

Chapter 12

Consumer-Resource Interactions on an Environmental Mosaic

The Role of Top-Down and Bottom-Up Forcing of Ecological Interactions along the Rocky Shores of the Temperate South-Eastern Pacific

Moisés A. Aguilera, Bernardo R. Broitman,
Julio A. Vásquez and Patricio A. Camus

12.1 Introduction

Over the past three decades, the biogeography, phylogeography and ecology of the diverse and unique species assemblage that inhabits the subtropical and temperate Pacific shores of South America (5–42°S) has received increasing scientific attention. Different studies have taken place in an interdisciplinary context and are matched with major developments in our understanding of coastal oceanographic processes along the region's shorelines (e.g., Broitman et al., 2001; Navarrete et al., 2005; Lagos et al., 2007; Tapia et al., 2009, 2014). Following seminal work by Camus (2001), the historical biogeographic division of Pacific South America into a warm-temperate Peruvian region (5–42°S) and a cool subantarctic region (42–54°S), has revealed a more complex biogeographic structure than previously thought (e.g., Thiel et al. 2007; Rivadeneira et al. 2012; Valdovinos et al. 2003; see Figure 12.1). The northern warm-temperate Peruvian sector appears separated from the

subantarctic province by a diffuse transitional region that spans from 30 to 41°S. Along this region, breaks in species distributions (see Figure 12.2) are clumped around areas where rapid and persistent changes in circulation and hydrographic conditions occur, which are usually associated to large headlands and abrupt changes in the width of the continental shelf (e.g., Hormazábal et al., 2004). These topographically locked oceanographic features determine a persistent spatial structure of the coastal environment along the transitional region, with implications for phylogeography and ecology (e.g., Broitman et al., 2001, 2011; Wieters et al., 2003; Rivadeneira et al., 2012; Haye et al., 2014).

First, and propelled by advances in molecular genetics, studies of the region's biota have revealed the presence of several cryptic species among some of the dominant and habitat-forming algal species of the mid- and low-intertidal zones of the rocky shore, the corticated algae *Mazzaella* and kelps like *Lessonia*, respectively (Tellier et al., 2011; Montecinos et al., 2012). The locations of the breaks between the

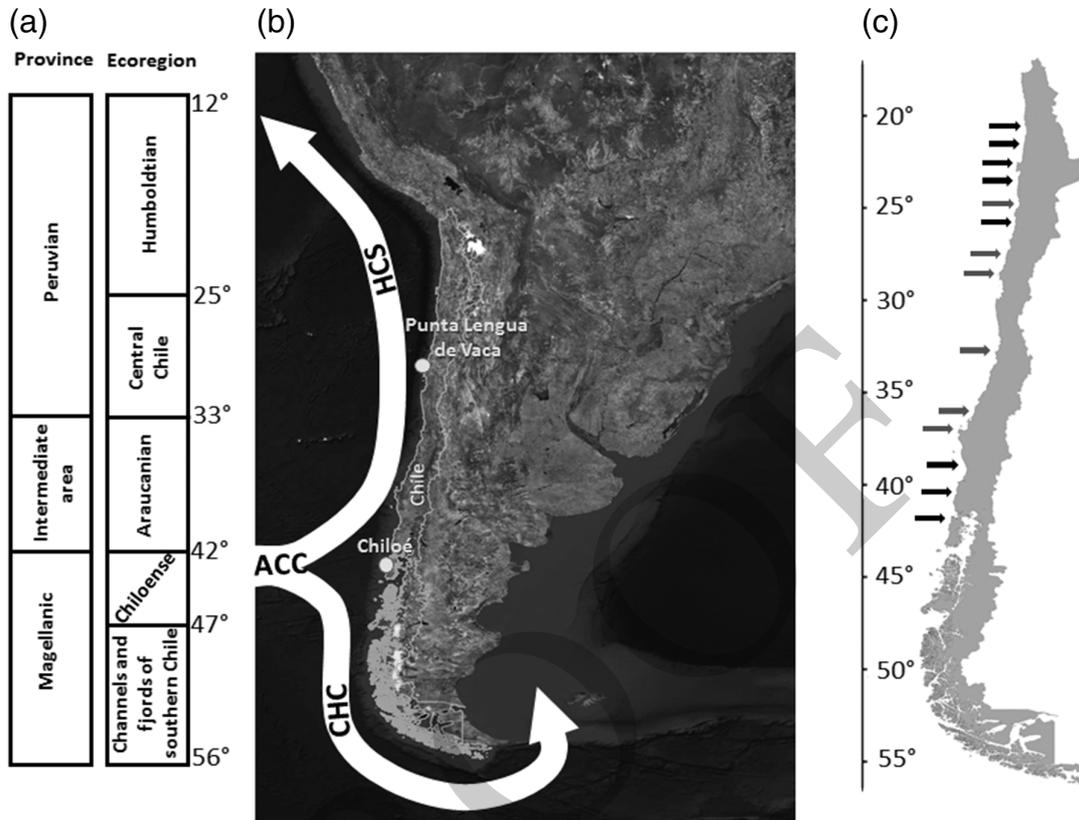


Fig. 12.1 (a) Biogeographic provinces (after Camus, 2001; Thiel et al., 2007) and ecoregions (after Spalding et al., 2007) along the southeast Pacific coast, indicating their latitudinal boundaries. (b) Simplified view of the major cold flows (white arrows) off western South America, originating from the Antarctic Circumpolar Current (ACC) after reaching the Chilean coast: the poleward Cape Horn Current (CHC), encompassing the southern cone, and the equatorward (HCS), an eastern boundary current formed actually by coastal and oceanic branches. Yellow dots indicate the location of two places often referred to in the text because of their ecological or biogeographical importance. (c) Fine-grained latitudinal breaks in species diversity (after UACH, 2006) along the Chilean coast (excluding the area south of 45°S), detected in analyses combining multiple littoral taxa from rocky and sandy shores. Breaks (associated with the latitude axis on the left) correspond to significant spatial changes in beta diversity (black arrows) and in both alpha and beta diversity (blue arrows). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section)

cryptic species corresponds well with the geographical template dictated by coastal oceanography (Hormazábal et al., 2004; Tapia et al., 2009, 2014) and is further supported by the phylogeographic structure of many other coastal species (see Haye et al., 2014). In this context, one of the most important questions is what are the consequences of such distributional changes on species interactions in the rest of the community? For example, different regions separated by the biogeographic break could evidence changes

in the functional structure of consumer assemblages (i.e., herbivores and carnivores). That could be related to a replacement from tropical to temperate species occurrences across the HCS (e.g., Lancellotti and Vásquez, 1999; Valdovinos et al., 2003; Hernández et al., 2005; Moreno et al., 2006a). Spatial turnover of species could be influenced by large-scale processes like the El Niño southern oscillation (ENSO), which can generate a gradient in water temperature across this region (Iriarte and González, 2004) affecting

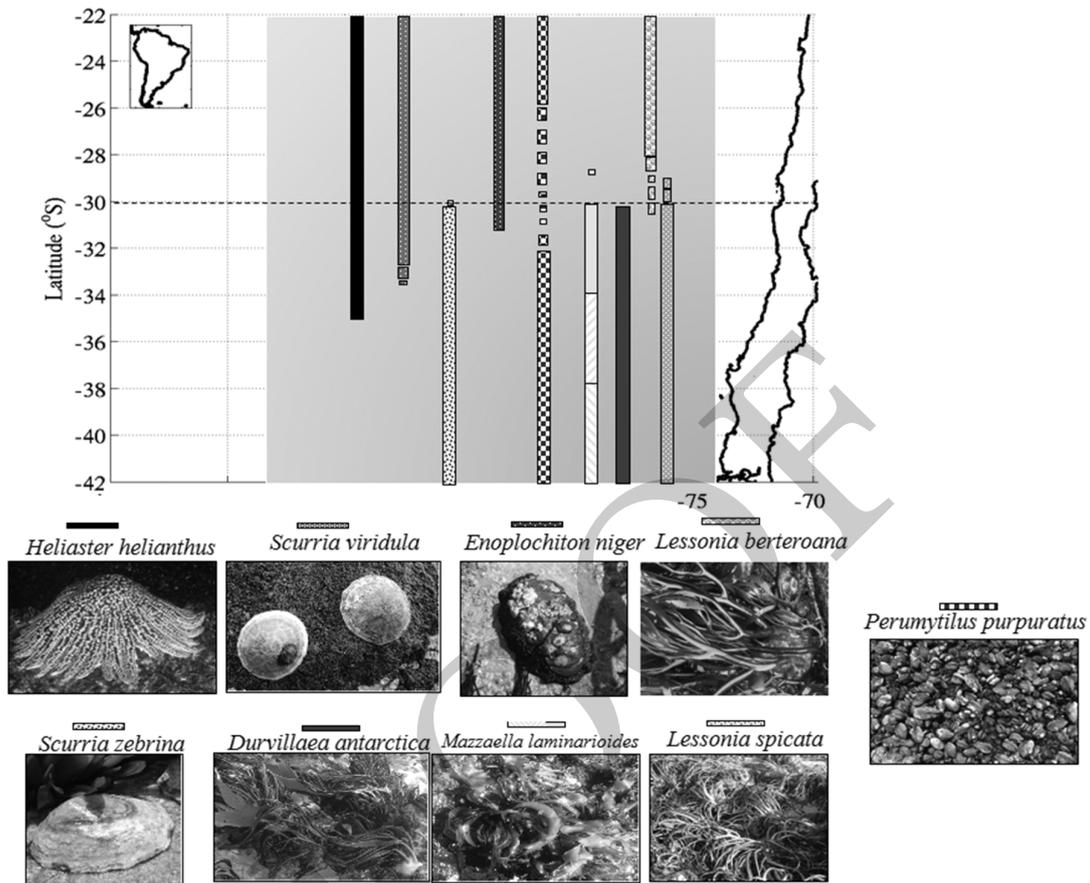


Fig. 12.2 Scheme of the geographic distributional pattern of different intertidal species, (i.e., distributional species mosaic) present across north and central-south Chile. Most species find their polar or equatorial range edge between the biogeographic transitional zone at Punta Lengua de Vaca (PLV, 30°S), and near 36°S. The sunstar *Heliaster helianthus* and the grazer species; *Scurria viridula*, *Scurria zebrina* and *Enoplochiton niger* are the main consumers in intertidal levels across the range considered. The corticated alga *Mazzaella laminarioides* is dominant in mid- and high-intertidal levels south 30°S, where three clades are reported (see yellow bars, Montecinos et al., 2012). The furoid *Durvillaea antarctica* and the kelp *Lessonia spicata* are also dominant south PLV in low-intertidal levels. North of this region, these algae are replaced by *Lessonia berteriana* (green bars, e.g., Tellier et al., 2011). Segmented bars correspond to small population densities, or small patches, of invertebrates and algae species present across the biographic transitional zone. For example, the mussel *Perumytilus purpuratus* (brown-grid bars) showed a discontinuous distribution across the transitional zone at 30°S, while a relatively continuous distribution is observed for this species both south and north of this range (Navarrete et al., 2005). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section)

rocky shore consumer assemblage composition through affecting their early developmental stages in the plankton (e.g., Escribano et al., 2004). Alternatively, there could be a spatially shifting mosaic of consumer functional structure (Aguilera et al. unpublished data) along the two sides of the biogeographic break underlying

changes in species composition (e.g., Rivadeneira and Fernández, 2005; Rivadeneira et al., 2012; see Figure 12.2) and matching the patchy spatial structure of oceanographic conditions across the HCS (e.g., Valle-Levinson et al., 2003; Montecinos and Lange, 2009; Thiel et al., 2007; Tapia et al., 2009, 2014; see Figure 12.1).

The deep temporal signature of coastal oceanography on coastal biogeography and phylogeography is underpinned by the spatial structure of bottom-up effects of ecological processes (e.g., Wieters et al., 2003; Wieters, 2005; Nielsen and Navarrete, 2004; Navarrete et al., 2005). Nutrients derived from coastal upwelling determine intertidal algal growth patterns (Wieters et al., 2003; Wieters, 2005), which, in turn, define the role of some herbivores as controllers of algal biomass and important drivers of community composition (Nielsen and Navarrete, 2004; Aguilera and Navarrete, 2012a; Aguilera et al., 2015a). In this way, ecological interactions like the consumer–resource interaction can be strongly modulated by oceanographic context (Nielsen and Navarrete, 2004), providing a mechanistic basis for the seemingly diffuse nature of transitional biogeographic regions.

Across the Pacific coasts, herbivores and carnivores play an important role regulating the structure of rocky shore communities (e.g., Jara and Moreno, 1984; Castilla and Durán, 1985; Paine et al., 1985; Moreno et al., 1986; Vásquez and Buschmann, 1997; Navarrete and Castilla, 2003; Aguilera, 2011). Specifically, given the diversity of impacts that herbivores can have on algal recruitment, abundance and diversity, they can have strong and differentiated effects on rocky shore community succession (Aguilera and Navarrete, 2012a) and overall seascape spatial heterogeneity (Aguilera et al., 2015a). Most species have negative direct effects on their target resource (e.g., algae), but a number of species can have significant positive indirect effects on established algal species (Aguilera et al., 2015b and see later). The tightly linked functional structure results in a low functional compensatory potential in the face of local species loss or extinctions (Aguilera and Navarrete, 2012a), which can be caused by intense human harvesting (Oliva and Castilla, 1986; Castilla, 1999; Moreno, 2001) and/or distributional changes of herbivorous species following climate change (e.g., Rivadeneira and Fernández, 2005).

One of the main challenges for the study of the ecology of rocky shore ecosystems on the temperate Eastern Pacific today, is to examine how coastal oceanographic processes regulate species range expansion and introduction, or contraction,

and how biotic interactions and environmental filtering define dynamic biogeographic patterns along spatially structured marine environments (Valdivia et al., 2015). Thus, there is a great interest in exploring the spatial structure of interacting stressors that may shape local and regional ecosystem vulnerability in the face of unprecedented environmental change.

12.2 Historical Biogeography of the Temperate Eastern Pacific

Along the south-east Pacific and the Chilean coast (18.5–56°S) in particular, geographic patterns of species diversity are closely linked to meso- and large-scale physical determinants. For instance, mid-low latitudes are dominated by upwelling and land–sea interactions with large oscillations in patterns of physico-biological coupling driven by inter-annual variations and equatorial forcing (Strub et al., 1998; Takesue et al., 2004; Lagos et al., 2007; Thiel et al., 2007). On the other hand, mid-high latitudes are deeply influenced by physical interactions between coastal geomorphology and the ACC (Ahumada et al., 2000; Camus, 2001; Barker and Thomas, 2004; Thiel et al., 2007). On a very large scale, however, the primary importance of the ACC (the world's strongest current) is reflected in the matching between biogeographical patterns and the spatial structure and extent of its two branches, which form after the ACC impinges the coast of South America around 40–45°S (see Figure 12.1). First, the poleward-flowing CHC, that continues eastwards into the Atlantic, forming the equatorwards Malvinas Current, dominates the surface ocean flow around southern South America. Second, the equatorward-flowing Humboldt Current is an eastern boundary current exerting a strong cooling influence up to ~5°S (Sepúlveda et al. 2016). The onset of the ACC, linked to the break-up of Gondwana and the opening of the Drake Passage, involved a substantial reversal of the warm conditions in the late Paleogene (Pfuhl and McCave, 2005), and was the most influential event in the origin of modern biogeographic provinces (see review by Camus, 2001).

Even with some departures reflecting the idiosyncratic histories of some taxa or methodological aspects (e.g., invertebrates: Lancellotti and Vásquez, 1999; Haussermann and Forsterra, 2009; Navarrete et al., 2014; red and brown algae: Meneses and Santelices, 2000; ectoparasites: González and Moreno, 2005), coastal taxa as a whole exhibit a congruent pattern of distributional breaks (Camus, 2001; Thiel et al., 2007) forming three major units (arrows in Figure 12.1), from which the first two show biogeographic anomalies. The first is the warm-temperate Peruvian province (5–30/33°S) that encompasses the coasts of Peru, which are dominated by subtropical taxa, and northern Chile, which is dominated instead by temperate taxa, with a marked paucity of warm-water species (see Santelices, 1980; Brattström and Johanssen, 1983; Camus, 2001). The second is an intermediate area (30/33–42°S) encompassing central-southern Chile, which is dominated by temperate and subantarctic taxa without a common history and showing no gradual pattern of biotic replacement, thus lacking the distinctive biogeographical character of a province or a transition zone. Finally, the cold-temperate Magellanic province (42–56°S, although extended into the Atlantic up to 42.5°S in Argentina), encompasses austral Chile from Chiloé Island to Cape Horn, a complex system of islands, peninsulas, fjords, channels and inner seas shaped by glacial and tectonic action in the Pleistocene. This cold province is characterised by protected hyposaline environments dominated by subantarctic taxa (see Velásquez et al., 2016). The origin of this provincial pattern can be traced back to the establishment of the cold HCS, which is connected with two major events that largely account for the modern irregularities in northern Chile and the intermediate area (Thiel et al., 2007). These events involve the retreat of the former warm-water biota to lower latitudes along with the northward advance of the subantarctic biota (see Brattström and Johanssen, 1983; Camus, 2001) and the onset of the oxygen minimum zone, concurrent with mass extinctions in the current Peruvian province (e.g., about 70 per cent of bivalve species; Rivadeneira and Marquet, 2007). However, extralimital fossil assemblages reveal that strong or long-lasting warming

(ENSO-like) events led to repeated invasions of northern Chile by tropical species throughout the Quaternary (Llagostera, 1979; Ortlieb, 1995; Ortlieb et al., 2003), uncovering a complex scenario of extinctions and recolonisations, which may have also been frequent over the last 10,000 years, where ENSO has been continuously active with peaks of high-frequency clusters of events at about 2,000 year intervals (Moy et al., 2002). In fact, phenomena such as isolated or correlated local extinctions and community-wide changes are still common in northern Chile during strong or moderate El Niño events, but they are not observed south of 30°S, where ENSO impacts are comparatively negligible (for reviews and case studies see Castilla and Camus, 1992; Camus, 1994, 2008; Thiel et al., 2007).

The interplay between past and present biogeographic factors in north-central Chile is reflected in the fact that many dominant species show phylogeographic breaks at 30°S, which originated either in the Neogene, the Pleistocene or the Holocene (e.g., Sánchez et al., 2011; Martin and Zuccarello, 2012; Montecinos et al., 2012; Haye et al., 2014). These genetic signatures remain strong in low-dispersal species, but were partially or entirely erased in high-dispersal species following modern gene flow across 30°S (Haye et al., 2014). For instance, major breaks in eddy kinetic activity, wind stress and coastal versus offshore productivity (Hormazábal et al., 2004; Thiel et al., 2007) reveal a physical transition around 30°S that seems to play a crucial biogeographical role (e.g., as a differential barrier to larval transport and dispersal; see Figure 12.2). This putative barrier helps to explain the abrupt distributional breaks at that latitude by numerous taxa with different origins, life cycles, ecologies or habitats (Thiel et al., 2007; Broitman et al., 2011), even including the cephalopod fauna, which is formed entirely by non-endemic, widely ranging and mostly eurithermic species (Ibáñez et al., 2009). In addition, these and other physical factors (analysed in detail in the next section) are among the forcing agents considered by Spalding et al. (2007; based on Sullivan and Bustamante, 1999) to define six coastal ecoregions nested in only two provinces along the temperate south-east Pacific. The larger of these two

provinces (warm-temperate south-eastern Pacific) subsumes the Peruvian province and the intermediate area outlined in this chapter (Figure 12.1), although the latter two are supported by the current information. Moreover, fine-grained analyses integrating databases for several rocky- and sandy-shore taxa (UACH, 2006) detected an unusual array of spatial breaks in species richness and beta diversity along the Chilean coast, suggesting that current biogeographical classifications could be masking a more complex patterning of biodiversity.

12.3 Species Distribution Patterns and Biotic–Environmental Coupled Processes across Rocky Shores of the Temperate Eastern Pacific

Benthic assemblage composition across the temperate Eastern Pacific rocky shores is dominated by a diverse group of algae and invertebrates endemic to the Peruvian or Magellanic provinces (see Broitman et al., 2001; Moreno et al., 2006a; Rivadeneira et al., 2012). These two biogeographic provinces are abutted by very clear boundaries defined by large-scale oceanographic transitions (Camus, 2001; see Figure 12.1). On the southern end of Pacific South America, the Drake Passage, around 56°S, and energetic ACC flowing through it mark the polar boundary of the Magellanic or subantarctic province. Similarly, the equatorial boundary of the Peruvian province is marked by the Paita Peninsula (~ 5°S), where the coast of western South America turns east and the westward-flowing trade winds, running along the equatorial guideline, separate the temperate and tropical realms (Longhurst, 1998). These two biogeographic provinces meet around 40°S, on Chiloé Island, where the eastward-flowing west wind drift impinges on the coast of western South America, determining the ACC (Chaigneau and Pizarro, 2005). The cold, northward-flowing branch of the ACC is commonly known as the Humboldt Current. However, the HCS is made by an ensemble of

equatorward- and poleward-flowing currents, some of them superficial or on the subsurface, in proximity to the coast or offshore (Strub et al., 1998). The complex structure of the alongshore flow of the HCS is driven by the spatial and temporal variability of the wind patterns, which is many times locked to coastal geomorphology. Equatorward winds blowing along the coast pushes surface waters along shore which lifts the thermocline (Ekman transport) and following the rotation of the earth (the Coriolis effect) displaces the surface waters to the west. This wind-driven offshore divergence of the equatorward-flowing coastal current brings cold, nutrient-rich waters from the poleward-flowing subsurface waters to the surface, a process known as coastal upwelling (Strub et al., 1998). Importantly, the influx of nutrients to the photic zone in association to coastal upwelling along the HCS maintains some of the most productive fisheries on the planet (Bakun and Weeks, 2008).

12.3.1 Productivity Patterns and Invertebrate Larval Supply

The large productivity of the HCS is a defining characteristic of the Peruvian province, where upwelling dynamics also drive energy along and cross-shelf transport process (Hormazábal et al., 2004). The nearshore flow field is an important process influencing the dispersal of planktonic larvae from benthic populations (Poulin et al., 2002). A broad region, limited to the north by a large headland located around 30°S, PLV is recognised as the largest upwelling foci along the region (Aguirre et al., 2012) and marks a division between the Peruvian province to the north and a transitional region that extends to the south until the well-established boundary at Chiloé Island (Thiel et al., 2007 and see earlier). In particular, PLV delimits a region where the rates of larval arrival of rocky shore intertidal invertebrates are up to three orders of magnitude higher than the region northwards (Navarrete et al., 2002, 2005; Valdivia et al., 2015). This spatial pattern seems to be related to coastal geomorphology where bays on the lee of headlands can retain larvae from benthic species, increasing local recruitment (Palma et al., 2006) and the intensity of year-round upwelling around 30°S. The coast

north of PLV has also fewer sheltered bays and a narrower continental shelf, thus providing fewer opportunities for nearshore larval retention. In addition, north of PLV, upwelling-favourable winds show a reduced seasonality, implying that, although they are not as strong and intense as in the southern sector, they tend to blow year-round, a process that is related to the latitudinal migration of the South Pacific anticyclone (Rahn et al., 2014). Hence, the narrower continental shelf and temporal distribution of upwelling-favourable winds provide a transport-driven mechanistic underpinning of the ecological and biogeographic patterns discussed later.

12.3.2 Environmental Processes across 30°S Transitional Zone

Recent insights from molecular phylogenetics have somehow modified prevailing views of the biogeographic structure of the Peruvian province (Cárdenas et al., 2009; Brante et al., 2012; Haye et al., 2014). A region around the PLV headland is the location where an important number of ecologically important species find their poleward or equatorial boundary (see Figure 12.2 and previous section). In the case of poleward boundaries, some notable examples are the large grazers, the chiton *E. niger* and the limpet *Stictidula* (Broitman et al., 2011; Aguilera et al., 2013a, 2013b). On the other hand, the limpet *S. zebrina* and two algae, the fucoid *D. antarctica* and the gigartinacea *M. laminarioides* have their equatorward boundaries at PLV (see Figure 12.2). As mentioned earlier, molecular phylogenetics have greatly contributed to consolidate the transitional nature of the region (Haye et al., 2014). The modified biogeographic structure has also important ecological implications, as dominant species of the rocky intertidal zone have turned out to be cryptic species with their southern/northern range limit around PLV. For example, *M. laminarioides* is a species complex that actually comprises three species (see yellow bars in Figure 12.2), with the northernmost species having a restricted geographic range around PLV (small yellow dot in Figure 12.2), which seemed to have acted as a refuge during the last glacial maximum about 18,000 years BP (Montecinos et al., 2012). A striking example is the kelp *Lessonia nigrescens*,

which dominates the low-intertidal zone along the Peruvian province and is a key component of the assemblage (Thiel et al., 2007 and see later). *Lessonia* has been recently recognised as comprised of two cryptic species, *L. berteriana* to the north and *L. spicata* to the south (green bars in Figure 12.2). The distribution limit between these two cryptic species is a geographic mosaic; i.e., interspersed patches of both species that spans the great Coquimbo bay and extends from PLV up to 29°S (Tellier et al., 2011; González et al., 2012; Figure 12.2). This also corresponds to the area where the northernmost populations of the mid-intertidal species *M. laminarioides* are located (Aguilera et al., 2015b). Several other examples are related to the contrasting phylogeographic structure of other benthic species, not all of them from rocky shores (Haye et al., 2014).

Intertidal zonation patterns across the region are characterised by a low-intertidal zone dominated by a conspicuous belt of kelps of the genus *Lessonia*, which dominate primary space on the low-intertidal shore along with calcareous or fleshy, crustose algae, chiefly the calcareous *Lithothamnion* spp. and the non-calcareous species *Hildenbrandia lecanelli*, respectively. Fleshy species are more common south of PLV (Broitman et al., 2011), where other corticated algae such as several species of *Gelidium*, and the fucoid *D. antarctica*, among other species, also occupy an important proportion of primary space. Fleshy algae species and *Gelidium* present between *Lessonia* and *Durvillaea* clumps are browsed by large keyhole limpets, mainly *Fissurella limbata* and *Fissurella maxima* while periphyton (microalgae, cyanobacteria and sporelings of macroalgae) are grazed by several chitons, most noticeably the large *Acanthopleura echinata* and *E. niger*, ~~the latter only lives north of PLV~~ (Broitman et al., 2011; Aguilera et al., 2015a). Sea urchin species, *Loxechinus albus* and *Tetrapygus niger*, commonly graze on adult and juvenile *Lessonia* and fleshy algae on rock pools. The small balanoid barnacles, *Nothobalanus flosculus* and *Balanus laevis*, and large clumps of the mussel *Semimytilus algosus* are seasonally abundant in the low shore, but they are rapidly extirpated by carnivores (see later). The mid-intertidal zone to the south of PLV is dominated by the mussel *P. purpuratus*, which are

conspicuously absent to the north except for isolated patches inside sheltered bays (Broitman et al., 2001; Navarrete et al., 2005; see brown-mesh bars in Figure 12.2). Corticated algae interspersed or atop mussel beds are abundant, notably the *M. laminarioides* complex and several other species of Gigartinaceae south of 36°S. Small chthamaloid barnacles, mainly *Jehlius cirratus* and *Notochthamalus scabrosus* are common space occupiers (Shinen and Navarrete, 2010), particularly north of PLV where they are the most abundant sessile invertebrates of the mid-intertidal zone. Grazers are abundant, particularly limpets from the genus *Scurria* and several species of chiton, particularly *Chiton granosus* (Aguilera and Navarrete, 2007). The keyhole limpet *Fissurella crassa* is also abundant, especially inside *Perumytilus* beds. The large seastar *H. helianthus* and the muricid gastropod *Concholepas concholepas* are key carnivores across the intertidal zone, exerting strong top-down pressure on invertebrate prey.

The studies highlighted point out to the large role played by environmental filtering, like upwelling intensity and sea water temperature, which can constrain/allow larval settlement and recruitment through large scales (dozens of kilometres; Valdivia et al., 2015). These processes can shape species composition of local assemblages across the large region encompassed by our review. For example, changing coastal wind patterns under climate change in the region are forecasted to increase in intensity and change to poleward direction (Sydeman et al., 2014; Rykaczewski et al., 2015). In turn, this intensification is expected to homogenise coastal upwelling regions (Wang et al., 2015), suppressing the rich spatial structure observed across the HCS. Alternatively, locally intensified upwelling in a warming world may provide for spatially persistent refugia that reinforce the alongshore relationship of oceanographic spatial structure with species composition patterns (Hu and Guillemin, 2016; Lourenço et al., 2016). In this way, a major challenge ahead is to increase our ability to combine environmental models that integrate species' distributions and their physiological limits, and incorporate trophic interactions as determinants of local ecological structure.

12.4 Consumer–Resource Interaction: Diversity in Response to Local Environmental Gradients

12.4.1 Herbivore–Alga Interaction in Space and Time

Herbivory is related to the consumptive effects that animals impose on populations or communities of plants, and is considered one of the most important ecological processes in marine ecosystems around the world (Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983; Poore et al., 2012). Marine herbivores can determine temporal and spatial distribution of algae in both intertidal and subtidal habitats (Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983; Jenkins et al., 2005; Poore et al., 2012). Through consumption of mature algae and spores, different herbivores can affect successional pathways, determining algal species composition and abundance (Hawkins and Hartnoll, 1983). As herbivores are also consumed by carnivores, including humans, they also have a central importance in food web dynamics and ecosystem functioning (e.g., Paine, 1980; Ling et al., 2009; Poore et al., 2012).

Seminal studies by Paine (e.g., 1980, 1992) on the functional structure of benthic herbivore assemblages on northern Pacific coasts, showed that very few species have strong impacts on algal community structure. Thus, low compensatory potential was observed for grazers with strong per capita impacts (Paine, 1992; see also Sala and Graham, 2002 for kelp forest ecosystems). Along the coast of Chile, on the southern Pacific, the benthic herbivore guild is characterised by species with diverse functional roles (e.g., Moreno and Jaramillo, 1983; Jara and Moreno, 1984; Nielsen and Navarrete, 2004; Aguilera and Navarrete, 2007, 2012a; and see Vásquez and Buschmann, 1997 and Aguilera, 2011 for review). Keyhole limpets (*Fissurella* spp.), chitons (e.g., *C. granosus*, *E. niger*, *Tonicia* spp.), Scurrinid limpets (e.g., *S. zebрина*, *Scurria ceciliana*, *S. viridula*) and sea urchins (*T. niger*, *L. albus*) are the most abundant herbivores present in rocky intertidal habitats

along the Chilean coast (see Vásquez and Buschmann, 1997 and Aguilera, 2011 for review). In subtidal systems, kelp-associated species like the fish *Scartichthys viridis*, the sea urchin *L. albus* and the turban snail *Tegula atra* are among the most important strict herbivore species (Ojeda and Muñoz, 1999; Vásquez and Buschmann, 1997). Omnivorous fish species like *Aplodactylus punctatus* and *Girella laevis* are also kelp-associated species (Pérez-Matus et al., 2007), and they can exert important grazing/browsing control of different algae species (Pérez-Matus et al., 2012).

In intertidal habitats, most benthic grazers have strong negative effects on more palatable early successional species (e.g., *Ulva* spp.), that dominate the seascape in the absence of herbivores or under reduced densities of them (see Aguilera, 2011 for review). Thus, equivalence or redundancy in consumptive effects on ephemeral algae is expected for most species of the herbivore assemblage. Experimental studies have shown that most species have diverse functional roles throughout the different stages of community succession (Aguilera and Navarrete, 2012a). Specifically, most herbivores have redundant effects during early succession, but differentiated effects are common during late succession when corticated algae are more dominant (Aguilera and Navarrete, 2012a). Even the magnitude and direction of effects on periphyton (i.e., microalgae and cyanobacteria) community structure can differ among herbivorous species (Aguilera et al., 2013a). Exceptionally, keyhole limpets (*F. crassa*, *Fissurella picta*) have a more differentiated and strong negative effect during late succession consuming the dominant corticated alga *M. laminarioides* (Moreno and Jaramillo, 1983; Aguilera and Navarrete, 2012a). Thus, low compensatory potential in controlling *M. laminarioides* biomass is expected for the other benthic herbivore species if *Fissurella* spp. are absent or if densities of these limpets are reduced by human harvesting, which is intense on Chilean coasts (e.g., Moreno et al., 1984; Oliva and Castilla, 1986; Moreno, 2001; and see later). In the same context, medium-sized grazers (20–30 cm) like chitons and scurrinid limpets tend to have a more positive indirect effect on *M. laminarioides*

(Aguilera and Navarrete, 2012a; Aguilera et al., 2015a). It is not clear, however, if positive effects on abundance and recovery of the corticated alga by the 'grazer/scrapper' functional group is additive and mediated through removal of the opportunistic, potentially competitive dominant, green algae.

Different studies have shown that, despite phylogenetic inertia i.e., the similarity in phenotypic traits shared by sister species (see Webb et al. 2002), in either diet (e.g., Santelices et al., 1986; Camus et al., 2008) or morphology (e.g. Espoz et al., 2004) among mollusc species, limited redundancy (*sensu* Bellwood et al., 2003; Hoey and Bellwood, 2009) in both temporal and spatial distribution of effects would be expected in this herbivore assemblage. This could be partly related to their broad distribution of body sizes and micro-scale habitat use patterns within the assemblage (e.g., Firth and Crowe, 2008; Aguilera, 2011), which could also mediate herbivore coexistence as observed in other ecosystems (e.g., grasslands; Ritchie and Olff, 1999). Coexistence can also be related to different physiological and/or behavioural responses (Chapman and Underwood, 1992, Klein et al., 2011), which together can account for a functional niche differentiation (see Rosenfeld, 2002 functional model). Both direct and indirect effects, commonly related to differences in behaviour and habitat use at micro-scales (centimetres) observed in some grazers of this guild (e.g., Muñoz et al., 2005; Aguilera and Navarrete, 2011, 2012b), can contribute to the differences in the functional roles different species play on the Chilean rocky intertidal community. Consequently, spatial distribution of algae and bare rock could correlate either negatively or positively with the microspatial (a few centimetres) distribution of herbivores during foraging (Chapman and Underwood, 1992), which creates heterogeneity at the scales of dozens of centimetres to metres in the seascape (Aguilera et al., 2015b). Therefore, within the herbivore guild, some species segregate their functional roles at different successional times, independent of the taxonomic affinities and similarity in feeding capabilities, which were previously considered key traits for functional characterisation (Steneck and Watling, 1982).

Commonly, magnitude of per capita effects of benthic herbivores present on Chilean coasts seem directly related to species body size (Aguilera, 2011; Aguilera and Navarrete, 2012a). Thus, a monotonical increase in effect (per capita) is expected for a given body mass of individual herbivore species present in the guild (Wood et al., 2010). No clear relationship has been observed between body size and the homing range of different species (Aguilera and Navarrete, 2011), modifying the general pattern suggested for the amplitude of different consumer effects. For example, large (i.e., ~7.6 cm shell length) molluscan grazer species like *Fissurella* spp. and/or chitons (e.g., *C. granosus*) exhibit a homing behaviour and have well-constrained foraging ranges (45–120 cm length) (Aguilera and Navarrete, 2011). In addition, factors like predation risk can also constrain the spatial amplitude and frequency of grazing beyond body size per se, determining higher metabolic demands and the consequent (net effect) high grazing pressure in the resource community (e.g., Espoz and Castilla, 2000; Escobar and Navarrete, 2011; Manzur et al., 2014). Thus, non-trophic interactions (e.g., behaviourally mediated effects) are one of the main processes shaping herbivore–algae interaction network and influencing community structure in this system (see Kéfi et al., 2012, 2015).

There is still scant knowledge regarding the role of bottom-up processes influencing herbivore–algae interactions in this system. A study by Nielsen and Navarrete (2004) showed that upwelling intensity can determine variation in grazers' roles on different functional groups of algae over the mesoscale (over 10s to 100s of kilometres). Corticated algae dominate sites with intense upwelling, while ephemeral algae are abundant at sites not exposed to upwelling (Nielsen and Navarrete, 2004). This pattern could define the role that functionally distinct herbivores (i.e., 'scrapers-grazers'; *C. granosus*, *Scurria araucana*, versus 'browsers-grazers'; keyhole limpets, *Siphonaria lessoni*) play at different upwelling regimes. For example, since facultative 'browser' herbivores like *Fissurella* spp. and some fish species like *S. viridis* are capable of controlling dominant corticated algae, like *M. laminarioides* during late successional stages of the community,

the role of these herbivores might be greater under intense upwelling. However, human harvesting of these herbivores (see Oliva and Castilla, 1986; Castilla, 1999; Moreno, 2001; Godoy et al., 2010) can reduce their densities, and their demographic pattern (e.g., sex ratio; Borges et al., 2016 and see Fenberg and Roy, 2008 for review), to levels that do not allow them to control dominant late successional algal forms (Nielsen and Navarrete, 2004).

Given the spatial structure of upwelling front across the coast of Chile from north to southern coasts (e.g., Montecinos and Lange, 2009; Tapia et al., 2014 and discussed earlier), herbivore–algae interaction patterns seem to be mostly influenced by nutrient effect rather than latitudinal effects, contrary to previous hypotheses (see Poore et al., 2012 for discussion). This could be also reflected across the northern biogeographic transitional zone (e.g., 30°S), where both quantitative and qualitative characteristics of herbivore–algae interactions can be strongly variable across the biogeographic boundary as can be derived from differences in life history dynamics of populations living at the range edge of their distributions (e.g., Fenberg and Rivadeneira, 2015).

12.4.2 Predator Guild Structure in Rocky Shore Habitats; Keystone versus Weak Interactors

Predator–prey interaction strength analyses have provided important insights into the factors that regulate the structure of consumer guilds in marine community structure (e.g., Paine, 1992; Menge et al., 1994; Navarrete and Menge, 1996; Berlow et al., 1999; Sala and Graham, 2002). In Chilean rocky intertidal communities, different quantitative estimates of predation intensity have helped to develop substantial recommendations about conservation and resource management (e.g., Castilla and Durán, 1985; Castilla and Fernández, 1998; Fernández et al., 2000; Gelcich et al., 2010). On the wave-exposed rocky intertidal zone of central Chile, the predator guild preferentially consumes important habitat-forming species such as mussels and barnacles, freeing space for the recruitment of other invertebrate and algal species (Castilla and Paine, 1987; Navarrete and Castilla, 2003). The seastar *H.*

helianthus and the muricid gastropod *C. concholepas* can be considered keystone predators (Navarrete and Castilla, 2003), because they have strong per capita effects on beds of the competitively dominant mussel, *P. purpuratus*, triggering dramatic changes in overall community structure (Castilla and Durán, 1985, Paine et al., 1985; Navarrete and Castilla, 2003). Predatory crabs *Acanthocyclus gayi* and *Acanthocyclus hassleri* also prey on mussels and barnacles at fairly high rates, and can coexist with *Concholepas* and *Heliaster* (e.g., Castilla and Durán, 1985; Navarrete and Castilla, 1988, 1990). Nonetheless, low per capita effects on mussel and barnacle species are observed for these crabs compared with *Concholepas* and *Heliaster* (Navarrete and Castilla, 2003). Also, juveniles and adults of the omnivorous clingfish *Sicyases sanguineus* occasionally feeds on mussels and barnacles at mid- and low-intertidal levels, with low impacts on these species (Cancino and Castilla, 1988). The whelks *Acanthina monodon* and *Crassilabrum crassilabrum* are commonly found on the very-low-intertidal fringe and shallow subtidal areas generating moderate to low per capita impacts on habitat-forming species. Therefore, field and laboratory evidence suggest that few large interactors and multiple weak-interacting species characterises the predator guild in intertidal rocky shore communities present in central Chile (Navarrete and Castilla, 2003). Experimental exclusion of humans from a portion (~500 m long) of the coast in 1982 (actually the marine reserve at Las Cruces: i.e., Estación Costera de Investigaciones Marinas), showed rapid increase of the commercially exploited gastropod *Concholepas* which drastically affected the biomass and productivity of herbivores and algae in the rocky intertidal community (e.g., Castilla and Durán, 1985, Botsford et al., 1997; Fernández et al., 2000; and see also Godoy and Moreno, 1989 for indirect effects of human exclusion). Therefore, studies conducted in the predator guild present in central-northern Chile (see earlier references) are at the core of the most important and challenging ecological research topics dealing with how changes in predator density/diversity can propagate through food webs, influencing ecosystem functioning (Otto et al., 2008). It is not clear, however, if

interspecific competition is a strong structuring factor in the predator guild, as observed in molluscan herbivores present in this (Godoy and Moreno, 1989; Aguilera and Navarrete, 2012b) and in other southern coastal systems (e.g., Branch, 1976; Fletcher and Underwood, 1987; Underwood, 1992).

In kelp-dominated subtidal habitats, characterised mainly by *Lessonia trabeculata*, and *Macrocystis intergrifolia*, the predator guild presents from subtropical to temperate habitats is characterised by diverse fish species (e.g., *Graus nigra*; *Semicossyphus pulcher*; *Cheilodactylus variegatus*; *Pinguipes chilensis*; Pérez-Matus et al., 2012). Most species seem to have a strong direct effect on invertebrate assemblages (e.g., shrimps, bivalves, polychaetes, gastropods amphipods, etc.) through feeding on juvenile and adult individuals (Ojeda and Muñoz, 1999; Pérez-Matus et al., 2012). Other important carnivorous species are echinoderms such as *Meyenaster gelatinosus*, *Stichaster striatus*, *H. helianthus* and *Luidia magellanica*, and the omnivorous sea urchins *T. niger* and *L. albus*, all of which share food resources with fish species (Vásquez, 1993a; Pérez-Matus et al., 2012; Vásquez and Donoso, 2013), and therefore can alter the habitat available to fish species in kelp forests (Pérez-Matus et al., 2007). Experimental studies suggest the seastar *M. gelatinosus* has keystone effects on subtidal invertebrate assemblages through intraguild predation on *Heliaster*, one of the stronger interactors of the rocky intertidal (Gaymer and Himmelman, 2008, and see earlier). Large body size (radial amplitude) and higher movement rates seems to confer an advantage to *Meyenaster* over *Heliaster* (Viviani, 1979), with non-lethal effects (behaviourally mediated effect) of the former having considerable impacts on individual performances of the latter. Notwithstanding, poor performances of *Meyenaster* compared with *Heliaster* on wave-exposed habitats suggest the latter could have a predominant role on shallow subtidal communities more exposed to wave action (Viviani, 1979).

Currently, intense harvesting of subtidal kelp species (*Lessonia*, *Macrocystis*, see later) is reducing habitat availability for predatory species, conforming the guild with additional impacts from fishing eroding the functional structure of this

kelp-associated predator guild (Godoy et al., 2010). For example, unregulated spearfishing has shifted the guild structure from large carnivorous species towards smaller-sized omnivores and herbivorous species in temperate reef fish communities (Godoy et al., 2010, 2016). Erosion of the functional structure of this guild correlates with similar human-induced impacts reported in other subtidal ecosystems where depletion of the fish assemblage had entailed a critical regime shift (e.g., coral reefs; Bellwood et al., 2004). Reduction of fish predators can shift the structure of the ecosystem to one where sea urchins (e.g., *Tetrapygus/Loxechinus*) reduce algal productivity and create urchin barrens in subtidal hard-bottom habitats (Vásquez and Donoso, 2013; see Ling et al., 2009 for similar effects for range-shifted sea urchin). Little knowledge is still available on the potential for *Meyenaster* or *Heliaster* to compensate fishing impacts and structuring subtidal invertebrate communities. Redundancy in controlling *Tetrapygus* abundances among the predator species might forestall ecosystem regime shift (from kelp to coralline or bare rock areas; e.g., see Ling et al., 2009 for examples of impacts of fishing spiny lobster *Jasus edwardsii* on sea urchin catastrophic effects on kelps). However, as kelp harvesting is intense in both subtidal and intertidal habitats in northern Chile (e.g., Vásquez et al., 2012; Oróstica et al., 2014; Vega et al., 2014), there would be low potential for overall compensatory effects (Ghedini et al., 2015) in this system. Therefore, management strategies are urgently needed to regulate kelp harvesting and fishing in order to control the reef fish crisis and seemingly inevitable regime shift (e.g., Gelcich et al., 2009, 2010).

12.4.3 The Role of Parasite–Host Interactions in Coastal Ecosystems

In general, parasite–host interactions are one of most overlooked interactions in marine communities despite their outstanding ecological and economic effects (Poulin, 1999; Lafferty et al., 2015). In Chile, some studies have focussed on patterns of diversity and richness of parasitic infracommunities (host like molluscs and fish species; e.g; George-Nascimento et al., 2002;

Muñoz and George-Nascimento, 2002; González and Moreno, 2005) and their geographic distribution patterns (Oliva and González, 2005). Other studies have considered the primary transmission pathways from primary to final host species in intertidal systems (especially for parasitic trematode species; Loot et al., 2008; Aldana et al., 2009). In this context, more focussed studies have reported on the direct impact of fishing and human activities on the parasitic transmission pathways, infracommunity structure and prevalence (e.g., Loot et al., 2008; Wood et al., 2013). For example, different species like the fish *C. variegatus* and *A. punctatus*, the limpet *Fissurella latimarginata* and the sea urchin *L. albus* are target species for subsistence fisheries in central Chile (33°S), and their densities are commonly low in unprotected areas (Godoy et al., 2016). Different parasites infect these species, and both prevalence and incidence were high in host populations present inside a marine protected area (MPA; Wood et al., 2013). These results showed that fishing drives a decline in parasite abundance at the population level, through reducing the availability of hosts and resource for parasites (Wood et al., 2013).

No studies have explored the alteration of consumer behaviour to parasite load (e.g., Thomas and Poulin, 1998), which can have important indirect consequences on consumer–resource interactions (Poulin, 1999). Similarly, few studies have reported on the direct parasite transmission pathways, which can help to incorporate the parasite–host dimension in these well-studied food webs (Lafferty et al., 2006, 2015). Notwithstanding, the importance of parasite load on interspecific interaction of marine mammal species (i.e., sea lions and fur seals) has been previously suggested (George-Nascimento et al., 1992). Little information is thus available to address the direct and indirect impact of parasites on other consumer interactions, like predator–prey or herbivore–algae dynamics, and also their role as a structuring factor of host communities in this system (see Poulin, 1999 for review). Further studies are thus needed to include parasite–host interactions in the highly diverse food web present in coastal marine ecosystems of Chile (Kéfi et al., 2015).

12.5 Drivers for Coastal Biodiversity in Subtidal Kelp-Dominated Ecosystems

Kelps dominate shallow subtidal rocky-bottom areas in temperate and cold seas to a depth of ~40 m (Dayton et al., 1984; Harrold and Pearse, 1987; Vásquez, 1992; Graham et al., 2007). In the south-east Pacific the geographic and local distribution of subtidal Laminarian species are variable: *L. trabeculata* dominates rocky subtidal environments to a depth of ~40 m (Villouta and Santelices, 1984; Vásquez, 1992) and *Macrocystis pyrifera* forms shallow beds south of 42°S. *M. pyrifera* forms coastal belts to intertidal zone to ~15 m in northern-central latitudes (Vega et al., 2005), and to Cape Horn including the fjord zone and the Atlantic coast up to Chubut area in Argentina (Buschmann et al., 2004).

Shallow subtidal environments structured by kelp species (ecosystem engineering; *sensu* Jones et al., 1994) are highly productive and harbour high diversity and abundance of invertebrates and fishes. Kelp holdfasts constitute feeding areas, refuges against predation and bottom currents, spawning, settlement areas and nursery sites (Vásquez and Buschmann, 1997; Vásquez et al., 1998, 2001b; Graham et al., 2007; Teagle et al., 2017; Walls et al., 2017). A wide diversity of algae live under kelp canopy including several Corallinales, *Asparagopsis armata*, *Halopteris paniculata* and *Gelidium* spp; some barnacles and other sessile invertebrates (*Pyura chilensis*, *Phragmatopoma moerchi*, *Aulacomya atra*) are also part of the associated species sheltered by the kelp canopy (Vásquez et al., 1993a, 1993b, 2001a, 2001b; Vásquez and Vega, 2004; Thiel et al., 2007). Invertebrate predators such as the muricid snail *C. concholepas*, seastars (*M. gelatinosus*, *S. striatus*, *H. helianthus* and *L. magellanica*) and intermediate-size coastal fishes (*C. variegatus*, *Semicossyphus darwini* and *Pinguipes chilensis*) constitute the predator guild in kelp forests along the Chilean coastline. The omnivorous-herbivore guild presents in kelp forest ecosystems include sea urchins (*T. niger* and *L. albus*), gastropods (*Tegula* spp. and *Fissurella* spp.), as well as fishes

(*A. punctatus*, *G. laevifrons* and *Kyphosus analogus*; Pérez-Matus et al. 2007, 2012). Marine mammals such as the sea lion *Otaria flavescens* and the sea otter *Lontra felina* distribute widely along the coastal zone of the Humboldt Current, and also use kelp beds as feeding areas (Vega et al., 2005, Vásquez et al., 2006; Thiel et al., 2007).

In absence of kelp assemblages, subtidal rocky reefs commonly form alternative states dominated by crustose coralline algae ('barren-ground'; *sensu* Lawrence, 1975, and see Ling et al., 2009). The most important grazer determining this state are the sea urchins *T. niger* (Molina) and the sympatric but less common species *L. albus* (Molina) (Rodríguez and Ojeda, 1993). The sea urchin *T. niger* is an omnivore, while *L. albus* is an herbivore and feeds on foliose algae and drifting algal rafts (Rodríguez and Ojeda, 1993; Thiel et al. 2007; Vásquez and Donoso, 2013). Although both species can completely destroy kelp beds on a local scale (see Dayton, 1985; Buschmann et al., 2003), *T. niger* is primarily responsible for generation and maintenance of barren areas typically observed in northern Chile (Vásquez and Buschmann, 1997).

The distribution, abundance and diversity patterns of subtidal kelp communities along the south-east Pacific coastline are the result of complex life history strategies and interactions with environmental factors like water movement, nutrient availability, distribution of surface temperature associated with El Niño-La Niña fluctuation, herbivory pressure and a high and intense harvesting by fishermen (Muñoz et al., 2004; Vega et al., 2005; Buschmann et al., 2006; Vásquez et al., 2006; Graham et al., 2007).

Long-term studies of subtidal communities before and after El Niño (Vásquez et al., 2006) suggest that different bottom-up and top-down factors might control ecosystem changes in northern Chile, including the intensity and frequency of upwelling, buffering the positive thermal anomalies of superficial seawater temperature and favoring the persistence of kelps.

Site-dependent oceanographic conditions may generate optimal scenarios for spawning, larval development and recruitment of the echinoderm *T. niger*, which is the main grazer in subtidal

rocky coastal areas, and also may decouple the correlation between carnivore abundances and population dynamics of sea urchins. In this context, abundance variability of some predator species as *L. magellanica* or *H. helianthus* may promote population increase of the urchin *T. niger* during El Niño events. These events might thus promote the development of two alternate states: (1) environments dominated by kelp versus and (2) barren ground areas dominated by urchins and coralline crustose algae (Graham et al., 2007; Ling et al., 2009). Nevertheless, other areas of the south-eastern Pacific during El Niño 1997–1998 showed that superficial warming decreased the abundance of kelp on shallow bottoms, inducing migrations of grazers to deeper zones (Fernández et al., 2000; Llellish et al., 2001). In a wider context, El Niño–La Niña events include large-scale bottom-up and top-down effects which involves various levels of marine subtidal food webs, most of them difficult to predict. In this context, impacts of relative frequency of these large-scale environmental processes on kelps are commonly coupled with changes in human impacts like direct kelp harvesting. For example, human impact involving the landings of brown macroalgae in Chile reaches 4,000,000 wet t year⁻¹ (Vásquez et al., 2012), constituting the world's largest landings from natural populations. As was previously mentioned, most of the brown macroalgae are foundation species of marine ecosystems (Graham et al., 2007), forming the basis of coastal food webs (Halpern et al., 2006). In Chile, brown macroalgae contribute significantly to the total biomass of subtidal ecosystems (Santelices et al., 1980; Santelices and Ojeda, 1984). Similarly, brown macroalgae are highly connected with all trophic levels (Vásquez et al., 2006; Thiel et al., 2007), generating a significant impact on the ecosystem in an ecological and evolutionary context (Steinberg et al., 1995; Seeley and Schlesinger, 2012).

Recent comparative studies done in MPAs versus open access areas present in northern Chile show that harvesting has been affecting the population dynamics of kelps and the structure of their associated communities (Vega et al., 2014). Inside MPAs, *Lessonia* recruitment, density and biomass have temporal patterns similar to

those described when populations of this brown macroalgae had less extraction (i.e., during 2000). By contrast, in open access areas, the lack of surveillance or assignments of use and property to artisanal fisherman (see Gelcich et al. 2008, 2009) promotes an indiscriminate harvest. Intensification of harvesting negatively affect the structure and population dynamics of subtidal communities associated with kelps compared with populations in areas with some conservation strategies like marine parks or co-management areas with sustainable management plans (Vásquez et al., 2012).

Kelps are useful sentinels of change because they are highly responsive to environmental conditions (Wernberg et al., 2013; Bell et al., 2015; Smale and Vance, 2016) and are directly exposed to many human activities that impact the coastal zone (e.g., harvesting, pollution, sedimentation, invasive species, fishing, recreation). In a global analysis of kelp forest changes over the past fifty years, Krumhansl et al. (2016) identified a high degree of variability in the magnitude and direction of changes across the geographic range of kelps. Although most of the changes worldwide are well correlated with warming or cooling of water surface associated with climate change, the decline of kelps in northern and central Chile is significantly related with the intensity of commercial harvest, despite a regional cooling trend (Krumhansl et al., 2016). This information shows that subtidal kelp ecosystem dynamics in the south-east Pacific, contrary to other coasts, is strongly controlled by processes directly related to disturbances generated by human harvesting, which are directly coupled with economic variation related to kelp exportation rates and market price fluctuations.

12.6 Concluding Remarks: Gaps in the Knowledge

Given the advances in understanding the processes influencing variation in distributional patterns and species interactions in rocky shore habitats in this ecosystem, further studies are needed to make explicit predictions regarding

the persistence and dynamics of multiple species ranges and changing ecological interactions among species in the face of intensified human harvesting and global change (e.g., Ling et al., 2009; Firth et al., 2009). Hence, the main challenges are thus related, but not constrained to, examining the persistence of biogeographic transitional zones and species range shift under climate-driven impacts (e.g., changes in currents: e.g., Ling et al., 2009; heat waves: Sunday et al., 2012; homogenisation of upwelling patterns: Wang et al., 2015) by examining the stability of species geographic range edges. In this context, information of the geographic variability in the intensity and direction of consumer effects could be of great interest, i.e., under which condition or environmental context herbivore positive effects are more frequent than negative impacts on algal biomass or diversity? Global change is driving rapid variation in assemblage structure in the face of changing environmental conditions (Parmesan and Yohe, 2003; Poloczanska et al., 2008; Sunday et al., 2012; Sydeman et al., 2014). Species ranges are changing in different coasts as a consequence of the synergistic effect of climate warming and human harvesting (e.g., Lima et al., 2006; Parmesan, 2006; Smale and Wernberg, 2013; Fenberg and Rivadeneira, 2015 and see Burrows et al., 2011 and Mieszowska et al., 2014 for reviews). Thus, one of the most important questions is: how the shift in consumer species (i.e., herbivores, predators) distribution patterns can influence variation in community structure and ecosystem functioning (e.g., Ling et al., 2009)? Recent evidence suggests that the ranges of some herbivore species are shifting across the temperate Eastern Pacific coast (Rivadeneira and Fernández, 2005; Aguilera et al., 2013b). Clear cooling trends (i.e., negative temperature anomalies) are observed across the HCS (e.g., Lima and Wethey, 2012; Rykaczewski et al., 2015; Wang et al., 2015), human harvesting is intensifying (e.g., consumers: Fernández et al., 2000; Godoy et al., 2016; kelps: Krumhansl et al., 2016) and there is potential for the presence of coastal artificial infrastructure could trigger species range shifts as recent studies suggest in other systems (e.g., Airolidi et al., 2015; Dong et al., 2016, and see Firth et al., 2016 for review).

Another important concern is the impact of exotic non-native species on community structure and functioning along the coast of Chile (Camus, 2005; Castilla et al., 2005). At least fifty-one marine non-indigenous invertebrate and algae species have been reported across the country (Castilla and Neill, 2009). However, given the scarce localities studied along Chilean coast the number of exotic species in Chile may be underestimated (see Villaseñor-Parada et al., 2017 for review). Most of these non-native species have been associated with aquaculture operations (e.g., *Codium fragile* var. *tomentosoides*, *Ciona intestinalis*; Neill et al., 2006 and see Naylor et al., 2001 and Villaseñor-Parada et al., 2017 for review) and transported by ships (e.g., *Pyura praeputialis*) (Castilla and Neill, 2009, see Keller et al., 2011 for discussion). Few studies, however, have been conducted in Chile (but see Dumont et al., 2011) on the role of artificial infrastructures (e.g., pilings) as a habitat for different non-indigenous or exotic species (e.g., Bulleri and Airolidi, 2005; Airolidi et al., 2015 and see Firth et al., 2016 for review). Given the recent proliferation of coastal infrastructure in Chile (e.g., artificial breakwaters; see Aguilera, 2018), an increase of suitable habitat for the spread and establishment of intertidal and subtidal non-indigenous species could be expected (see Firth et al., 2016). Many of the introduced species in Chile also correspond to parasites of both native and exotic (e.g., from aquaculture) host species (Moreno et al., 2006b), which have impacts on the structure of natural communities and on economic activities associated with aquaculture. In addition, there is an important number of introduced bio-engineer species like the ascidian *P. praeputialis* and the sea grass *Heterozostera tasmanica* which provide habitat for a diverse range of intertidal species (Ortiz and Wolff, 2002; Castilla et al., 2005). In contrast to the fact that most exotic species (non-target species) exert negative impacts on economic activities (e.g., like fouling species), the ascidian *P. praeputialis*, which is found exclusively inside the Bay of Antofagasta, ~24°S, is currently under intense exploitation by small-scale fisheries in northern Chile (Castilla et al., 2005; Manríquez et al., 2016). Thus, there is a challenge to deal with the presence and future introduction of

non-native species to natural habitats along the coast of Chile (see Soto et al., 2001; Camus, 2005; Castilla and Neill, 2009 for discussion). On the one hand, environmental monitoring plans are required to prevent introduction, and ongoing research based on ballast water risk assessments (Camus et al., unpublished data) will soon provide the first official protocols to be applied in Chilean ports. On the other hand, appropriated strategies are required to restore natural ecosystem through non-native species eradication/control (e.g., Glen et al., 2013), and also to delineate species-specific conservation plans for species which provide important ecosystem services.

A rich ecological knowledge has been accumulated through the study of trophic and non-trophic community interactions along the Chilean rocky shores. Studies have reached a level of resolution that has allowed ecosystem-scale exploration about the structure of complex networks (see Kéfi et al. 2012, 2015). There is still scant knowledge, however, on the consequences of the range contraction or expansion of species on influencing community homogenisation or diversification (e.g., Olden et al., 2004, but see Vergés et al., 2016). For example, through range expansions or invasions, consumer species might displace native species with similar traits or those with a strong overlap in niche space through competitive effects (i.e., as the limiting similarity hypothesis suggests; MacArthur and Wilson, 1967). The functional replacement can drive widespread and unpredictable changes in the functioning of ecosystem through modified interactions at different trophic levels (Stachowicz et al., 2008 and see Ling et al., 2009 for cascade effects of sea urchin range expansion). Conversely, loss of key consumers could diminish resistance of native assemblages to species introductions (Bulleri et al., 2009). Species functional identity, richness and competitive potential seem to be critical traits to predict changes in the community composition and the consumer functional structure (e.g., Arenas et al., 2006; Firth et al., 2009). Thus, field experiments are needed to forecast community responses to changes in community structure driven by human-induced alteration, which operate at different temporal and spatial scales on coastal ecosystems present

across the large and heterogeneous south-east temperate Pacific coast.

Strong and consistent changes in the timing, intensity and spatial heterogeneity of coastal upwelling in response to future warming by climate change impacts are predicted for most eastern boundary upwelling systems (Sydeman et al., 2014; Rykaczewski et al., 2015; Wang et al., 2015). For the HCS, an increase in upwelling intensity and duration will result in a substantial reduction of the latitudinal variation in coastal upwelling (Wang et al., 2015). Because there is a strong linkage between upwelling and marine ecosystem productivity, the projected geographic homogenisation in the intensity, timing and spatial structure of coastal upwelling may influence the geographical distribution of marine biodiversity across the south-east temperate Pacific coast owing to biotic homogenisation (e.g., Olden et al., 2004). Hence, synergistic effects of upwelling homogenisation and coastal impacts on local ecosystems through intensive harvesting, urbanisation and associated exotic species proliferation are expected in this system. These large-scale changes pose a strong challenge on the persistence and stability of the large-scale spatial variation in species diversity present across Chile, and on the opportunities to develop general ecosystem management and conservation strategies. This will be a central research topic in the future to contribute to conservation and restoration of local coastal ecosystems tightly connected across the HCS.

Acknowledgements

MAA was financed by Fondecyt grant # 1160223 and PAI-CONICYT #79150002. BRB was supported by the ICM Center for the study of Multiple drivers of marine Socio-Ecological Systems (MUSELS, NC120086). We thank EcoUrbe-lab for camaraderie and friendship.

REFERENCES

Aguilera, M. A. (2011). The functional roles of herbivores in the rocky intertidal systems in Chile: a

- review of food preferences and consumptive effects. *Revista Chilena de Historia Natural*, **84**, 241–61.
- Aguilera, M. A. (2018). Artificial defences in coastal marine ecosystems in Chile: opportunities for spatial planning to mitigate habitat loss and alteration of the marine community structure. *Ecological Engineering*, **120**, 601–10. <http://doi.org/10.1016/j.ecoleng.2017.04.021>.
- Aguilera, M. A. and Navarrete, S. A. (2007). Effects of *Chiton granosus* (Frembly, 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. *Journal of Experimental Marine Biology and Ecology*, **349**, 84–98.
- Aguilera, M. A. and Navarrete, S. A. (2011). Distribution and activity patterns in an intertidal grazer assemblage: temporal and spatial organization influence inter-specific associations. *Marine Ecology Progress Series*, **431**, 119–36.
- Aguilera, M. A. and Navarrete, S. A. (2012a). Functional identity and functional structure change through succession in a rocky intertidal marine herbivore assemblage. *Ecology*, **93**, 75–89.
- Aguilera, M. A. and Navarrete, S. A. (2012b). Interspecific competition for shelters in territorial and gregarious intertidal grazers: consequences for individual behaviour. *Plos One*, **7**(9), e46205.
- Aguilera, M. A., Navarrete, S. A. and Broitman, B. R. (2013a). Differential effects of grazer species on periphyton of a temperate rocky shore. *Marine Ecology Progress Series*, **484**, 63–78.
- Aguilera, M. A., Valdivia, N. and Broitman, B. R. (2013b). Spatial niche differentiation and coexistence at the edge: co-occurrence distribution patterns in *Scurria limpets*. *Marine Ecology Progress Series*, **483**, 185–98.
- Aguilera, M. A., Valdivia, N. and Broitman, B. R. (2015a). Herbivore-alga interaction strength influences spatial heterogeneity in a kelp-dominated intertidal community. *Plos One*, **10**(9), e0137287.
- Aguilera, M. A., Valdivia, N. and Broitman, B. R. (2015b). Facilitative effect of a generalist herbivore on the recovery of a perennial alga: consequences for persistence at the edge of their geographic range. *Plos One*, **10**, e0146069.
- Aguirre, C., Pizarro, O., Strub, P. T., Garreaud, R. and Barth, J. A. (2012). Seasonal dynamics of the near-surface alongshore flow off central Chile. *Journal of Geophysical Research: Oceans*, **117**, 1–17.
- Ahumada, R. B., Pinto, L. and Camus, P. A. (2000) The Chilean Coast. In C. R. C. Sheppard, eds. *Seas at the Millennium: An Environmental Analysis*. Pergamon Press, Oxford, pp. 699–717.
- Airoldi, L., Turon, X., Perkol-Finkel, S. and Rius, M. (2015). Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Diversity and Distributions*, **21**, 1–14.
- Aldana, M., González, K., Loot, G., Pulgar, J. and Marquet, P. (2009). First intermediate host of the Digenean Trematode *Proctoeces lintoni* (Fellodistomidae) in Chile. *Journal of Parasitology*, **95**, 1408–14.
- Arenas, F., Sánchez, I., Hawkins, S. J. and Jenkins, S. R. (2006). The invasibility of marine algal assemblages: role of functional diversity and identity. *Ecology*, **87**, 2851–61.
- Bakun, A. and Weeks, S. J. (2008). The marine ecosystem off Peru: what are the secrets of its fishery productivity and what might its future hold? *Progress in Oceanography*, **79**, 290–9.
- Barker, P. F. and Thomas, E. (2004). Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. *Earth-Science Reviews*, **66**, 143–62.
- Bell, T. W., Cavanaugh, K. C., Reed, D. C. and Siegel, D. A. (2015). Geographic variability in the controls of giant kelp biomass dynamics. *Journal of Biogeography*, **42**, 2010–21.
- Bellwood, D. R., Hughes, T., Folke, C. and Nystrom, M. (2004). Confronting the coral reef crisis. *Nature*, **429**, 827–33.
- Bellwood, D. R., Hoey, A. S. and Choat, J. H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters*, **6**, 281–5.
- Berlow, E. L., Navarrete, S. A., Briggs, C. J., Power, M. E. and Menge, B. A. (1999). Quantifying variation in the strengths of species interactions. *Ecology*, **80**, 2206–24.
- Borges, C. D., Hawkins, S. J., Crowe, T. P. and Doncaster, C. P. (2016). The influence of simulated exploitation on *Patella vulgata* populations: protandric sex change is size-dependent. *Ecology and Evolution*, **6**, 514–31.
- Botsford, L. W., Castilla, J. C. and Peterson, C. H. (1997). The management of fisheries and marine ecosystems. *Science*, **277**, 509–15.
- Branch, G. (1976). Interspecific competition experienced by South African *Patella* species. *Journal of Animal Ecology*, **45**, 507–29.
- Brante, A., Fernández, M. and Viard, F. (2012). Phylogeography and biogeography concordance in the marine gastropod *Crepidipatella dilatata* (calyptraeidae) along the southeastern pacific coast. *Journal of Heredity*, **103**, 630–7.
- Brattström, H. and Johanssen, A. (1983). Ecological and regional zoogeography of the marine benthic fauna of Chile. *Sarsia*, **68**, 289–339.

- Broitman, B., Navarrete, S. A., Smith, F. and Gaines, S. (2001). Geographic variation of southeastern Pacific intertidal communities. *Marine Ecology Progress Series*, **224**, 21–34.
- Broitman, B. R., Véliz, F., Manzur, T. et al. (2011). Geographic variation in diversity of wave exposed rocky intertidal communities along central Chile. *Revista Chilena de Historia Natural*, **84**, 143–54.
- Bulleri, F. and Airoldi, L. (2005). Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology*, **42**, 1063–72.
- Bulleri, F., Tamburello, L. and Benedetti-Cecchi, L. (2009). Loss of consumers alters the effects of resident assemblages on the local spread of an introduced macroalga. *Oikos*, **118**, 269–79.
- Burrows, M. T., Schoeman, D. S., Buckley, L. B. et al. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, **334**, 652–5.
- Buschmann, A. H., García, C., Espinoza, C., Filún, L. and Vásquez, J. A. (2003). Sea Urchin and Kelp (*Macrocystis pyrifera*) Interaction in Protected Areas in Southern Chile. In J. Lawrence, ed. *Sea Urchins and Fisheries*. CRC, Boca Raton, FL, pp. 120–30.
- Buschmann, A. H., Vásquez, J. A., Osorio, P. et al. (2004). The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp (Phaeophyta) at different latitudes. *Marine Biology*, **145**, 849–62.
- Buschmann, A. H., Moreno, C., Vásquez, J. A. and Hernández-Carmona, M. (2006). Reproduction strategies of *Macrocystis pyrifera* (paheophyta) in southern Chile: the importance of population dynamics. *Journal of Applied Phycology*, **18**, 575–82.
- Camus, P. A. (1994). Recruitment of the intertidal kelp *Lessonia nigrescens* Bory in northern Chile: successional constraints and opportunities. *Journal of Experimental Marine Biology and Ecology*, **184**, 171–81.
- Camus, P. A. (2001). Marine biogeography of continental Chile. *Revista Chilena de Historia Natural*, **74**, 587–617.
- Camus, P. A. (2005). Introducción de especies en ambientes marinos chilenos: no solo exóticas, no siempre evidentes. *Revista Chilena de Historia Natural*, **78**, 155–9.
- Camus, P. A. (2008). Understanding biological impacts of ENSO on the eastern Pacific: an evolving scenario. *International Journal of Environment and Health*, **2**, 5–19.
- Camus, P. A., Daroch, K. and Opazo, F. L. (2008). Potential for omnivory and apparent intraguild predation in rocky intertidal herbivore assemblages from northern Chile. *Marine Ecology Progress Series*, **361**, 35–45.
- Cancino, J. and Castilla, J. C. (1988). Emersion behaviour and foraging ecology of the common clingfish *Sicyases sanguineus* (Pisces: Gobiesocidae). *Journal of Natural History*, **22**, 249–61.
- Cárdenas, L., Castilla, J. C. and Viard, F. (2009). A phylogeographical analysis across three biogeographical provinces of the south-eastern Pacific: the case of the marine gastropod *Concholepas concholepas*. *Journal of Biogeography*, **36**, 969–81.
- Castilla, J. C. (1999). Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology and Evolution*, **7**, 280–3.
- Castilla, J. C. and Camus, P. A. (1992). The Humboldt-El Niño scenario: coastal benthic resources and anthropogenic influences, with particular reference to the 1982/83 ENSO. *South African Journal of Marine Science*, **12**, 111–19.
- Castilla, J. C. and Durán, L. R. (1985). Human exclusion from the rocky intertidal zone of Central Chile: the effects on *Concholepas Concholepas* (Gastropoda). *Oikos*, **45**, 391–9.
- Castilla, J. C. and Fernández, M. (1998). Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. *Ecological Applications*, **8**, S124–32.
- Castilla, J. C. and Neill, P. (2009). Marine Bioinvasions in the Southeastern Pacific: Status, Ecology Economic Impacts, Conservation and Management. In G. Rilov and J. A. Crooks, eds. *Biological Invasions*. Springer-Verlag, Berlin.
- Castilla, J. C. and Paine, R. T. (1987). Predation and community organization in Eastern Pacific, temperate zone, rocky intertidal shores. *Revista Chilena de Historia Natural*, **60**, 131–51.
- Castilla, J. C., Uribe, M., Bahamonde, N. et al. (2005). Down under the southeastern Pacific: marine non-indigenous species in Chile. *Biological Invasions*, **7**, 213–32.
- Chaigneau, A. and Pizarro, O. (2005). Mean surface circulation and mesoscale turbulent flow characteristics in the eastern South Pacific from satellite tracked drifters. *Journal of Geophysical Research*, **110**, 1–17.
- Chapman, M. and Underwood, A. J. (1992). Foraging Behaviour of Marine Benthic Grazers. In D. M. John, S. J. Hawkins and J. H. Price, eds. *Plant–Animal Interactions in the Marine Benthos*. Clarendon Press, Oxford, pp. 289–317.
- Dayton, P. K., Currie, V., Gerrodette, T. et al. (1984). Patch dynamic and stability of some Californian kelp communities. *Ecological Monographs*, **54**, 253–89.

- Dayton, P. K. (1985). Ecology of kelp communities. *Annual Review of Ecology, Evolution, and Systematics*, **16**, 215–45.
- Dong, Y., Huang, X., Wang, W., Li, Y. and Wang, J. (2016). The marine 'great wall' of China: local- and broad-scale ecological impacts of coastal infrastructure on intertidal macrobenthic communities. *Diversity and Distributions*, **22**, 731–44.
- Dumont, C. P., Harris, L. G. and Gaymer, C. F. (2011). Anthropogenic structures as a spatial refuge from predation for the invasive bryozoan *Bugula neritina*. *Marine Ecology Progress Series*, **427**, 95–103.
- Escobar, J. and Navarrete, S. A. (2011). Risk recognition and variability in escape responses among intertidal molluscan grazers to the sun star *Heliaster helianthus*. *Marine Ecology Progress Series*, **421**, 151–61.
- Escribano, R., Daneri, G., Farías, L. et al. (2004). Biological and chemical consequences of the 1997–1998 El Niño in the Chilean coastal upwelling system: a synthesis. *Deep Sea Research Part II: Topical Studies in Oceanography*, **51**, 2389–411.
- Espoz, C. and Castilla, J. C. (2000). Escape responses of four Chilean intertidal limpets to seastars. *Marine Biology*, **137**, 887–92.
- Espoz, C., Lindberg, D. R., Castilla, J. C. and Simison, B. (2004). Los patelogastrópodos intermareales de Chile y Perú. *Revista Chilena de Historia Natural*, **77**, 257–83.
- Fenberg, P. B. and Rivadeneira, M. M. (2015). Range limits and geographic patterns of abundance of the rocky intertidal owl limpet, *Lottia gigantea*. *Journal of Biogeography*, **38**, 2286–98.
- Fenberg, P. B. and Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology*, **17**, 209–20.
- Fernández, M., Jaramillo, E., Marquet, P. et al. (2000). An overview of the diversity, biogeography and dynamics of nearshore ecosystems in Chile: foundation for marine conservation ecology. *Revista Chilena de Historia Natural*, **73**, 797–830.
- Firth, L. B. and Crowe, T. P. (2008). Large-scale coexistence and small-scale segregation of key species on rocky shores. *Hydrobiologia*, **614**, 233–41.
- Firth, L. B., Crowe, T. P., Moore, P., Thompson, R. C. and Hawkins, S. J. (2009). Predicting impacts of climate-induced range expansion: an experimental framework and a test involving key grazers on temperate rocky shores. *Global Change Biology*, **15**, 1413–22.
- Firth, L. B., Knights, A. M., Bridger, D. et al. (2016). Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanography and Marine Biology: An Annual Review*, **54**, 193–269.
- Fletcher, W. J. and Underwood, A. J. (1987). Interspecific competition among subtidal limpets: effect of substratum heterogeneity. *Ecology*, **68**, 387–400.
- Gaymer, C. F. and Himmelman, J. H. (2008). A keystone predatory sea star in the intertidal zone is controlled by a higher-order predatory sea star in the subtidal zone. *Marine Ecology Progress Series*, **370**, 143–53.
- Gelcich, S., Godoy, N. and Castilla, J. C. (2009). Artisanal fisher's perceptions regarding coastal co-management policies in Chile and their potentials to scale-up marine biodiversity conservation. *Ocean and Coastal Management*, **52**, 424–32.
- Gelcich, S., Kaiser, M. J., Castilla, J. C. and Edward-Jones, G. (2008). Engagement in co-management of marine benthic resources influences environmental perceptions of artisanal fishers. *Environmental Conservation*, **35**, 36–45.
- Gelcich, S., Hughes, T. P., Olsson, P. et al. (2010). Navigating transformations in governance of Chilean marine coastal resources. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 16794–9.
- George-Nascimento, M., Lima, M. and Ortiz, E. (1992). A case of parasite-mediated competition? Phenotypic differentiation among hookworms *Uncinaria* sp. (Nematoda: Ancylostomatidae) in sympatric and allopatric populations of South American sea lions *Otaria byronia*, and fur seals *Arctocephalus australis* (Carnivora: Otariidae). *Marine Biology*, **112**, 527–33.
- George-Nascimento, M., Garcías, F. and Muñoz, G. (2002). Parasite body volume and infracommunity patterns in the southern pomfret *Brama australis* (Pisces: Bramidae). *Revista Chilena de Historia Natural*, **75**, 835–9.
- Ghedini, G., Russell, B. D. and Connell, S. D. (2015). Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. *Ecology Letters*, **18**, 182–7.
- Glen, A. S., Atkinson, R., Campbell, K. J. et al. (2013). Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? *Biological Invasions*, **15**, 2589–603.
- Godoy, C. and Moreno, C. A. (1989). Indirect effects of human exclusion from the rocky intertidal in Southern Chile: a case of cross-linkage between herbivores. *Oikos*, **54**, 101–6.
- Godoy, N., Gelcich, S., Vásquez, J. A. and Castilla, J. C. (2010). Spearfishing to depletion: evidence from temperate reef fishes in Chile. *Ecological Applications*, **20**, 1504–11.
- Godoy, N., Gelcich, S., Castilla, J. C., Lima, M. and Smith, A. (2016). Artisanal spearfishing in temperate

- nearshore ecosystems of Chile: exploring the catch composition, revenue, and management needs. *Marine and Coastal Fisheries Dynamics, Management and Ecosystem Science*, **8**, 436–47.
- González, A., Beltrán, J. and Hiriart-Bertrand, L. B. (2012). Identification of cryptic species in the *Lessonia nigrescens* complex (Phaeophyceae, Laminariales). *Journal of Phycology*, **48**, 1153–65.
- González, M. T. and Moreno, C. A. (2005). The distribution of the ectoparasite fauna of *Sebastes capensis* from the southern hemisphere does not correspond with zoogeographical provinces of free-living marine animals. *Journal of Biogeography*, **32**, 1539–47.
- Graham, M. H., Vásquez, J. A. and Buschmann, A. H. (2007). Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanography and Marine Biology: An Annual Review*, **45**, 39–88.
- Halpern, B. S., Cottenie, K. and Broitman, B. R. (2006). Strong top-down control in southern California kelp forest ecosystems. *Science*, **312**, 1230–2.
- Harrold, C. and Pearse, J. S. (1987). The Ecological Role of Echinoderms in Kelp Forests. In M. Jangoux and J. M. Lawrence, eds. *Echinoderm Studies*, vol. 2. Balkema, Rotterdam, pp. 137–233.
- Haye, P. A., Segovia, N. I., Muñoz-Herrera, N. C. et al. (2014). Phylogeographic structure in benthic marine invertebrates of the southeast Pacific coast of Chile with differing dispersal potential. *Plos One*, **9**(2), e88613.
- Haussermann, V. and Forsterra, G. (2009). *Marine Benthic Fauna of Chilean Patagonia*. Nature in Focus, Puerto Montt, p. 1000.
- Hawkins, S. J. and Hartnoll, R. G. (1983). Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: An Annual Review*, **21**, 195–282.
- Hernández, C. E., Moreno, R. A. and Rozbaczylo, N. (2005). Biogeographical patterns and Rapoport's rule in southeastern Pacific benthic polychaetes of the Chilean coast. *Ecography*, **28**, 363–73.
- Hoey, A. and Bellwood, D. (2009). Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems*, **12**, 1316–28.
- Hormazábal, S., Shaffer, G. and Leth, O. (2004). Coastal transition zone off Chile. *Journal of Geophysical Research*, **109**, C01021.
- Hu, Z. M. and Guillemin, M.-L. (2016). Coastal upwelling areas as safe havens during climate warming. *Journal of Biogeography* **43**: 2513–2514.
- Ibáñez, C. M., Camus, P. A. and Rocha, F. J. (2009). Diversity and distribution of cephalopod species off the coast of Chile. *Marine Biology Research*, **5**, 374–84.
- Iriarte, J. L. and González, H. E. (2004). Phytoplankton size structure during and after the 1997/98 El Niño in a coastal upwelling area of the northern Humboldt current system. *Marine Ecology Progress Series*, **269**, 83–90.
- Jara, F. and Moreno, C. (1984). Herbivory and structure in a midlittoral rocky community: a case in southern Chile. *Ecology*, **65**, 28–38.
- Jenkins, S., Coleman, R., Santina, P., Hawkins, S., Burrows, M. and Hartnoll, R. (2005). Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Marine Ecology Progress Series*, **287**, 77–86.
- Jones, C. G., Lawton, J. H. and Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, **69**, 73–386.
- Kéfi, S., Berlow, E. L., Wieters, E. A. et al. (2012). More than a meal... integrating non-feeding interactions into food webs. *Ecology Letters*, **15**, 291–300.
- Kéfi, S., Berlow, E. L., Wieters, E. A. et al. (2015). Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology*, **96**, 291–303.
- Keller, R. P., Drake, J. M., Drew, M. B. and Lodge, D. M. (2011). Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Diversity and Distributions*, **17**, 93–102.
- Klein, J. C. Underwood, A. J. and Chapman, M. G. (2011). Urban structures provide new insights into interactions among grazers and habitat. *Ecological Applications*, **21**, 427–38.
- Krumhansl, K. A., Okamoto, D. K., Rassweiler, A. et al. (2016). Global patterns of kelp forest change over the past half-century. *Proceedings of National Academy of Science of the United States of America*, **113**, 13785–90.
- Lafferty, K. D., Dobson, A. P. and Kuris, A. M. (2006). Parasites dominate food web links. *Proceeding of the National Academy of Sciences of the United States of America*, **103**, 11211–16.
- Lafferty, K. D., Harvell, C. D., Conrad, J. M. et al. (2015). Infectious disease affect marine fisheries and aquaculture economics. *Annual Review of Marine Science*, **7**, 471–96.
- Lagos, N. A., Tapia, F. J., Navarrete, S. A. and Castilla, J. C. (2007). Spatial synchrony in the recruitment of intertidal invertebrates along the coast of central Chile. *Marine Ecology Progress Series*, **350**, 29–39.
- Lancellotti, D. A. and Vásquez, J. A. (1999). Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. *Journal of Biogeography*, **26**, 1001–6.

- Lawrence, J. M. (1975). On the relationships between marine plants and sea urchins. *Oceanography and Marine Biology: an Annual Review*, **13**, 213–86.
- Lima, F. P. and Wethey, D. S. (2012). Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nature Communications*, **3**, 1–13.
- Lima, F. P., Queiroz, N., Ribeiro, P. A., Hawkins, S. J. and Santos, A. M. (2006). Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. *Journal of Biogeography*, **33**, 812–22.
- Ling, S. D., Johnson, C. R., Frusher, S. D. and Ridgway, K. R. (2009). Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 22341–5.
- Llagostera, A. (1979). 9700 years of maritime subsistence on the Pacific: an analysis by means of bioindicators in the north of Chile. *American Antiquity*, **44**, 309–23.
- Llellish, J., Fernández, E. and Hooker, Y. (2001). Disturbancia del bosque submareal de *Macrocystis pyrifera* durante El Niño 1997–1998 en la Bahía de Pucusana. In K. Alveal and T. Antezana, eds. *Sustentabilidad de la biodiversidad. Un problema actual: bases científico técnicas, teorizaciones y proyecciones*. Ediciones Universidad de Concepción, Concepción, pp. 331–50.
- Loot, G., Blanchet, S., Aldana, M. and Navarrete, S. A. (2008). Evidence of plasticity in the reproduction of a trematode parasite: the effect of host removal. *Journal of Parasitology*, **94**, 23–7.
- Longhurst, A. (1998). *Ecological Geography of the Sea*. Academic Press, San Diego, CA.
- Lourenço, C. R., Zardi, G. I., McQuaid, C. D. et al. (2016). Upwelling areas as climate change refugia for the distribution and genetic diversity of a marine macroalga. *Journal of Biogeography*, **43**, 1595–607.
- Lubchenco, J. and Gaines, S. D. (1981). A unified approach to marine plant–herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics*, **12**, 405–37.
- MacArthur, R. and Wilson, E. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Manríquez, P. H., Castilla, J. C., Ortiz, V. and Jara, M. E. (2016). Empirical evidence for large-scale human impact on intertidal aggregations, larval supply and recruitment of *Pyura praeputialis* around the Bay of Antofagasta, Chile. *Austral Ecology*, **41**, 701–14.
- Martin, P. and Zuccarello, G. C. (2012). Molecular phylogeny and timing of radiation in *Lessonia* (Phaeophyceae, Laminariales). *Phycological Research*, **60**, 276–87.
- Manzur, T., Vidal, F., Pantoja, J. F., Fernández, M. and Navarrete, S. A. (2014). Behavioural and physiological responses of limpet prey to a seastar predator and their transmission to basal trophic levels. *Journal of Animal Ecology*, **83**, 923–33.
- Meneses, I. and Santelices, B. (2000). Patterns and breaking points in the distribution of benthic algae along the temperate Pacific coast of South America. *Revista Chilena de Historia Natural*, **73**, 615–23.
- Menge, B. A., Berlow, E. L., Blanchette, C. A., Navarrete, S. A. and Yamada, S. B. (1994). The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs*, **64**, 249–86.
- Mieszkowska, N., Sugden, H., Firth, L. B. and Hawkins, S. J. (2014). The role of sustained observations in tracking impacts of environmental change on marine biodiversity and ecosystems. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences*, **372**, 20130339.
- Montecinos, V. and Lange, C. B. (2009). The Humboldt current system: ecosystem components and processes, fisheries, and sediment studies. *Progress in Oceanography*, **83**, 65–79.
- Montecinos, A., Broitman, B., Faugeron, S., Haye, P. A., Tellier, F. and Guillermin, M. L. (2012). Species replacement along a lineal coastal habitat: phylogeography and speciation in the red alga *Mazzaella laminarioides* along the south east Pacific. *BMC Evolutionary Biology*, **12**, 1–17.
- Moreno, C. A. (2001). Community patterns generated by human harvesting on Chilean shores: a review. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **11**, 19–30.
- Moreno, C. A. and Jaramillo, E. (1983). The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. *Oikos*, **41**, 73–6.
- Moreno, C. A., Sutherland, J. and Jara, F. (1984). Man as predator in the intertidal zone of southern Chile. *Oikos*, **42**, 155–60.
- Moreno, C. A., Lunecke, K. M. and López, M. I. (1986). The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in Southern Chile and the effects on benthic sessile assemblages. *Oikos*, **46**, 359–64.
- Moreno, R. A., Hernández, C. E., Rivadeneira, M. M., Vidal, M. A. and Rozbaczylo, N. (2006a). Patterns of endemism in south-eastern Pacific benthic polychaetes of the Chilean coast. *Journal of Biogeography*, **33**, 750–9.
- Moreno, R. A., Neill, P. E. and Rozbaczylo, N. (2006b). Native and non-indigenous boring polychaetes in Chile: a threat to native and commercial mollusc species. *Revista Chilena de Historia Natural*, **79**, 263–78.

- Moy, C. M., Seltzer, G. O., Rodbell, D. T. Y. and Anderson, D. M. (2002). Variability of El Niño/southern oscillation activity at millennial timescales during the Holocene epoch. *Nature*, **420**, 162–5.
- Muñoz, G. and George-Nascimento, M. (2002). *Spiracanthus bovichthys* n. gen. n. sp. Acanthocephala: Arhythmacanthidae, a parasite of littoral fishes of the central-south coast of Chile. *Journal of Parasitology*, **88**, 141–5.
- Muñoz, J., Finke, R., Camus, P. and Bozinovic, F. (2005). Thermoregulatory behavior, heat gain and thermal tolerance in intertidal snails: the case of the periwinkle *Echinolittorina peruviana* in central Chile. *Comparative Biochemistry and Physiology A*, **142**, 92–8.
- Muñoz, V., Hernandez, M. C., Buschmann, A. H., Graham, M. H. and Vásquez, J. (2004). Variability in *per capita* oogonia and sporophyte production from giant kelp gametophyte (*Macrocystis pyrifera*, Phaeophyceae). *Revista Chilena de Historia Natural*, **77**, 639–47.
- Navarrete, A. H., Lagos, N. A. and Ojeda, F. P. (2014). Latitudinal diversity patterns of Chilean coastal fishes: searching for causal processes. *Revista Chilena de Historia Natural*, **87**, 1–11.
- Navarrete, S. A. and Castilla, J. C. (1988). Foraging activity of Chilean intertidal crabs *Acanthocyclus gayi* Milne-Edwards et Lucas and *A. hassleri* Rathburn. *Journal of Experimental Marine Biology and Ecology*, **118**, 115–36.
- Navarrete, S. A. and Castilla, J. C. (1990). Resource partitioning between intertidal predatory crabs: interference and refuge utilization. *Journal of Experimental Marine Biology and Ecology*, **143**, 101–12.
- Navarrete, S. A. and Menge, B. A. (1996). Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs*, **66**, 409–29.
- Navarrete, S. A., Broitman, B., Wieters, E. A., Finke, G. R., Venegas, R. M. and Sotomayor, A. (2002). Recruitment of intertidal invertebrates in the southeast Pacific: interannual variability and the 1997–1998 El Niño. *Limnology and Oceanography*, **47**, 791–802.
- Navarrete, S. A. and Castilla, J. C. (2003). Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. *Oikos*, **100**, 251–62.
- Navarrete, S. A., Wieters, E. A., Broitman, B. and 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 of the United States of America*, **102**, 18046–51.
- Naylor, R., Williams, S. and Strong, D. (2001). Aquaculture – a gateway for exotic species. *Science*, **294**, 1655–6.
- Neill, P. E., Alcalde, O., Faugeton, S., Navarrete, S. A. and Correa, J. A. (2006). Invasion of *Codium fragile* ssp. *tomentosoides* in northern Chile: a new threat for *Gracilaria* farming. *Aquaculture*, **259**, 202–10.
- Nielsen, K. J. and Navarrete, S. A. (2004). Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. *Ecology Letters*, **7**, 31–41.
- Ojeda, F. P. and Muñoz, A. (1999). Feeding selectivity of the herbivorous fish *Scartichthys viridis*: Effects on macroalgal community structure in a temperate rocky intertidal coastal zone. *Marine Ecology Progress Series*, **184**, 219–29.
- Oliva, D. and Castilla, J. C. (1986). The effects of human exclusion on the population structure of keyhole limpets *Fissurella crassa* and *Fissurella limbata* in the coast of Central Chile. *Marine Ecology*, **7**, 201–17.
- Oliva, M. and González, M. T. (2005). The decay of similarity over geographical distance in parasite communities of marine fishes. *Journal of Biogeography*, **32**, 1327–32.
- Olden, J. D., Poff, N. L., Douglas, M. R., Douglas, M. E. and Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, **19**, 18–24.
- Oróstica, M., Aguilera, M. A., Donoso, G., Vásquez, J. and Broitman, B. R. (2014). Effect of grazing on distribution and recovery of harvested stands of *Lessonia berteriana* kelp in northern Chile. *Marine Ecology Progress Series*, **511**, 71–82.
- Ortiz, M. and Wolff, M. (2002). Trophic models of four benthic communities in Tongoy Bay (Chile): comparative analysis and preliminary assessment of management strategies. *Journal of Experimental Marine Biology and Ecology*, **268**, 205–35.
- Ortlieb, L. (1995). Paleoclimas cuaternarios en el norte grande de Chile. In J. Argollo and P. Mourguiart, eds. *Cambios Cuaternarios en América del Sur*, ORSTOM-Bolivia, La Paz, pp. 225–46.
- Ortlieb, L., Guzmán, N. and Marquardt, C. (2003). A Longer-Lasting and Warmer Interglacial Episode during Isotopic Stage 11: Marine Terrace Evidence in Tropical Western Americas. In A. W. Droxler, R. Z. Poore and L. H. Burckle, eds. *Earth's Climate and Orbital Eccentricity: The Marine Isotope Stage 11 Question*. American Geophysical Union, Washington, DC, Geophysical Monograph 137, pp. 157–80.
- Otto, S. B., Berlow, E. L., Rank, N. E., Smiley, J. and Brose, U. (2008). Predator diversity and identity drive

- interaction strength and trophic cascades in a food web. *Ecology*, **89**, 134–44.
- Paine, R. T. (1980). Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, **49**, 666–85.
- Paine, R. T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*, **355**, 73–5.
- Paine, R. T., Castilla, J. C. and Cancino, J. (1985). Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand, and Washington State. *The American Naturalist*, **125**, 679–91.
- Palma, A. T., Pardo, L. M., Veas, R. et al. (2006). Coastal brachyuran decapods: Settlement and recruitment under contrasting coastal geometry conditions. *Marine Ecology Progress Series*, **316**, 139–53.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, **37**, 637–69.
- Parnesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pérez-Matus, A., Ferry-Graham, L. A., Cea, A. and Vásquez, J. A. (2007). Community structure of temperate reef fishes in kelp-dominated subtidal habitats of northern Chile. *Marine and Freshwater Research*, **58**, 1069–85.
- Pérez-Matus, A., Pledger, S., Díaz, F. J., Ferry, L. A. and Vásquez, J. A. (2012). Plasticity in feeding selectivity and trophic structure of kelp forest associated fishes from northern Chile. *Revista Chilena de Historia Natural*, **85**, 29–48.
- Pfuhl, H. A. and McCave, N. I. (2005). Evidence for late Oligocene establishment of the Antarctic Circumpolar Current. *Earth and Planetary Science Letters*, **235**, 715–28.
- Poloczanska, E., Hawkins, S. J., Southward, A. J. and Burrows, M. T. (2008). Modeling the response of populations of competing species to climate change. *Ecology*, **89**, 3138–49.
- Poore, A. G. B., Campbell, A. H., Coleman, R. A. et al. (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, **15**, 912–22.
- Poulin, E., Palma, A. T., Leiva, G. et al. (2002). Avoiding offshore transport of competent larvae during upwelling events: The case of the gastropod *Concholepas concholepas* in central Chile. *Limnology and Oceanography*, **47**, 1248–55.
- Poulin, R. (1999). The functional importance of parasites in animal communities: many roles at many levels? *International Journal of Parasitology*, **29**, 903–14.
- Rahn, D. A., Rosenbluth, B. and Rutlland, J. A. (2014). Detecting subtle seasonal transitions of upwelling in North-Central Chile. *Journal of Physical Oceanography*, **45**, 854–68.
- Rivadeneira, M. and Fernández, M. (2005). Shifts in southern endpoints of distribution in rocky intertidal species along the south-eastern Pacific coast. *Journal of Biogeography*, **32**, 203–9.
- Rivadeneira, M. M. and Marquet, P. A. (2007). Selective extinction of late Neogene bivalves on the temperate Pacific coast of South America. *Paleobiology*, **33**, 455–68.
- Rivadeneira, M. M., Hernández, P., Baeza, J. A. et al. (2012). Testing the abundant-centre hypothesis using intertidal porcelain crabs along the Chilean coast: linking abundance and life-history variation. *Journal of Biogeography* **37**, 486–98.
- Ritchie, M. E. and Olff, H. (1999). Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, **400**, 557–60.
- Rodríguez, S. R. and Ojeda, F. P. (1993). Distribution patterns of *Tetrapyrgus niger* Echinodermata: Echinoidea off the central Chilean coast. *Marine Ecology Progress Series*, **101**, 157–62.
- Rosenfeld, R. (2002). Functional redundancy in ecology and conservation. *Oikos*, **98**, 156–62.
- Rykcaczewski, R. R., Dunne, J. P., Sydeman, W. J., García-Reyes, M., Black, B. A. and Bograd, S. J. (2015). Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. *Geophysical Research Letters*, **42**, 6424–31.
- Sala, E. and Graham, M. H. (2002). Community-wide distribution of predator-prey interaction strength in kelp forests. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 3678–83.
- Sánchez, R., Sepúlveda, R. D., Brante, A. and Cárdenas, L. (2011). Spatial pattern of genetic and morphological diversity in the direct developer *Acanthina monodon* (Gastropoda: Mollusca). *Marine Ecology Progress Series*, **434**, 121–31.
- Santelices, B. (1980). Phytogeographic characterization of the temperate coast of Pacific South America. *Phycologia*, **19**, 1–12.
- Santelices, B., Castilla, J. C., Cancino, J. and Schmiede, P. (1980). Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in central Chile. *Marine Biology*, **59**, 119–32.
- Santelices, B. and Ojeda, P. (1984). Recruitment, growth and survival of *Lessonia nigrescens* (Phaeophyta) at various tidal levels in exposed habitats of central Chile. *Marine Ecology Progress Series*, **19**, 73–82.

- Santelices, B., Vásquez, J. and Meneses, I. (1986). Patrones de distribución y dietas de un gremio de moluscos herbívoros en habitats intermareales expuestos de Chile central. In *Simposio Internacional. Usos y funciones de las algas marinas bentónicas*, 147–71.
- Seeley, R. H. and Schlesinger, W. H. (2012). Sustainable seaweed cutting? The rockweed (*Ascophyllum nodosum*) industry of Maine and the Maritime Provinces. *Annals of the New York Academy of Sciences*, **1249**, 84–103.
- Sepúlveda, R. D., Camus, P. A. and Moreno, C. A. (2016). Diversity of faunal assemblages associated with ribbed mussel beds along the South American coast: relative roles of biogeography and bioengineering. *Marine Ecology*, **37**, 943–56.
- Shinen, J. L. and Navarrete, S. A. (2010). Coexistence and intertidal zonation of chthamalid barnacles along central Chile: Interference competition or a lottery for space? *Journal of Experimental Marine Biology and Ecology*, **392**, 176–87.
- Smale, D. A. and Wernberg, T. (2013). Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B*, **280**, 2012–29.
- Smale, D. A. and Vance, T. (2016). Climate-driven shifts in species' distributions may exacerbate the impacts of storm disturbances on North-east Atlantic kelp forests. *Marine and Freshwater Research*, **67**, 65–74.
- Soto, D., Jara, F. and Moreno, C. (2001). Escaped salmon in the inner southern Chile: facing ecological and social conflicts. *Ecological Applications*, **11**, 1750–62.
- Spalding, M. D., Fox, H. E., Allen, G. R. et al. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, **57**, 573–83.
- Stachowicz, J. J., Graham, M., Bracken, M. and Szoboszlai, A. (2008). Diversity enhances cover and stability of seaweed assemblage: the role of heterogeneity and time. *Ecology*, **89**, 3008–19.
- Steneck, R. S. and Watling, L. (1982). Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Marine Biology*, **68**, 299–319.
- Steinberg, P. D., Estes, J. A. and Winter, F. C. (1995). Evolutionary consequences of food chain length in kelp forest communities. *Proceedings of the National Academy of Sciences of the United States of America*, **92**, 8145–8.
- Strub, P., Mesías, J., Montecino, V., Rutlant, J. and Salinas, S. (1998). Coastal Ocean Circulation off Western South America Coastal Segment. In A. Robinson and K. H. Brink, eds. *Global Coastal Ocean*, vol. 11. Harvard University Press, Cambridge, MA.
- Sydemann, W. J., García-Reyes, M., Schoeman, M. S. et al. (2014). Climate change and wind intensification in coastal upwelling ecosystems. *Science*, **345**, 77–80.
- Sullivan, K. and Bustamante, G. (1999). *Setting Geographic Priorities for Marine Conservation in Latin America and the Caribbean*. The Nature Conservancy, Arlington, VA, p. 141.
- Sunday, J. M., Bates, A. E. and Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–90.
- Takesue, R. K., van Geen, A., Carriquiry, J. D. et al. (2004). Influence of coastal upwelling and El Niño-southern oscillation on nearshore water along Baja California and Chile: shore-based monitoring during 1997–2000. *Journal of Geophysical Research-Oceans*, **109**, C03009.
- Tapia, F. J., Navarrete, S. A., Castillo, M. et al. (2009). Thermal indices of upwelling effects on inner-shelf habitats. *Progress in Oceanography*, **83**, 278–87.
- Tapia, F. J., Largier, J., Castillo, M., Wieters, E. A. and Navarrete, S. A. (2014). Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. *Plos One*, **9**, e110841.
- Teagle, H., Hawkins, S. J., Moore, P. J. and Smale, D. A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*, <http://doi.org/10.1016/j.jembe.2017.01.017>.
- Tellier, F., Tapia, J., Faugeton, S., Destombe, C. and Valero, M. (2011). The *Lessonia nigrescens* species complex (Laminariales, phaeophyceae) shows strict parapatry and complete reproductive isolation in a secondary contact zone. *Journal of Phycology*, **47**, 894–903.
- Thiel, M., Macaya, E., Acuña, E. et al. (2007). The Humboldt current system of northern-central Chile: oceanographic processes, ecological interactions and socio-economic feedback. *Oceanography and Marine Biology: An Annual Review*, **45**, 195–345.
- Thomas, F. and Poulin, R. (1998). Manipulation of a mollusc by a trophically transmitted parasite: convergent evolution or phylogenetic inheritance? *Parasitology*, **116**, 431–6.
- UACH. (2006). Actualización y validación de la clasificación de las zonas biogeográficas litorales. Universidad austral de Chile, Informe Final proyecto FIP 204-28. Fondo de Investigación Pesquera, Santiago, www.fip.cl/Archivos/Hitos/Informes/inffinal%202004-28.pdf.
- Underwood, A. J. (1992). Competition and Marine Plant–Animal Interactions. In D. M. John, S. J. Hawkins and J. H. Price, eds. *Plant–Animal Interactions in the Marine Benthos*. Clarendon Press, Oxford, pp. 443–75.
- Valle-Levinson, A., Atkinson, L. P., Figueroa, D. and Castro, L. (2003). Flow induced by upwelling winds

- in an equatorward facing bay: Gulf of Arauco, Chile. *Journal of Geophysical Research*, **108**, 1–14.
- Valdivia, N., Aguilera, M. A., Navarrete, S. A. and Broitman, B. R. (2015). Disentangling the effects of propagule supply and environmental filtering on the spatial structure of a rocky shore metacommunity. *Marine Ecology Progress Series*, **538**, 67–79.
- Valdovinos, C., Navarrete, S. A. and Marquet, P. (2003). Mollusk species diversity in the Southeastern Pacific: why are there more species towards the pole? *Ecography*, **26**, 139–44.
- Vásquez, J. A. (1992). *Lessonia trabeculata*, a subtidal bottom kelp in northern Chile: a case of study for a structural and geographical comparison. In U. Seeliger, ed. *Coastal Plant Communities of Latin America*. Academic Press Inc., San Diego, CA, pp. 77–89.
- Vásquez, J. A. (1993a). Patrones de distribución de poblaciones submareales de *Lessonia trabeculata* (Laminariales, Phaeophyta) en el norte de Chile. *Serie Ocasional, Facultad de Ciencias del Mar, Universidad Católica del Norte*, **2**, 187–211.
- Vásquez, J. A. (1993b). Abundance, distributional patterns and diets of main herbivorous and carnivorous species associated with *Lessonia trabeculata* kelp beds in northern Chile. *Serie Ocasional, Facultad de Ciencias del Mar, Universidad Católica del Norte*, **2**, 213–29.
- Vásquez, J. A. and Buschmann, A. (1997). Herbivory-kelp interactions in subtidal Chilean communities: a review. *Revista Chilena de Historia Natural*, **70**, 41–52.
- Vásquez, J. A., Camus, P. A. and Ojeda, F. P. (1998). Diversidad, estructura y funcionamiento de ecosistemas costeros rocosos del norte de Chile. *Revista Chilena de Historia Natural*, **71**, 479–99.
- Vásquez, J. A., Fonck, E. and Vega, J. A. M. (2001a). Comunidades submareales rocosas dominadas por macroalgas en el norte de Chile: diversidad, abundancia y variabilidad temporal. In K. Alveal and T. Antezana, eds. *Sustentabilidad de la biodiversidad. Un problema actual, bases científico-técnicas, teorizaciones y perspectivas*. Universidad de Concepción, Concepción, pp. 281–92.
- Vásquez, J. A., Veliz, D. and Pardo, L. M. (2001b). Biodiversidad bajo las grandes algas. In K. Alveal and T. Antezana, eds. *Sustentabilidad de la biodiversidad. Un problema actual, bases científico-técnicas, teorizaciones y perspectivas*. Universidad de Concepción, Concepción, pp. 293–308.
- Vásquez, J. A. and Vega, J. M. A. (2004). El Niño 1997–1998 en el norte de Chile: efectos en la estructura y en la organización de comunidades submareales dominadas por algas pardas. In S. Avaria, J. Carrasco, J. Rutland and E. Yañez, eds. *El Niño-La Niña 1997-2000: su efecto en Chile*. Comité Oceanográfico Nacional, Valparaíso, pp. 115–36.
- Vásquez, J. A., Vega, J. M. A. and Buschmann, A. H. (2006). Long term studies on El Niño-La Niña in northern Chile: effects on the structure and organization of subtidal kelp assemblages. *Journal of Applied Phycology*, **18**, 505–19.
- Vásquez, J. A., Piaget, N. and Vega, J. M. A. (2012). Chilean *Lessonia nigrescens* fishery in northern Chile: how do you harvest is more important than how much do you harvest. *Journal of Applied Phycology*, **24**, 417–26.
- Vásquez, J. A. and Donoso, G. (2013). *Loxechinus albus: Biology and Ecology*. Development in Aquaculture and Fisheries Science. Elsevier, Amsterdam.
- Vega, J. M. A., Vásquez, J. A. and Buschmann, A. H. (2005). Population biology of the subtidal kelps *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in an upwelling ecosystem of northern Chile: interannual variability and El Niño 1997–98. *Revista Chilena de Historia Natural*, **78**, 33–50.
- Vega, J. M. A., Broitman, B. R. and Vásquez, J. A. (2014). Monitoring the sustainability of *Lessonia nigrescens* complex (Laminariales, Phaeophyta) in northern Chile under string harvest pressure. *Journal Applied Phycology*, **26**, 791–801.
- Velásquez, C., Jaramillo, E., Camus, P. A., Manzano, M. and Sánchez, R. (2016). Biota del intermareal rocoso expuesto de la Isla Grande de Chiloé, Archipiélago de Chiloé, Chile: Patrones de diversidad e implicancias ecológicas y biogeográficas. *Revista de Biología Marina y Oceanografía*, **51**, 33–50.
- Vergés, A., Doropoulos, C., Malcolm, H. A. et al. (2016). Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proceeding of the National Academy of Science*, **113**, 13791–6.
- Villaseñor-Parada, C., Pauchard, A. and Macaya, E. C. (2017). Ecology of marine invasions in continental Chile: what do we know and we need to know? *Revista Chilena de Historia Natural*, **52**, 17.
- Villouta, E. and Santelices, B. (1984). Estructura de la comunidad submareal de *Lessonia* (Phaeophyta, Laminariales) en Chile norte y central. *Revista Chilena de Historia Natural*, **57**, 111–22.
- Viviani, C. (1979). Ecogeografía del litoral chileno. *Studies on Neotropical Fauna and Environment*, **14**, 65–123.
- Walls, A. M., Edwards, M. D., Firth, L. B. and Johnson, M. P. (2017). Successional changes of epibiont fouling communities of the cultivated kelp *Alaria esculenta*: predictability and influences. *Aquaculture Environment Interactions*, **9**, 55–69.

- Wang, D., Gouhier, T. C., Menge, B. A. and Ganguly, A. R. (2015). Intensification and spatial homogenization of coastal upwelling under climate change. *Nature*, **518**, 390–4.
- Webb, O. C., Ackerly, D. D., McPeck, M. A. and Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Wernberg, T., Smale, D. A., Tuya, F. et al. (2013). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, **3**, 78–82.
- 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., Kaplan, D. M., Navarrete, S. A. et al. (2003). Alongshore and temporal variability in chlorophyll a concentration in Chilean nearshore waters. *Marine Ecology Progress Series*, **249**, 93–105.
- Wood, S., Lilley, S., Schiel, D. and Shurin, J. (2010). Organismal traits are more important than environment for species interactions in the intertidal zone. *Ecology Letters*, **13**, 1160–71.
- Wood, C. L., Micheli, F., Fernández, M., Gelcich, S., Castilla, J. C. and Carvajal, J. (2013). Marine protected areas facilitate parasite populations among four fished host species of central Chile. *Journal of Animal Ecology*, **82**, 1276–87.