^2), swamping abundance estimates for all other taxa. To examine geographic patterns of community similarity, we used the multivariate methods of Clarke (1993) and the PRIMER 6.1.3 (Plymouth Routines in Multivariate Ecological Research) software package. The data matrix of taxon abundances was fourth root transformed to reduce the contribution of very abundant species and increase that of rare species. A similarity matrix was constructed using the Bray–Curtis similarity coefficient and we used 2-dimensional plots constructed by, non-metric multidimensional scaling (nMDS) to examine regional segregation among communities (Kruskal and Wish, 1978).

4. Results

4.1. SST patterns

There were strong spatial and temporal patterns of variability in SST across the four main regions. Long-term mean SST was very similar (approximately 15 °C) in both the Benguela and Humboldt regions from approximately 29–32°S latitude, and diverged in opposite directions (Benguela warmer and Humboldt colder) from 32°S latitude poleward (Fig. 2a). Both the California and New Zealand systems were typified by a decline of approximately 6 °C from equatorward to poleward latitudes. In California the drop in SST was particularly steep (approximately 5 °C) over a relatively short range in latitude near 34°N. The percentage of variance in SST contained in the seasonal cycle was relatively high and relatively constant (approximately 70–80%) across all systems at latitudes equatorward of 32–33° latitude (Fig. 2b). The California and Humboldt regions displayed a decline in the proportion of seasonal cycle variance of temperature at latitudes poleward of 32° latitude, albeit more variable among sites in the Humboldt. The California system displayed the broadest range of variation in seasonal cycle variance across all systems. The New Zealand system was characterized by a relatively constant and high (70–90%) proportion of seasonal cycle variance across all latitudes.

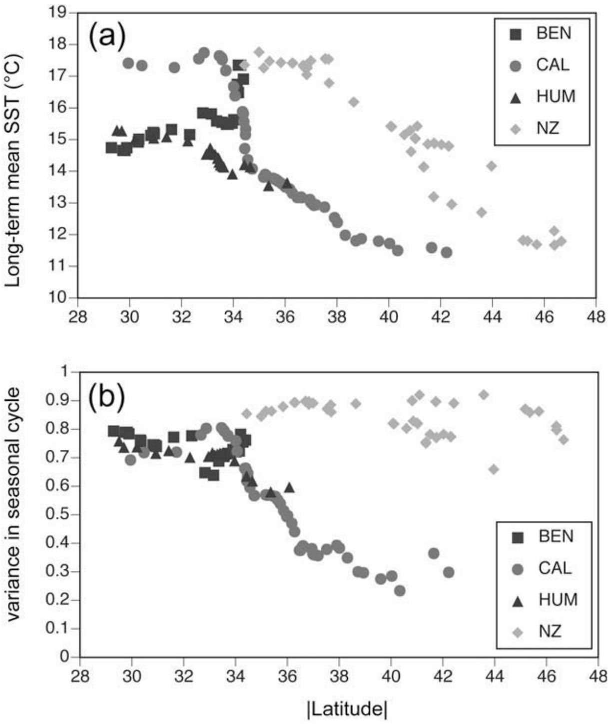

Fig. 2. (a) Long-term (1985–2005) mean satellite SST and (b) fraction of variance in the seasonal cycle (pentod climatology as a function of absolute latitude just offshore (<8 km) from intertidal sites in each of the 4 main regions: Benguela (squares), California (circles) Humboldt (triangles) and New Zealand (diamonds).

4.2. Species richness

Jackknifed estimates of taxon richness varied broadly across systems with California as the most diverse, followed by NZ, Benguela and the Humboldt as the least diverse (Fig. 3a). The

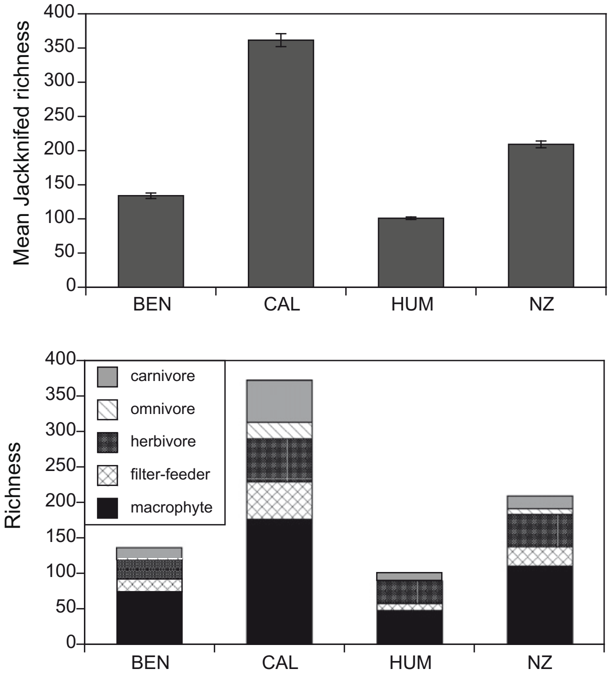

Fig. 3. (a) Mean (±1s.e.) of jackknifed estimates of taxonomic richness among the four regions and (b) Taxonomic richness of carnivores (solid gray), omnivores (hashed) herbivores (dotted) filter-feeders (crossed) and macrophytes (solid black) in each of the four main study regions.

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

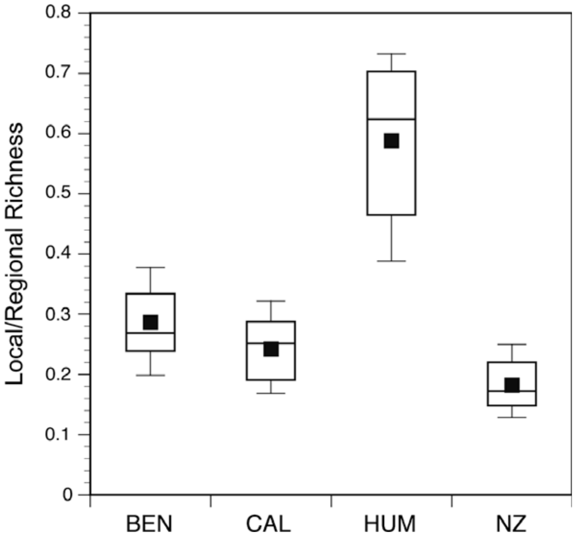

Fig. 4. The relationship of local (site scale) to regional (all sites in region) taxonomic richness (number of species) for each of the four main study regions. The top, bottom, and line through the middle of the box correspond to the 75th percentile (top quartile), 25th percentile (bottom quartile), and 50th percentile (median), respectively. The whiskers on the bottom extend from the 10th percentile (bottom decile) and top 90th percentile (top decile) and the square represents the mean.

proportional taxon richness across trophic groups was remarkably similar among all four regions (Fig. 3b). Approximately 50% of the total taxon richness in each region was composed of primary producers. Top-level consumers were the least speciose in each region, and middle-level trophic groups (herbivores and filter-feeders) accounted for approximately 30% of the total taxon richness across all four regions. Although the Humboldt region was characterized by the lowest overall taxon richness, the proportion of local to regional richness (site richness/regional richness) was significantly higher than any of the other regions, indicating that most of the taxa found at any one site are also found broadly across the region (Fig. 4). The local/regional richness in the two highest diversity regions (California and New Zealand) was relatively low, indicating high species turnover throughout the region. Across all four regions we found a significant negative relationship between local taxon richness and percent of variation explained by the seasonal cycle in temperature ($R^2 = 0.46$, $p < 0.0001$) (Fig. 5).

4.3. Functional composition

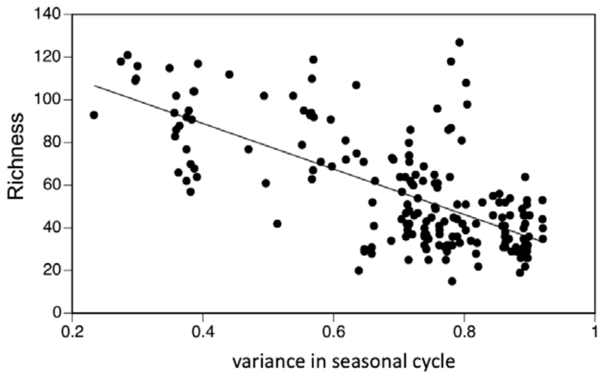

Fig. 5. Local taxonomic richness as a function of the fraction of variance explained by the seasonal SST cycle for all sites and regions.

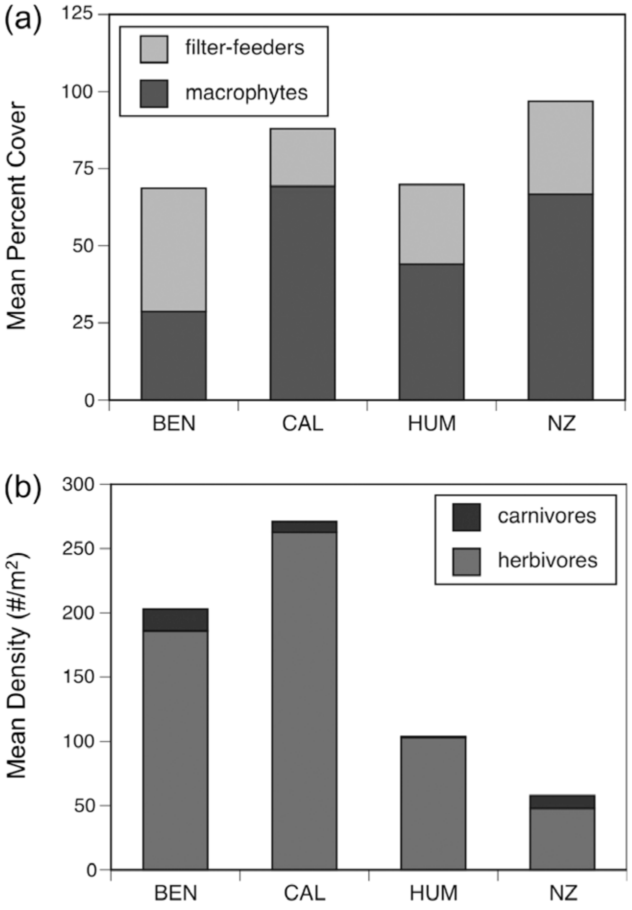

Fig. 6. (a) Mean percentage cover of filter-feeders (gray) and macrophytes (black); and (b) mean densities of herbivores (black) and carnivores (gray) across the four main regions.

Across all regions, primary producers and filter-feeders (mainly barnacles and mussels) occupied well over 60% of primary space. In California and New Zealand, the two most taxon-rich regions, primary producers occupied most of the space (c. 70%) and were the dominant taxa (Fig. 6a). Primary producers occupied nearly 50% of the primary space in the Humboldt region and were slightly more abundant than filter-feeders. The Benguela is the only system in which filter-feeders occupied the largest proportion of space (c. 67%) and were more abundant than primary producers. The abundance of consumers across all systems was greatly dominated by herbivores (Fig. 6b). Herbivore densities were lowest in New Zealand and highest in California, approximately five times the densities of New Zealand herbivores. Although carnivore densities were low in all regions, they were noticeably scarce in the Humboldt region and had greatest proportional abundance in the Benguela region. These differences in functional group composition are more pronounced when examined by site within each region, and were apparent in the nMDS plot (Fig. 7). The relative spatial separation among sites coded by regions indicates high compositional similarity within regions. The Benguela and New Zealand regions were completely separated from other regions, while the Humboldt and California regions displayed some overlap. Within regions, sites generally cluster close together, although there is some scatter, particularly in California and New Zealand, which are relatively large regions geographically. An ANOSIM test between the four regions detected significant differences in community structure between all regions (Global $r = 0.656$, $p < 0.01$).

5. Discussion

Our results highlight broad similarities in the structure of rocky intertidal ecosystems of major upwelling regions worldwide. These

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

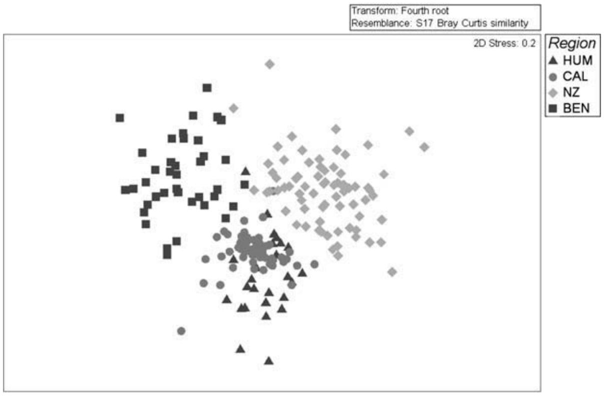

Fig. 7. Non-metric multidimensional ordination plot (stress = 0.20) based on the fourth root transformed taxon abundance data for each site within each of the four main regions; Benguela (squares), California (circles) Humboldt (triangles) and New Zealand (diamonds).

communities tend to be dominated by a mixture of sessile invertebrates and seaweeds of similar functional groups, but the combinations of plants and animals found within each region are distinctive, similar to the findings of Stephenson (1960) in his comparisons of the Pacific coast of North America, the European North Atlantic and South Africa. Although the systems studied here share broad similarities in functional group structure, they were found to differ greatly in biodiversity, which is not surprising given their different evolutionary histories, phylogeography, and heterogeneous coastlines. Interestingly, however, we found a significant negative relationship between taxon richness and the percentage of environmental variability explained by predictable seasonal patterns as captured by the 21-year climatological pentad SST mean. This suggests that differences in species richness across systems may be linked to temporal environmental variability. Many hypotheses have been proposed to account for diversity, several of which incorporate some aspect of stability or variation in the availability or provision of resources. Along topographically complex coastlines bathed in generally nutrient-rich waters, broad-scale diversity patterns may reflect a complex interaction of many spatially and temporally correlated, and possibly confounded, processes (Broitman and Kinlan, 2006). these attributes. Our results suggest that taxonomic richness may be linked to environmental variability, and that patterns of SST variance are a useful proxy for some of the processes driving diversity. If is unknown how well this relationship may hold across broader scales and in non-temperate systems. More work is needed to investigate mechanisms linking oceanographic variability with diversity along coastlines. Bearing these caveats in mind, we discuss some of possible interpretations and implications of these findings below.

5.1. Environmental variability and species richness

Ecologists have long debated the relative importance of factors that cause gradients in species diversity. Many of the hypotheses deal with time (Fischer, 1960), spatial heterogeneity (Simpson, 1964), competition (Dobzhansky, 1950) and predation (Paine, 1966). However several ideas have linked diversity to aspects of the environment (Connell and Orias, 1964; Sanders, 1968). The productivity hypothesis (Connell and Orias, 1964) essentially states that greater productivity should result in greater diversity, everything else being equal. The range of estimated productivity among the upwelling systems described here gives us an opportunity to evaluate this idea. Most estimates (Carr, 2002; Cushing, 1969) have ranked the Benguela as the most productive of the world's systems, followed by the Humboldt and then California. New Zealand, which is not an eastern boundary upwelling system, is thought to be the least productive. Our results are clearly at odds with the productivity hypothesis. We found the highest richness in the California and New Zealand systems, the two least productive areas, with a nearly twofold drop in richness to the Benguela system, considered to be most productive. There are several reasons why diversity and productivity may be uncorrelated in our study. The spatial scale of our study sites for both the Benguela and Humboldt systems is restricted to a limited portion of the region typically considered to represent the entire upwelling region from which productivity estimates are derived. Furthermore, estimates of productivity based on satellite observations of Chl-*a* (Carr, 2002) are not necessarily representative of productivity in intertidal regions due to land-masking (Siegel et al., 2005) and spatial patchiness in chlorophyll in the nearshore (Wieters et al., 2003). It is also possible that there is no relationship between productivity and diversity; the lack of support for this hypothesis in our data is consistent with results of some other studies from marine and freshwater ecosystems (e.g. Bonada et al., 2008; Harmsworth and Whiteside, 1968).

Other ideas have linked diversity to the stability of the environment. Sanders (1968) proposed the "stability-time" hypothesis, suggesting that the more stable the environmental parameters, the more species will be present. Non-equilibrium theories of community structure purport that diversity peaks at intermediate levels of disturbance, which is necessary to remove competitively dominant species (Connell, 1978). These ideas have been applied to stream systems, which exhibit seasonal cycles of flooding, and where diversity is related to the frequency and intensity of flooding (Power, 2006; Sousa, 1984). In our study we attempted to gauge environmental stability using variance in temperature over a long period of time (21 years). SST is a relevant, universal and easily measured environmental metric across this broad spatial scale. Since our study focused on temperate systems, characterized by seasonality, we measured predictability of the environment as the proportion of annual variance in temperature accounted for by the long-term average seasonal cycle. Deviations from the annual cycle represent inter- or intra-annual variation that is less predictable. Our findings suggest that more predictable environments (more variance in the seasonal cycle) have lower richness than less predictable environments. This relationship between diversity and environmental variability is consistent with non-equilibrium theories and ideas based on niche overlap (May and Macarthur, 1972; Chesson, 2000).

5.2. Trophic structure

Much of the literature on upwelling ecosystems has focused on the highly productive, nearshore pelagic environment characterized by a broad assemblage of plankton, planktivorous and piscvivorous fishes (Bakun, 1996). This focus is understandable, given the great importance of these upwelling systems to world fisheries. The intertidal regions of these systems provide an interesting comparison to offshore ecosystems in that they experience similar environmental conditions. However, in comparison to the offshore regions, most intertidal regions do not support large commercial fisheries and harvest pressure is generally low (with a few notable exceptions, particularly in Chile). Similar to comparisons of offshore upwelling ecosystems, we found a remarkable consistency in the trophic structure of intertidal communities across these systems. Benthic macrophytes occupied the vast majority of space and accounted for the largest component of taxonomic richness across regions. Across all regions, the higher trophic levels generally contained increasingly lower taxonomic diversity. This is in contrast to the classic "wasp-waist" structure found in nearshore upwelling

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

regions (Cury et al., 2000) where a very small number of species dominate intermediate trophic levels.

There are several factors that could obscure a wasp-waist structure in intertidal ecosystems. First, many intertidal herbivores graze on epilithic microalgae (e.g. benthic diatoms), which are not easily quantified in surveys (Thompson et al., 2004). Second, sessile, filter-feeding invertebrates, such as barnacles and mussels, typically feed on phytoplankton, which is also difficult to quantify in the very nearshore environment, and not sampled in intertidal surveys. Finally, top-level predators such as birds, which forage both inside and outside the intertidal zone and are patchily distributed in space and time, may play an important role in controlling herbivore abundances (Coleman et al., 1999; Kurle et al., 2008; Lindberg et al., 1998; Wootton, 1992). Despite these differences between offshore and intertidal systems, our results suggest that intermediate trophic level herbivores (e.g. limpets and snails) may play a crucial role in these systems (Hawkins and Hartnoll, 1983; Hunt and McKinnell, 2006; Paine, 2002). Similar to the pelagic ecosystem, herbivores occupy a central position ("hub") in the food web, and are highly connected to other species in the network (Brose et al., 2005; Williams et al., 2002). Across all regions, we found herbivores to be by far the most abundant consumers. In contrast to the wasp-waist structure of offshore systems dominated by a few key trophic intermediates, the intertidal grazer assemblages reflected a diverse suite of species. Intertidal grazers, particularly limpets, are known to have large and spatially variable effects on intertidal macroalgae, (Coleman et al., 2006; Jenkins et al., 2001). In South Africa, intertidal productivity has been shown to be correlated with overall biomass of the herbivore guild (Bustamante et al., 1995). It is interesting to note that in New Zealand, where sessile taxa (macrophytes and invertebrates) occupied nearly all the primary space, mobile consumers were least abundant. Additionally all systems except New Zealand contain a diverse group of herbivores ranging from very large and abundant grazers (*Scutellastra* spp. in the Benguela, *Fissurella* spp. in the Humboldt and *Lottia gigantea* and *Haliotis* spp. in California) to a speciose group of small limpets, snails and chitons. Similarly, the carnivore group in all regions except the Benguela is dominated by ecologically important and large predatory seastars (*Pisaster ochraceus* in California, *Heliaster helianthus* in the Humboldt and *Stichaster australis* in New Zealand). Although carnivores are numerically abundant in the Benguela system, this group tends to contain mostly smaller-bodied whelks. These differences in body size and biomass across systems highlights an important limitation of this study and others based on percent cover and numerical abundance for examining questions of energy flow through an ecosystem. For example, the total biomass of herbivores in Benguela may well be greatest among all regions, even though densities are not highest, given the large sizes of grazers in this system. Despite these shortcomings, we feel that estimates of density and percent cover across systems are relevant to many questions regarding population and community ecology, particularly in systems where intense competition for space, recruitment limitation, and top-down control by predators are known to be important. Although the present study focuses on structure rather than dynamics of intertidal food webs, the observed patterns hint at differences in importance of top-down and bottom-up processes across regions, which have previously been suggested and may be linked to oceanographic differences (Menge et al., 1997a,b; Schiel, 2004).

5.3. Community convergence

Intercontinental comparisons of community attributes have a long tradition in ecology and biogeography, and several authors have hypothesized that community attributes should be similar when comparing climatically similar regions of the world (Cody and Mooney, 1978). Comparisons of communities across climatically similar regions of the world have provided evidence of community convergence in birds (Cody, 1974; Recher, 1969), lizards (Fuentes, 1976; Pianka, 1973) grasslands (Paruelo et al., 1998) and stream invertebrates (Bonada et al., 2008). Although our study is not a direct test of the convergence hypothesis, we found strong functional and trophic similarities in richness and community structure across four of the major temperate intertidal upwelling ecosystems of the world. Despite these similarities, sites within the four regions grouped together in the nMDS based on their functional structure. The differences among regions are likely driven by a variety of factors (e.g. geology, coastal topography, evolutionary history, biogeographic context, habitat diversity, as well as other environmental factors) that are beyond the scope of this study. Our use of SST as a proxy for oceanographic variability is only a first attempt at exploring the mechanisms underlying variation in intertidal community structure among world upwelling systems. For example, although we have not measured habitat diversity in this study we suspect that differences in heterogeneity along coastlines may account for some of the differences in diversity among regions. Both California and New Zealand have relatively high regional diversity (the total number of taxa found within the region) but a relatively low proportion of those taxa are found at any one site (local diversity). The habitat diversity in New Zealand is likely highest among all regions due to the aspect and orientation of the coastline to prevailing ocean conditions. In comparison, habitat diversity in the Humboldt is likely to be lowest among all regions due to the consistent west-facing exposure of the entire coastline to the Pacific. The Humboldt system has the lowest regional diversity; however the ratio of local/regional diversity was highest across all systems, which may reflect relatively low habitat diversity.

The results presented here represent an important step towards a global biogeographic perspective on intertidal community structure in temperate upwelling ecosystems. We hope that broad-scale comparisons, such as this, provide valuable context for mechanistic syntheses across systems. Such efforts are important because, in part, because improved ecosystem management requires greater understanding of interactions among and between species as well as their environment (Larkin, 1996). Currently, we know very little about variation in the dynamics of species interactions within and among these region. We anticipate that future experimental studies aimed at understanding the processes driving variation within and among systems will continue to provide insights useful to the conservation and management of marine ecosystems.

Acknowledgements

We thank the leaders of the ICORUMBA (International Consortium for Research on Upwelling Marine Biogeographic Areas) group, including B. Menge, J. Lubchenco, S. Gaines, S. Navarrete, J. Castilla and G. Branch. This group and much of the research presented here has been funded by the Andrew W. Mellon Foundation. This project was also funded by the Partnership for Interdisciplinary Studies of Coastal Oceans, the USA Minerals Management Service, the New Zealand Foundation for Research, Science and Technology (Coasts and Oceans OBI) and Fondap-Fondecyt 1501-001 to the Center for Advanced Studies in Ecology and Biodiversity (CASEB). We especially thank Lydia Ladah and the ICE group at CICESE, and MARINe. We thank the NZ sampling team: D. Taylor, M. Hickford, R. Dunmore, S. Wood, S. Lilley, P. South. The North America team was led by P. Raimondi and the following contributed greatly to the collection of field data: C. Engel, R. Gaddam, A. Kendall, J. Kovach, K. Kusic, H. Livingston, D. Lohse, E. Maloney, C. Miner, C. Palazzo, C. Svedlund, K. Walters, M. Williams and A.

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

Wyndham. Collection of data in Chile was aided by M. Fernández, M. Rivadeneira, F. Veliz, A. Haupt, T. Contador, A. Masuero, C. Broitman, C. Silva and C. Flores. We thank M. Pfaff, M. Wilhelm, K. Reaugh, and N. Steffani for help in the field and other logistic support in South Africa, while C. van der Westhuisen and C. Erasmus aided access to field sites. This is contribution 329 of the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO): A Long-Term Ecological Consortium funded by the David and Lucille Packard Foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2009.07.038.

References

Bakun, A., 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. University of California Sea Grant, San Diego, California.

Bakun, A., Nelson, C.S., 1991. The seasonal cycle of wind-stress curl in subtropical eastern boundary current regions. Journal of Physical Oceanography 21, 1815–1834.

Barber, R., Smith, R., 1981. Coastal upwelling ecosystems. In: Longhurst, A. (Ed.), Analysis of Marine Ecosystems. Academic Press, New York., pp. 31–68.

Blanchette, C., Miner, C., Raimondi, P., Lohse, D., Heady, K., Broitman, B., 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. Journal of Biogeography 35, 1593–1607.

Bonada, N., Rieradevall, M., Dallas, H., Davis, J., Day, J., Figueroa, R., Resh, V.H., Prat, N., 2008. Multi-scale assessment of macroinvertebrate richness and composition in mediterranean-climate rivers. Freshwater Biology 53, 772–788.

Branch, G.M., Griffiths, C., 1988. The Bengula ecosystem part v. The coastal zone. Oceanography and Marine Biology Annual Review 26, 395–486.

Broitman, B.R., Kinlan, B.P., 2006. Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. Marine Ecology Progress Series 327, 15–25.

Broitman, B.R., Navarrete, S.A., Smith, F., Gaines, S.D., 2001. Geographic variation of southeastern Pacific intertidal communities. Marine Ecology Progress Series 224, 21–34.

Brose, U., Berlow, E.L., Martinez, N.D., 2005. Scaling up keystone effects from simple to complex ecological networks. Ecology Letters 8, 1317–1325.

Bustamante, R.H., Branch, G.M., 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196, 1–28.

Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Keats, D., Jurd, M., McQuaid, C., 1995. Gradients of intertidal primary productivity around the coast of South-Africa and their relationships with consumer biomass. Oecologia 102, 189–201.

Carr, M.E., 2002. Estimation of potential productivity in eastern boundary currents using remote sensing. Deep-Sea Research Part II-Topical Studies in Oceanography 49, 59–80.

Castelao, R.M., Mavor, T.P., Barth, J.A., Breaker, L.C., 2006. Sea surface temperature fronts in the California current system from geostationary satellite observations. Journal of Geophysical Research-Oceans 111. doi:10.1029/2006JC003541.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31, 343–366.

Chiswell, S.M., Schiel, D.R., 2001. Influence of along-shore advection and upwelling on coastal temperature at Kaikoura Peninsula, New Zealand. New Zealand Journal of Marine and Freshwater Research 35, 307–317.

Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117–143.

Cody, M.L., 1974. Optimization in ecology. Science 183, 1156–1164.

Cody, M.L., Mooney, H.A., 1978. Convergence versus non-convergence in mediterranean-climate ecosystems. Annual Review of Ecology and Systematics 9, 265–321.

Coleman, R.A., Goss-Custard, J.D., Durell, S., Hawkins, S.J., 1999. *Limpet Patella* spp. Consumption by oystercatchers *Haematopus ostralegus*: a preference for solitary prey items. Marine Ecology-Progress Series 183, 253–261.

Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Aberg, P., Arenas, F., Arrontes, J., Castro, J., Hartnoll, R.G., Jenkins, S.R., Paula, J., Della Santina, P., Hawkins, S.J., 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. Oecologia 147, 556–564.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Connell, J.H., Orias, E., 1964. The ecological regulation of species diversity. American Naturalist 98, 399–414.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES Journal of Marine Science 57, 603–618.

Cushing, D., 1969. Upwelling and fish production. FAO Fisheries Technical Paper 84, 1–40.

Dobzhansky, T., 1950. Mendelian populations and their evolution. American Naturalist 84, 401–418.

Emanuel, B.P., Bustamante, R.H., Branch, G.M., Eekhout, S., Odendaal, F.J., 1992. A zoogeographic and functional-approach to the selection of marine reserves on the west-coast of South-Africa. South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap 12, 341–354.

Fernandez, M., Jaramillo, E., Marquet, P.A., Moreno, C.A., Navarrete, S.A., Ojeda, F.P., Valdovinos, C.R., Vasquez, J.A., 2000. Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. Revista Chilena de Historia Natural 73, 797–830.

Field, J., Shillington, F., 2006. Variability of the Benguela current system. The Sea 14, 833–861.

Fischer, A.G., 1960. Latitudinal variations in organic diversity. Evolution 14, 64–81.

Francis, A.P., Currie, D.J., 2003. A globally consistent richness-climate relationship for angiosperms. American Naturalist 161, 523–536.

Freon, P., Cury, P., Shannon, L., Roy, C., 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bulletin of Marine Science 76, 385–462.

Fuentes, E.R., 1976. Ecological convergence of lizard communities in Chile and California. Ecology 57, 3–17.

Goldstien, S., Schiel, D., Gemmell, N., 2006. Comparative phylogeography of coastal limpets across a marine disjunction in New Zealand. Molecular Ecology 15, 3259–3268.

Harmsworth, R., Whiteside, M., 1968. Relation of cladoceran remains in lake sediments to primary productivity of lakes. Ecology 49, 998–1000.

Hawkins, S.J., Hartnoll, R.G., 1983. Grazing of intertidal algae by marine-invertebrates. Oceanography and Marine Biology 21, 195–282.

Heath, R.A., 1985. A review of the physical oceanography of the seas around New-Zealand – 1982. New Zealand Journal of Marine and Freshwater Research 19, 79–124.

Hickey, B.M., Banas, N.S., 2003. Oceanography of the US Pacific northwest coastal ocean and estuaries with application to coastal ecology. Estuaries 26, 1010–1031.

Hunt, G.L., McKinnell, S., 2006. Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. Progress in Oceanography 68, 115–124.

Huyer, A., 1983. Coastal upwelling in the California current system. Progress in Oceanography 12, 259–284.

Jarre-Teichmann, A., 1998. The potential role of mass balance models for the management of upwelling ecosystems. Ecological Applications 8, S93–S103.

Jarre-Teichmann, A., Shannon, L.J., Moloney, C.L., Wickens, P.A., 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap 19, 391–414.

Jenkins, S.R., Arenas, F., Arrontes, J., Bussell, J., Castro, J., Coleman, R.A., Hawkins, S.J., Kay, S., Martinez, B., Oliveros, J., Roberts, M.F., Sousa, S., Thompson, R.C., Hartnoll, R.G., 2001. European-scale analysis of seasonal variability in limpet grazing activity and microalgal abundance. Marine Ecology-Progress Series 211, 193–203.

Kruskal, J.B., Wish, M., 1978. Multidimensional Scaling. Sage Publications, Beverly Hills, CA.

Kurle, C.M., Croll, D.A., Tershy, B.R., 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. Proceedings of the National Academy of Sciences of the United States of America 105, 3800–3804.

Larkin, P.A., 1996. Concepts and issues in marine ecosystem management. Reviews in Fish Biology and Fisheries 6, 139–164.

Lindberg, D., Estes, J., Warheit, K., 1998. Human influences on trophic cascades along rocky shores. Ecological Applications 8, 880–890.

Magurran, A., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton.

May, R.M., Macarthur, R., 1972. Niche overlap as a function of environmental variability. Proceedings of the National Academy of Sciences of the United States of America 69, 1109–1113.

McQuaid, C.D., Branch, G.M., 1985. Trophic structure of rocky intertidal communities – response to wave action and implications for energy-flow. Marine Ecology-Progress Series 22, 153–161.

Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997a. Benthic-pelagic links and rocky intertidal communities: bottom-up effects or top-down control? Proceedings of the National Academy of Sciences USA 94, 14530–14535.

Menge, B.A., Daley, B.A., Wheeler, P.A., Strub, P.T., 1997b. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography 42, 57–66.

Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist 130, 730–757.

Navarrete, S.A., Wieters, E.A., Broitman, B.R., Castilla, J.C., 2005. Scales of benthic–pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. Proceedings of the National Academy of Sciences USA 102, 18046–18051.

Norton, T.A., Hawkins, S.J., Manley, N.L., Williams, G.A., Watson, D.C., 1990. Scraping a living – a review of littorinid grazing. Hydrobiologia 193, 117–138.

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038

Padilla, D.K., Allen, B.J., 2000. Paradigm lost: reconsidering functional form and group hypotheses in marine ecology. Journal of Experimental Marine Biology and Ecology 250, 207–221.

Paine, R.T., 1966. Food web complexity and species diversity. American Naturalist 100, 65–75.

Paine, R.T., 2002. Trophic control of production in a rocky intertidal community. Science 296, 736–739.

Paruelo, J.M., Jobbagy, E.G., Sala, O.E., Lauenroth, W.K., Burke, I.C., 1998. Functional and structural convergence of temperate grassland and shrubland ecosystems. Ecological Applications 8, 194–206.

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

Pianka, E., 1973. The structure of lizard communities. Annual Review of Ecology Evolution and Systematics 4, 53–74.

Power, M.E., 2006. Environmental controls on food web regimes: a fluvial perspective. Progress in Oceanography 68, 125–133.

Recher, H.F., 1969. Bird species diversity and habitat diversity in Australia and North America. American Naturalist 103, 75–80.

Sanders, H.L., 1968. Marine benthic diversity – a comparative study. American Naturalist 102, 243–282.

Schiel, D.R., 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. Journal of Experimental Marine Biology and Ecology 309, 342.

Schoch, G.C., Menge, B.A., Allison, G., Kavanaugh, M., Thompson, S.A., Wood, S.A., 2005. Fifteen degrees of separation: latitudinal gradients of rocky intertidal biota along the California current. Limnology and Oceanography 51, 2564–2585.

Schoener, T.W., 1988. On testing the Macarthur–Wilson model with data on rates. American Naturalist 131, 847–864.

Shannon, L., 1985. The Benguela ecosystem part I. Evolution of the Benguela, physical features and processes. Oceanography and Marine Biology Annual Review 23, 105–182.

Shannon, L., Nelson, G., 1986. The Benguela: laarge scale features and processes and system variability. In: Wefer, G., Berger, W., Siedler, G., Webb, D. (Eds.), The South Atlantic: Present and Past Circulation. Springer, Berlin, pp. 163–210.

Shaw, A.G.P., Vennell, R., 2000. Variability of water masses through the Mernoo saddle, South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research 34, 103–116.

Siegel, D.A., Maritorena, S., Nelson, N.B., Behrenfeld, M.J., McClain, C.R., 2005. Colored dissolved organic matter and its influence on the satellite-based characterization of the ocean biosphere. Geophysical Research Letters 32. doi:10.1029/2005GL024310.

Simpson, G.G., 1964. Species density of North American recent mammals. Systematic Zoology 13, 57–73.

Sink, K.J., Branch, G.M., Harris, J.M., 2005. Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa. African Journal of Marine Science 27, 81–96.

Sommer, U., 1984. The paradox of the plankton – fluctuations of phosphorus availability maintain diversity of phytoplankton in flow-through cultures. Limnology and Oceanography 29, 633–636.

Sousa, W.P., 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15, 353–391.

Stanton, B.R., 1976. Oceanic frontal jet near norfolk-ridge northwest of New-Zealand. Deep-Sea Research 23, 821–829.

Stephenson, T.A., 1960. The southern cold temperate coasts, with special reference to South Africa. Proceedings of the Royal Society of London Series B-Biological Sciences 152, 635–638.

Stephenson, T.A., Stephenson, A., 1949. The universal features of zonation between tide-marks on rocky coasts. Journal of Ecology 37, 289–305.

Strub, P.T., Mesias, J.M., Montecino, V., Rutllant, J., Salinas, S., 1998. Coastal ocean circulation off western South America. The Sea 11, 273–313.

Thompson, R.C., Norton, T.A., Hawkins, S.J., 2004. Physical stress and biological control regulate the producer-consumer balance in intertidal biofilms. Ecology 85, 1372–1382.

Underwood, A.J., Petraitis, P.S., 1993. Structure of intertidal assemblages in different locations: How can local processes be compared? In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, Illinois, USA, London, England, UK, pp. 39–51.

Vincent, W.F., Howard-Williams, C., 1991. Distribution and biological properties of oceanic water masses around the south island, New-Zealand. New Zealand Journal of Marine and Freshwater Research 25, 21–42.

Wieters, E.A., 2005. Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. Marine Ecology Progress Series 301, 43–54.

Wieters, E.A., 2006. Benthic-pelagic coupling: rocky intertidal communities and nearshore oceanographic conditions across multiple scales. Department of Zoology, vol. PhD. University of Cape Town, Cape Town. p. 148.

Wieters, E.A., Broitman, B.R., Branch, G.M., 2009. Benthic community structure and spatiotemporal thermal regimes in two upwelling ecosystems: Comparisons between South Africa and Chile. Limnology and Oceanography 54, 1060–1072.

Wieters, E.A., Kaplan, D.M., Navarrete, S.A., Sotomayor, A., Largier, J., Nielsen, K.J., Veliz, F., 2003. Alongshore and temporal variability in chlorophyll a concentration in Chilean nearshore waters. Marine Ecology-Progress Series 249, 93–105.

Williams, R.J., Berlow, E.L., Dunne, J.A., Barabasi, A.L., Martinez, N.D., 2002. Two degrees of separation in complex food webs. Proceedings of the National Academy of Sciences of the United States of America 99, 12913–12916.

Wootton, J.T., 1992. Indirect effects, prey susceptibility, and habitat selection – impacts of birds on limpets and algae. Ecology 73, 981–991.

Please cite this article in press as: Blanchette, C.A., et al. Trophic structure and diversity in rocky intertidal upwelling ecosystems: A comparison of community patterns across California, Chile, South Africa and New Zealand. Prog. Oceanogr. (2009), doi:10.1016/j.pocean.2009.07.038