

THE HUMBOLDT CURRENT SYSTEM OF NORTHERN AND CENTRAL CHILE

OCEANOGRAPHIC PROCESSES, ECOLOGICAL INTERACTIONS AND SOCIOECONOMIC FEEDBACK

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Abstract The Humboldt Current System (HCS) is one of the most productive marine ecosystems on earth. It extends along the west coast of South America from southern Chile (~42°S) up to Ecuador and the Galapagos Islands near the equator. The general oceanography of the HCS is characterised by a predominant northward flow of surface waters of subantarctic origin and by strong upwelling of cool nutrient-rich subsurface waters of equatorial origin. Along the coast of northern and central Chile, upwelling is localised and its occurrence changes from being mostly continuous (aseasonal) in northern Chile to a more seasonal pattern in southern-central Chile. Several important upwelling centres along the Chilean coast are interspersed with long stretches of coast without or with sporadic and less intense upwelling. Large-scale climatic phenomena (El Niño Southern Oscillation, ENSO) are superimposed onto this regional pattern, which results in a high spatiotemporal heterogeneity, complicating the prediction of ecological processes along the Chilean coast. This limited predictability becomes particularly critical in light of increasing human activities during the past decades, at present mainly in the form of exploitation of renewable resources (fish, invertebrates and macroalgae). This review examines current knowledge of ecological processes in the HCS of northern and central Chile, with a particular focus on oceanographic factors and the influence of human activities, and further suggests conservation strategies for this high-priority large marine ecosystem. Along the Chilean coast, the injection of nutrients into surface waters through upwelling events results in extremely high primary production. This fuels zooplankton and fish production over extensive areas, which also supports higher trophic levels, including large populations of seabirds and marine mammals. Pelagic fisheries, typically concentrated near main upwelling centres (20–22°S, 32–34°S, 36–38°S), take an important share of the fish production, thereby affecting trophic interactions in the HCS. Interestingly, El Niño (EN) events in northern Chile do not appear to cause a dramatic decline in primary or zooplankton production but rather a shift in species composition, which affects trophic efficiency of and interactions among higher-level consumers. The low oxygen concentrations in subsurface waters of the HCS (oxygen-minimum zone, OMZ) influence predator-prey interactions in the plankton by preventing some species from migrating to deeper waters. The OMZ also has a strong effect on the bathymetric distribution of sublittoral soft-bottom communities along the Chilean coast. The few long-term studies available from sublittoral soft-bottom communities in northern and central Chile suggest that temporal dynamics in abundance and community composition are driven by interannual phenomena (EN and the extent and intensity of the OMZ) rather than by intra-annual (seasonal) patterns. Macrobenthic communities within the OMZ are often dominated in biomass by sulphide-oxidising, mat-forming bacteria. Though the contribution of these microbial communities to the total primary production of the system and their function in structuring OMZ communities is still scarcely known, they presumably play a key role, also in sustaining large populations of economically valuable crustaceans. Sublittoral hard bottoms in shallow waters are dominated by macroalgae and suspension-feeder reefs, which concentrate planktonic resources (nutrients and suspended matter) and channel them into benthic food webs. These communities persist for many years and local extinctions appear to be mainly driven by large-scale events such as EN, which causes direct mortality of benthic organisms due to lack of nutrients/food, high water temperatures, or burial under terrigenous sediments from river runoff. Historic extinctions in combination with local conditions (e.g., vicinity to upwelling centres or substratum availability) produce a heterogeneous distribution pattern of benthic communities, which is also reflected in the diffuse biogeographic limits along the coast of northern-central Chile. Studies of population connectivity suggest that species with highly mobile planktonic dispersal stages maintain relatively continuous populations throughout most of the HCS, while populations of species with limited planktonic dispersal appear to feature high genetic structure over small spatial scales. The population dynamics of most species in the HCS are further influenced by geographic variation in propagule production (apparently caused by local differences in primary production), by temporal variation in recruit supply (caused by upwelling

events, frontal systems and eddies), and topographically driven propagule retention (behind headlands, in bay systems and upwelling shadows). Adults as well as larval stages show a wide range of different physiological, ecological and reproductive adaptations. This diversity in life-history strategies in combination with the high variability in environmental conditions (currents, food availability, predation risk, environmental stress) causes strong fluctuations in stocks of both planktonic and benthic resources. At present, it remains difficult to predict many of these fluctuations, which poses particular challenges for the management of exploited resources and the conservation of biodiversity in the HCS. The high spatiotemporal variability in factors affecting ecological processes and the often-unpredictable outcome call for fine-scale monitoring of recruitment and stock dynamics. In order to translate this ecological information into sustainable use of resources, adaptive and co-participative management plans are recommended. Identification of areas with high biodiversity, source and sink regions for propagules and connectivity among local populations together with developing a systematic conservation planning, which incorporates decision support systems, are important tasks that need to be resolved in order to create an efficient network of Marine Protected Areas along the coast of northern-central Chile. Farther offshore, the continental shelf and the deep-sea trenches off the Chilean coast play an important role in biogeochemical cycles, which may be highly sensitive to climatic change. Research in this area should be intensified, for which modern research vessels are required. Biodiversity inventories must be accompanied by efforts to foster taxonomic expertise and museum collections (which should integrate morphological and molecular information). Conservation goals set for the next decade can only be achieved with the incorporation of local stakeholders and the establishment of efficient administrative structures. The dynamic system of the HCS in northern-central Chile can only be understood and managed efficiently if a fluent communication between stakeholders, administrators, scientists and politicians is guaranteed.

Introduction

The deep-blue colour of the water observed for a long time past gave place to a green colour, and on the whole there was a great change in the general character of the surface fauna, pointing to the nearness of a great continent, similar to what was observed off Japan and elsewhere. On November 18 [1875], the water was very green in colour, and the ship occasionally passed through large red or brown patches, which the tow-net showed to be due to immense numbers of red copepods, hyperids, and other Crustacea.

Murray (1895), on approaching Valparaíso aboard *H.M.S. Challenger*

Such a vivid language was rarely used by John Murray to refer to the abundance of planktonic organisms in surface waters. Only for the surface plankton from the Agulhas Bank off South Africa did he employ similar colourful language, referring to “myriads of Zoeae and a few larger Megalopae”. Scientists studying the plankton ecology of the Eastern Boundary Currents (EBCs) are used to the sight of these dense accumulations of zooplankton, which are often found in sharply defined patches. It is the intense upwelling of nutrient-rich waters in the EBCs that fuels the extraordinary high primary production (PP) in the EBCs, which forms the basis of the food web supporting some of the largest fisheries of the world. However, the frequency and intensity of upwelling within the EBCs varies, mainly depending on large-scale climatic forcing, latitudinal/seasonal signals and local factors, such as the width of the shelf, coastal topography, and sources of upwelled waters (Thomas et al. 2004). Although the overall importance of upwelling in these large marine ecosystems is relatively well known, the effects of temporal and spatial variability of upwelling on the ecology and productivity of the planktonic and benthic communities remain poorly understood. Herein these effects are explored, using the Humboldt Current System (HCS), one of the most

productive EBCs (Halpin et al. 2004, Montecino et al. 2005), as a model system. In the present paper knowledge on the HCS in northern-central Chile is reviewed because this area is characterised by a complex set of temporally changing and geographically variable conditions that represent a particular challenge to science and management (see also Artisanal benthic fisheries and following sections, p. 278ff). The aims of this review are 4-fold: to (1) review current knowledge, (2) reveal gaps in information, (3) indicate conservation priorities, and (4) propose future research avenues.

The HCS, by some authors named the Peru-Chile Current System, extends from $\sim 42^{\circ}\text{S}$ up to about the equator (Montecino et al. 2005). The main oceanographic features of this system are often described as cold nutrient-rich waters being transported northward and nutrient-enriched subsurface waters upwelled along the shorelines of Ecuador, Peru and northern Chile. Occasionally the nutrient-supply engine of the HCS is interrupted by influx of warm and nutrient-depleted equatorial waters; during such events (El Niño, EN) the northward flow of cool nutrient-rich waters is suppressed and upwelling intensity is often reduced (W. Palma et al. 2006). Individual cycles of this El Niño Southern Oscillation (ENSO) last for several years, but predictability of EN events is still very limited. On shorter temporal scales, there is a seasonal (predictable) pattern of climate and oceanography at high latitudes, which becomes aseasonal (and less predictable) at mid- and low latitudes (Blanco et al. 2001, Carr et al. 2002). It can be argued that the predictability of oceanographic conditions is lowest in the mid-region of the HCS (from 18°S to about 32°S ; see also Thomas et al. 2001a) because here the seasonal variations are occasionally overshadowed by the interannual ENSO cycles, whereas at low latitudes ($<18^{\circ}\text{S}$) the conditions may remain relatively stable for several years in a row, only being disturbed, but then severely, by EN events. To add to this variability, the HCS between 18°S and $\sim 40^{\circ}\text{S}$ features a complex coastal oceanography, where the main equatorward current is enveloped by a set of counter- and undercurrents, the width, location and intensity of which also vary in time. Herein we focus on this area between 18°S and $\sim 40^{\circ}\text{S}$ because the interaction between seasonal and interannual (ENSO) signals results in high temporal variability, which affects the ecological processes in this region.

Overall, the coastline of northern and central Chile (18° to $\sim 40^{\circ}\text{S}$) is relatively straight (Figure 1), but in the nearshore region small-scale geographic features produce a high spatial heterogeneity, which also influences oceanographic conditions in this area. Several bay systems are found along the coast of northern-central Chile. Circulation in these bays is complex with counterrotating gyres (Valle-Levinson et al. 2000) affecting larval transport and settlement patterns (A.T. Palma et al. 2006), most likely related to depth- and site-dependent retention or export scenarios (Yannicelli et al. 2006a). Headlands favour the generation of powerful coastal flow structures (squirts) transporting surface waters up to 100 km offshore (Marín et al. 2003a). In contrast, long stretches of exposed outer coast without headlands or bays, as found for example in northern Chile between 20° and 22°S , favour alongshore currents leading to relatively homogeneous conditions and downstream transport (W. Palma et al. 2006).

Numerous studies have examined the effects of oceanographic conditions on a variety of ecological processes in the HCS (e.g., Carrasco & Santander 1987, Tarazona et al. 1988a,b, Alheit & Niquen 2004, Arntz et al. 2006). Upwelling or ENSO-related conditions affect PP (Wieters et al. 2003, Iriarte & González 2004), zooplankton community composition (Escribano et al. 2004a), fish population dynamics (Halpin et al. 2004), dispersal of larvae (Poulin et al. 2002a,b), growth of benthic algae (Wieters 2005), benthic-pelagic coupling (Graco et al. 2006), population dynamics of benthos organisms (Castilla & Camus 1992), and a variety of other processes. Most of these studies have focused on direct cause-effect relationships between oceanographic factors and ecological responses. Recent studies in central Chile indicate complex interactions between upwelling, supply of recruits, and grazers or predators (Nielsen & Navarrete 2004, Wieters 2005). These studies show the importance of bottom-up and top-down processes, which may vary on small temporal and spatial scales, making predictions difficult. In this context, Navarrete et al. (2002) emphasised

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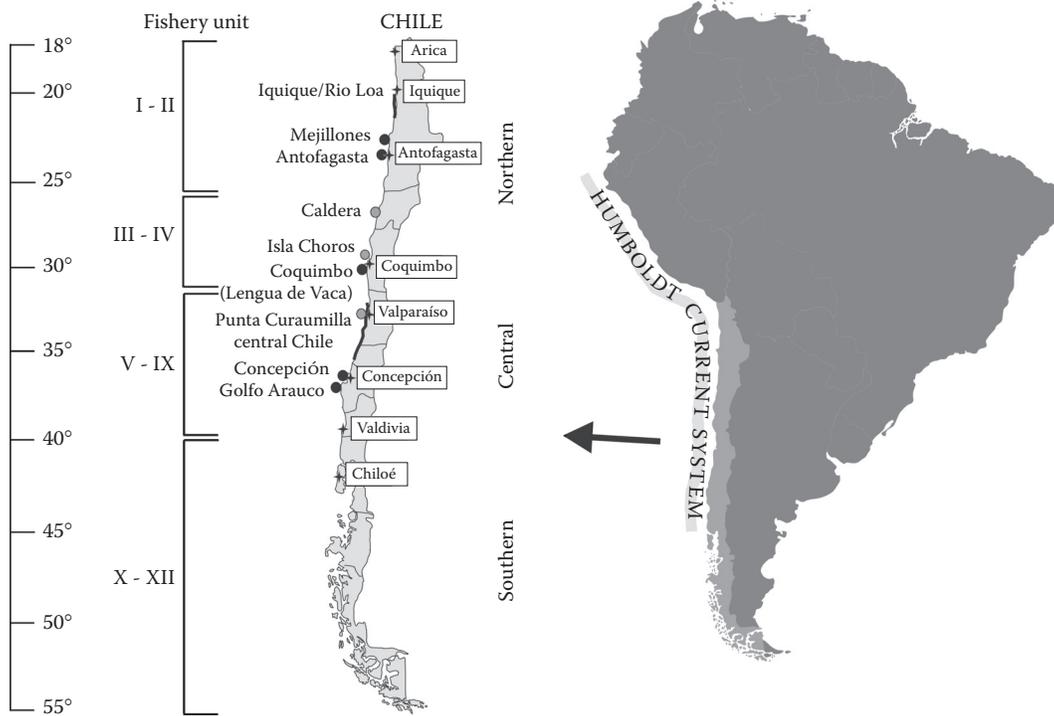


Figure 1 Study region in northern Chile with the main upwelling regions and localities mentioned throughout the text. Principal upwelling centers in black dots, other sites with frequent upwelling indicated with grey dots, coastal stretches with occasional upwelling shown as thick black line.

that “lack of consistent trends among sites ... shows that El Niño effects on interannual recruitment variation are not predictable”. Not only marine biologists but above all the organisms inhabiting the HCS are grappling with this limited predictability. How do these organisms deal with the difficulty of foreseeing the availability of dispersal windows, food, competitors or predators in the near future? Many of the following sections will explicitly or implicitly address this question. The main focus, though, will be on the outcomes of ecological processes in the HCS, the processes that govern them and their relevance in a socioeconomic and conservation context.

Variable distribution patterns and species interactions in the HCS are not only due to oceanographic processes but are also increasingly affected by human activities that reduce the abundance of some species while favouring others. When humans first started to use the natural resources of the HCS, they opportunistically reacted to the system and exploited natural resources where these were available and accessible. When a particular resource became scarce or inaccessible they either searched for the resource in other places or shifted to alternative resources (e.g., Llagostera 1979, Méndez & Jackson 2004). With increasing population pressure and technological advances, human pressure on the HCS has intensified. Wave-sheltered bays along the coast with dense human populations are impacted by intense shipping traffic, artificial coastline constructions and wastewater influx (Fernández et al. 2000). Mining and agriculture activities have resulted in severe contamination of some coastal areas, fishing pressure has intensified and extended into previously inaccessible regions and zones and finally climate change (increased ultraviolet (UV) radiation, global warming) has also reached the HCS. From being opportunistic users who responded to natural variations in resource abundance, humans have now become important actors who directly affect many of the

natural processes in the HCS. Recognition of this impact has called increasingly for planning and regulation of human activities. The limited predictability of oceanographic conditions and the ecological processes in the HCS, however, represents an enormous challenge for efficient management of this large marine ecosystem. Herein we strive to describe those aspects of the system that are comparatively predictable and to identify those that will require additional knowledge before they can be reliably predicted. In order to achieve this goal, this review provides (1) a brief overview of historic research activities, (2) a description of the main oceanographic conditions in the HCS of northern and central Chile, (3) an analysis of the pelagic environment and top consumers, (4) an introduction to benthic systems and nearshore biogeography, (5) a discussion of biological adaptations of organisms, (6) a portrayal of socioeconomic aspects related to the exploitation of natural resources, and finally (7) a scenario for marine conservation and an outlook identifying some of the main administrative and scientific tasks for the future.

A brief history of research on the Humboldt current system

First reports on a cool current in the southeastern Pacific

First written accounts of a cold current along the western coast of South America come from the European explorers. According to Gunther (1936), the history of the Humboldt Current began in 1515 when Vasco Nuñez de Balboa first sighted the South Sea. The knowledge of this oceanic current dates to the sixteenth century when several Europeans carried out observations suggesting that waters were cool: Pascual de Andagoya in 1522 was the first Spaniard to explore to the south of the Panamanian coast, Agustín de Zarate published in 1555 his *Historia del descubrimiento y Conquista de la Provincia del Peru*, and the Jesuit José de Acosta described in his *Historia Natural y Moral de Indias* (1591) the temperature conditions and their influence on the climate (Santibáñez 1944). Other travellers carried out additional observations (for details see Gunther 1936), but it was the German naturalist Alexander von Humboldt who took the first temperature measurements (Gunther 1936, Santibáñez 1944). Humboldt (1846), in his book *Cosmos*, wrote on page 301: “in the Southern Pacific Ocean, ... a current the effect of whose low temperature on the climate of the adjacent coast was first brought into notice by myself in the autumn of 1802. This current brings the cold water of high southern latitudes to the coast of Chile, and follows its shores and those of Peru northward”. Additionally, Humboldt also was the first to describe EN temperature anomalies in coastal waters (Kortum 2002).

From natural history to ecology to marine conservation

The first Chilean naturalist was Abate Juan Ignacio Molina. He published the following works in Italy: *Compendio della storia geografica, naturale, e civili del regno del Chile* (1776) and *Saggio sulla storia naturale del Chili* (1782), which include detailed descriptions of the mineral wealth and native flora and fauna based on the Linnaean system of classification (Ronan 2002). Claudio Gay, a French naturalist who arrived in Chile in 1828, as a result of 12 yr of exploring Chile under government contract, wrote his *Historia física y política de Chile*. In 29 volumes Gay described the history, botany and zoology of the country, including detailed descriptions of the marine fauna (e.g., 79 species of decapod crustaceans) (Jara 1997). Rodolfo Amando Philippi, who emigrated from Germany to Chile in 1851, was a physician by profession but a naturalist by inclination, and he is considered one of the most recognised and influential scientists in the development of natural sciences in Chile (Castro et al. 2006). He contributed numerous taxonomic descriptions to the knowledge of biological diversity of Chile. In a recent article, Castro et al. (2006) conclude that in comparison with other taxonomists, Philippi was the author of the largest number of presently

valid species in the Chilean biota. Other scientists who contributed enormously to the knowledge of the fauna and flora from the HCS of northern-central Chile included Alcide D'Orbigny, Eduard Friedrich Poeppig and Carlos Emilio Porter Mosso.

Most expeditions during the eighteenth and nineteenth centuries produced observations and collections that were gathered by individual scientists or 'naturalists' aboard global voyages of exploration and discovery. These voyages often had political, military and economic purposes, with science being a secondary or even incidental activity (Fiedler & Lavín 2006). After Humboldt's travels, several pioneer expeditions were carried out in the southern Pacific, but most of them rounded Cape Horn on their way into the Pacific, stopped in Concepción or more commonly in Valparaíso, and then turned off to Juan Fernández and from there progressed further into the southwest Pacific. The coasts of northern Chile were rarely visited by these expeditions. Also the U.S. Exploring Expedition (1838–1842), the main objective of which was to facilitate American commerce (Johnson 1995), left the coast of northern Chile untouched on its way from Valparaíso to Callao. Other expeditions took the same route on their return trips. For example, the Novara Expedition passed through Valparaíso in April 1859, coming from Tahiti. The corvette *H.M.S. Challenger* reached Valparaíso in November 1875 coming from Juan Fernández and then continued to the south. Later expeditions, such as the Fisheries Commission Steamer *Albatross*, with Alexander Agassiz on board, explored the northern parts of the HCS, but rarely reached farther south than Callao, Peru. A notable exception to this general pattern was the *H.M.S. Beagle* (1831–1836), with Charles Darwin aboard, which after leaving Valparaíso made stopovers in Coquimbo (30°S), Caldera (27°S) and Iquique (20°S) before continuing directly to Callao (Peru) (Darwin 1851, 1854).

Expeditions conducted during the first half of the twentieth century were mainly dedicated to the study of the local biodiversity. One of the most important expeditions during that time, the Lund University Chile Expedition in 1948–1949, explored the Chilean coast between Iquique and the Magellan Straits, but of the 277 stations visited, only 79 were located in northern and central Chile (Brattström & Dahl 1951). Only during the last half of the twentieth century have concentrated research efforts been directed toward the oceanography and ecology of the HCS in northern Chile (e.g., Gallardo 1963 and many others).

While those initial studies have provided important information on the description of species distribution and abundance in the HCS along the coast of Chile, research during the last quarter of the twentieth century became much more process oriented (Castilla & Largier 2002, Escribano et al. 2004a,b, Montecino et al. 2005 and citations therein). In particular during the past decade, marine conservation has become an important topic in the marine sciences literature of Chile (see, e.g., Castilla 1996, 2000, Fernández et al. 2000, Fernández & Castilla 2000, 2005, Moreno 2001). Thus, as in other regions of the HCS (e.g., Pauly et al. 1989), research in the HCS along the Chilean coast has shifted from a description of taxonomy and patterns to the examination of processes, which has also resulted in an increasing trend of interdisciplinary studies, in particular between ecologists and oceanographers.

Oceanographic conditions in the southeastern Pacific

The HCS is the equatorward-flowing, eastern portion of the basin-scale southeast Pacific anti-cyclonic gyre, bounded to the north by the equatorial current system and to the south by the West Wind Drift (WWD). The HCS is one of the four major global EBCs, characterised by dominant equatorward alongshore wind stress, offshore Ekman transport, coastal upwelling of cold, nutrient-rich subsurface water and highly productive fisheries (Hill et al. 1998). The narrow continental shelf and meridionally oriented coastline of South America allow efficient transmittal of atmospheric and oceanographic signals imposed from both lower latitudes through the equatorial current system and from higher latitudes where increasing seasonality in both wind forcing and oceanic response

is seen with increasing latitude. The coast can be divided into general zones based on physical characteristics. The shelf (200 m) off Peru is up to 100 km wide. Along the Chilean coast, four zones (Figueroa 2002) include the northern region (north of $\sim 32^\circ\text{S}$) with little freshwater influence and an extremely narrow shelf (<10 km), a widening shelf from 32°S to 36°S , a wider shelf (~ 70 km) from 36°S to 42°S with increased freshwater influence, especially in winter, and a high-latitude region ($>42^\circ\text{S}$) with a wider topographically complex, fjord-indented coastline and with strong freshwater influence.

Wind forcing in the southeast Pacific is dominated by the influence of the southeast Pacific subtropical anticyclone that creates equatorward, upwelling-favourable winds along most of the South American Pacific coast with latitudinally varying seasonality. Between 5°S and $\sim 35^\circ\text{S}$, monthly mean winds remain upwelling favourable throughout the year and are weakest along the northern Chilean coast $\sim 17\text{--}23^\circ\text{S}$ (Shaffer et al. 1999, Thomas et al. 2001a). Distinct phase differences in the annual maxima are evident as a function of latitude (Thomas et al. 2001a), where maximum upwelling strength shifts from austral autumn–winter off Peru (Bakun & Nelson 1991, Carr et al. 2002), to austral spring–summer off northern Chile (Blanco et al. 2001) and austral summer south of $\sim 30^\circ\text{S}$ (Shaffer et al. 1999). Upwelling is augmented by a decrease in alongshore wind stress near shore that creates a region of cyclonic (negative) wind stress curl in the coastal zone, lifting isotherms. Two regions of maximum alongshore wind stress are evident, centred at $\sim 15^\circ\text{S}$ and $\sim 30^\circ\text{S}$ (Shaffer et al. 1999, Thomas et al. 2001a, Hormazábal et al. 2004). North of 30°S , strong land–sea thermal contrast in austral summer enhances upwelling-favourable alongshore wind stress (Rutllant et al. 2004a). At the very lowest latitudes (north of $\sim 5^\circ\text{S}$), the annual meridional migration of the Inter-Tropical Convergence Zone (ITCZ) creates both wind and precipitation (and therefore stratification) seasonality. Beginning at $\sim 35^\circ\text{S}$ and extending poleward, seasonality in the strength of the subtropical anticyclone creates seasonal reversals between an austral summer upwelling maximum and mean winter conditions of poleward, downwelling-favourable winds driven by winter storms associated with the polar front (Shaffer et al. 1999, Rutllant et al. 2004a). The strength and duration of these winter conditions increases with latitude. South of $\sim 45^\circ\text{S}$, events associated with polar front activity create poleward alongshore monthly mean winds, downwelling conditions and strong precipitation in coastal regions throughout the year.

The large-scale equatorward surface flow of the HCS within the basin-scale gyre belies a complicated and still relatively poorly sampled flow structure closer to the coast. The following description is a general overview of commonly observed characteristics reviewed in more detail by Strub et al. (1998). The northern latitude at which the WWD approaches the continent shifts seasonally from 35°S to 40°S in austral winter to $\sim 45^\circ\text{S}$ in austral summer. Flow from the WWD branches north and south (Figure 2). The southern arm joins poleward coastal flow of the Cape Horn Current, a buoyancy-driven coastal current with input from local river runoff, which is strongest during austral winter. The northern arm forms the main flow of the Humboldt Current that proceeds equatorward along the basin margin and joins the westward-flowing South Equatorial Current at lowest latitudes, off northern Peru-Ecuador. This main flow of the Humboldt Current is located seaward ($\sim 75\text{--}85^\circ\text{W}$) of a system of narrower coastal flows. Closest to the coast and coupled to local wind forcing and coastal upwelling, the Chile Coastal Current (CCC) flows predominantly equatorward. In summer, equatorward flow is most latitudinally extensive, traceable to $35\text{--}40^\circ\text{S}$ (Atkinson et al. 2002) and flowing along the entire central and northern Chilean coast, continuous with the equatorward flowing Peru Coastal Current (PCC), also forced by local winds, as far as $\sim 5^\circ\text{S}$. In winter, the PCC strengthens in association with the winter maximum in alongshore wind stress. Off northern Chile ($18\text{--}24^\circ\text{S}$) the seasonal maximum of the CCC is in the autumn (Blanco et al. 2001), while south of $\sim 25^\circ\text{S}$ the CCC becomes increasingly seasonally variable. South of $\sim 35^\circ\text{S}$, in association with the seasonal reversal in alongshore wind stress, the CCC is predominantly

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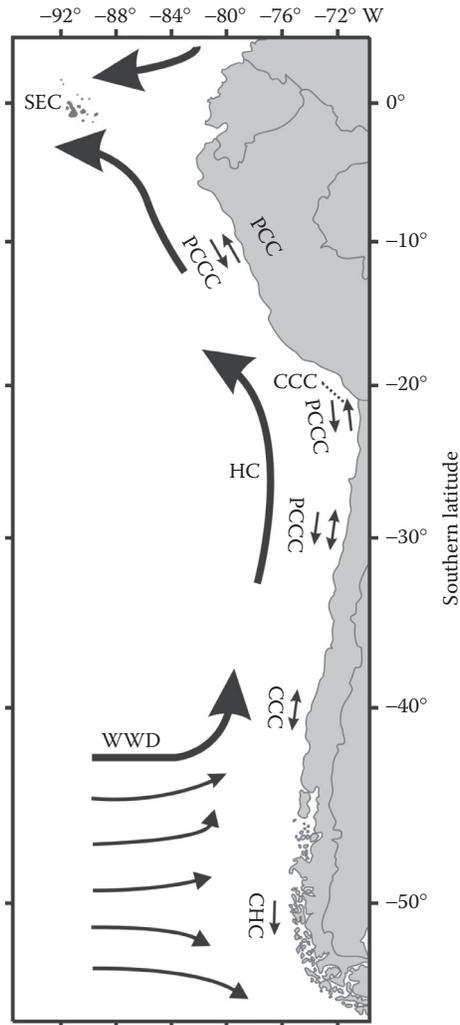


Figure 2 Overview of the surface currents in the eastern South Pacific that influence the north-central Chilean coast, showing the West Wind Drift (WWD), the main flow of the Humbolt Current (HC), the Cape Horn Current (CHC), the Chile Coastal Current (CCC), the Peru Coastal Current (PCC), the Peru-Chile Counter-current (PCCC) and the South Equatorial Current (SEC).

poleward in winter. Between these seasonal coastal currents and the more continuous equatorward flow of the main Peru-Chile Current is the poleward-flowing Peru-Chile Counter-current located ~100–300 km offshore, originating in equatorial regions likely as Equatorial Undercurrent water and continues to ~35°S. This flow is poorly resolved in drifter data (Chaigneau & Pizarro, 2005) but evident in altimeter data (Strub et al. 1995) and temperature-salinity characteristics (Strub et al. 1998). Beneath the coastal surface currents, a Poleward Undercurrent is continuous from northern Peru to latitudes as high as 45–50°S (Silva & Neshyba 1979). This undercurrent, located over the continental slope (Zuta & Guillén 1970, Shaffer et al. 1995, Leth et al. 2004), delivers relatively saline, nutrient-rich, low-oxygen water (equatorial subsurface water, ESSW) to coastal regions; it

is a primary contributor to upwelling off Peru and northern Chile (Huyer et al. 1987) and in Chilean coastal regions at least as far as 35°S (Fonseca 1989).

From 5°S to ~40°S, the primary coastal oceanographic characteristics are isotherms and isohalines of the upper ~100 m tilted upward toward the coast and associated with upwelling. Off Peru, the seasonally maximum winter winds and the small Coriolis term combine to create strong offshore Ekman transport with upwelling effects evident at least as far as 400 km offshore. Along the Chilean coast, four regions are recognised for especially strong upwelling, most likely due to topographic enhancement by headlands, at Antofagasta (23°S), Coquimbo (30°S), Valparaíso (33°S) and Concepción (37°S) (Figueroa & Moffat 2000, Mesías et al. 2003). Off southern-central Chile (36–40°S), coastal stratification imposed by freshwater runoff becomes important even during summer upwelling conditions (Atkinson et al. 2002).

Strong interannual variability is superimposed on mean seasonal patterns by ENSO signals propagating poleward along the coast from their equatorial source. These impose elevated sea levels, a deeper thermocline, positive sea-surface temperature (SST) anomalies and either a decrease or episodic reversal of coastal equatorward flow in the PCC and CCC (Figure 2) during the EN (warm) phase. Decreased coastal sea levels, shallower thermoclines, colder SST conditions and strengthened coastal equatorward flow occur during the La Niña (LN; cold) phase. Satellite data show that EN anomalies can extend south of 40°S to include the entire coast of South America (Carr et al. 2002, Strub & James 2002), but anomalies decrease with increasing latitude (Strub & James 2002, Montecinos et al. 2003, Escribano et al. 2004a). EN conditions can also be imposed by local anomalous winds, likely modulated via atmospheric teleconnections (Shaffer et al. 1999). Oceanic ENSO signals originate as eastward-propagating equatorial Kelvin waves that propagate poleward as coastally trapped waves (CTWs). Alongshore wind stress and offshore Ekman transport persist, or even strengthen during EN periods (Carr et al. 2002, Escribano et al. 2004a), but upwell warm, nutrient-poor water from above the deepened thermocline.

Mesoscale variability is evident as eddies and filaments that advect cold, high-pigment coastal water for hundreds of kilometres offshore, often originating at headlands (Thomas 1999, Sobarzo & Figueroa 2001, Mesías et al. 2003). Along the coast of central Chile, a transition zone of elevated eddy kinetic energy is observed (Hormazábal et al. 2004). A wide zone (800–1000 km) of relatively diffuse and low eddy kinetic energy is observed north of ~30°S where winds are weak but are persistently favourable to upwelling. Eddy kinetic energy is stronger and more closely associated with the coast (~600 km) in the region between ~30°S and 38°S where the winds, though stronger, are more variable (Hormazábal et al. 2004). Away from the coast (>300 km), altimeter and drifter data show two regions of maximum eddy kinetic energy, one along the Peru coast and another centred at ~30°S off Chile. This is consistent with patterns of surface temperature and satellite-measured ocean colour that show cold waters with high pigment concentrations associated with the upwelling extending furthest offshore off Peru and off central Chile (Montecino et al. 2005), while being restricted to an extremely narrow coastal band off northern Chile (Morales et al. 1999, Thomas et al. 2001b). CTWs propagate poleward along the entire Peru and Chile coastlines, traceable to wind fluctuations in equatorial regions (Hormazábal et al. 2001). CTWs raise and lower the pycnocline/nutricline, influencing the effectiveness of upwelling, with dominant frequencies of days to weeks off Peru (Enfield et al. 1987) and ~50-day periods off northern and central Chile (Shaffer et al. 1997, Hormazábal et al. 2001, Rutllant et al. 2004b). Ramos et al. (2006) show that variability of equatorial origin at both annual and semi-annual periods impose strong modulation on isotherm depth along the coast. CTWs appear especially energetic during EN periods and weaker during LN periods and austral winter (Shaffer et al. 1999). At the shorter time-/space scales, diurnal cycles in wind stress are important contributors to forcing along the arid northern Chilean coast, especially in summer (Rutllant et al. 1998), but become less important with increasing latitude, where

storm-mediated variability on 3- to 7-day cycles increases (Strub et al. 1998), with a maximum in austral winter.

Coastal oceanography

Coastal waters have been defined in many different ways depending upon the reason (e.g., scientific, geopolitical, international conventions, etc.) for their usage. Bowden (1983) defines them, from an oceanographic perspective, as “those on the continental shelf and the adjoining seas”. If such a definition would be used for the HCS, then the coastal strip would be rather narrow. Bottom depth in some areas of the HCS (i.e., Antofagasta) goes from less than 100 m at distances of 10 km from shore to more than 1000 m at 30 km. However, many characteristics of the plankton assemblages at those distances show that they are still largely influenced by the proximity of the coast. Thus, for the purposes of this analysis an alternative definition for coastal ocean is used: that part of the ocean where the proximity of the continents affects the circulation and ecological processes. This definition then includes coastal waters as defined by Bowden and the coastal transition zone defined by Hormazábal et al. (2004).

The analysis of any oceanographic system is scale dependent (Haury et al. 1978, Rutllant & Montecino 2002). Thus, if space–time is considered as a continuum, then isolating parts of it is an observer decision, which may be influenced by its epistemological background (Ramírez 2005a) and the characteristics of the ecosystem to be studied (Marín 2000). Haury et al. (1978), in a classical article on scales of analysis in oceanography, propose two terms (mesoscale and gross scale) to refer to those scales where the effects of flow structures such as filaments, squirts, meanders and eddies ($1\text{--}10^2$ km) are dominant and where ecosystem patterns are advective (influenced by the physics of the system) and biological. Coastal upwelling is one of the main mesoscale oceanographic processes affecting the dynamics and the spatial and temporal structure of coastal ecosystems along the EBCs (Strub et al. 1998, Montecino et al. 2005). Upwelling flow structures such as filaments (Sobarzo & Figueroa 2001), squirts (Marín et al. 2003a, Marín & Delgado 2007) and shadows (Castilla et al. 2002a, Marín et al. 2003b) have been described for the Chilean coast. Herein, information about those structures is succinctly reviewed and the potential effects on the ecology of the coastal ocean in the HCS are discussed.

The HCS, from the standpoint of coastal wind forcing, can be divided in two latitudinal areas near 26°S (Figueroa 2002). From 26°S to the north, meridional, upwelling-favourable winds are rather constant throughout the year; south of this latitude greater seasonality is observed. One important upwelling focus in the northern zone is the Mejillones Peninsula (23°S). Observational (Marín et al. 1993, Escribano et al. 2000, Marín et al. 2001, Olivares 2001, Sobarzo & Figueroa 2001, Escribano et al. 2002, Rojas et al. 2002, Marín et al. 2003b) and modelling studies (Escribano et al. 2004b) have shown that the dynamics of the coastal ecosystems in that area largely depend on the generation of upwelling filaments at Mejillones Peninsula. Indeed, the generation of filaments in the northern tip of the peninsula (Punta Angamos) has been identified as the main mechanism of nutrient enrichment in the surface layers (Marín & Olivares 1999). Furthermore, ‘upwelling shadows’ within Mejillones Bay, an equator-facing bay located in the northern end of the peninsula, have been dynamically linked to the generation of bifurcated filaments at Punta Angamos (Marín et al. 2003b). This shadow is an important physical structure within the bay, affecting PP (Marín et al. 2003b) and the retention of planktonic organisms (Olivares 2001). An alternative mechanism, described as an ‘upwelling trap’ by Castilla et al. (2002a) and also related to the coastal upwelling dynamics, generates higher temperatures inside Antofagasta Bay, a pole-facing bay at the southern end of the peninsula. In this case also the physically generated structure contributes to the retention of planktonic organisms. Thus, mesoscale flow features (upwelling shadows and upwelling traps),

associated with cold-water filaments, seem to play an important role not only in relation to the biological productivity of coastal upwelling regions but also as mechanisms for the retention of coastal planktonic species. If account is taken of the fact that Mejillones Peninsula is located in the area where upwelling-favourable winds occur year-round, then those areas may constitute recurrent retention zones.

Farther south, within the HCS area where upwelling is more seasonal, the Coquimbo Bay System (30°S) is another important coastal upwelling centre. This system is located within two coastal points (Punta Lengua de Vaca and Punta Pájaros) and is the site of intensive fisheries and eco-tourism (Ramírez 2005b). Filaments, including bifurcated upwelling filaments (Moraga et al. 2001), are known to generate at Punta Lengua de Vaca, contributing with cold, nutrient-high waters to the coastal system (Montecino & Quiroz 2000, Montecino et al. 2005). A recent Lagrangian study conducted within the bay (Marín & Delgado 2007) shows that the dominant equatorward flow is modulated at quasi-inertial frequencies, enhancing the coastal retention times. Furthermore, Marín et al. (2003a) have shown that cold-water squirts generate at the northern end of the bay system (near Punta Pájaros). Squirts seem to be geographically anchored to locations meeting the requirements for their generation (Strub et al. 1991). Thus, it is highly likely that indeed the squirts observed in the vicinity of Punta Pájaros are normally generated within the same area, making them a recurrent mesoscale flow feature. As a test of this idea a simple model was built using the ROMS model (Shchepetkin & McWilliams 2005) and initialised with the ROMSTOOLS package (Penven 2003). The study area was defined by longitudinal boundaries set at 74°W and 70°W and latitudinal boundaries at 32°S and 24°S (see also Figure 3). This model has been run for 2 yr in other eastern boundary systems such as the California Current System (Marchesiello et al. 2003) to obtain a statistical equilibrium condition. However, in the present test case a squirt was generated just after 17 days of integration, which closely resembles the squirt observed in an SST image obtained in January 2005 in shape, size and location (Figure 3). The interesting, and indeed serendipitous, observation resulting from this numerical exercise is that transient modes developed as perturbations (e.g., baroclinic instabilities) from climatological mean conditions generate coastal flow structures (squirts) which are recurrently found within the HCS. Satellite observations and Lagrangian drifter data (Marín & Delgado 2007) have in fact shown that this squirt is a recurrent feature in the area, reaching distances on the order of 140 km offshore. Squirt speeds, estimated both through feature-tracking analysis (Marín et al. 2003a) and Lagrangian drifters (Marín & Delgado 2007), range between 0.2 and 0.3 m s⁻¹. Thus, considering that the lifetime of a single squirt is related to the active period of equatorward wind events, which for the area range between 3 and 7 days (Rutllant et al. 2004a), coastal organisms trapped within the squirt are likely to reach 100–200 km offshore in a period of less than a week.

The conclusions that may be offered as a result of this brief, and highly condensed, analysis of the prevailing mesoscale coastal features of the HCS are nevertheless far reaching. In the first place, if these features are intrinsic to the HCS (generated as a result of coastline geometry, bottom topography and prevailing flow conditions including perturbations) and not dependent on large-scale, low-frequency forcing (e.g., ENSO), then a whole new array of multiscale (nested) models are necessary to generate predictable bio-oceanographic coastal patterns for the HCS. Second, coastal upwelling areas can be described as a dynamic mosaic of nearshore retention/offshore expatriation patches or sectors. Thus, for a planktonic organism, remaining in a specific location (i.e., local populations) within the HCS coastal zone becomes a probabilistic process. If, for example, larvae are entrained within an upwelling shadow then there is a high chance that they will remain in the same sector for a period close to a week. If, on the other hand, the larvae are entrained within a squirt, then in a period close to 24 h they will be expatriated offshore. However, since the seascape is dynamic and depends upon the upwelling condition, it is not possible to ensure that a given geographic location will always act as a retention or expatriation locality.

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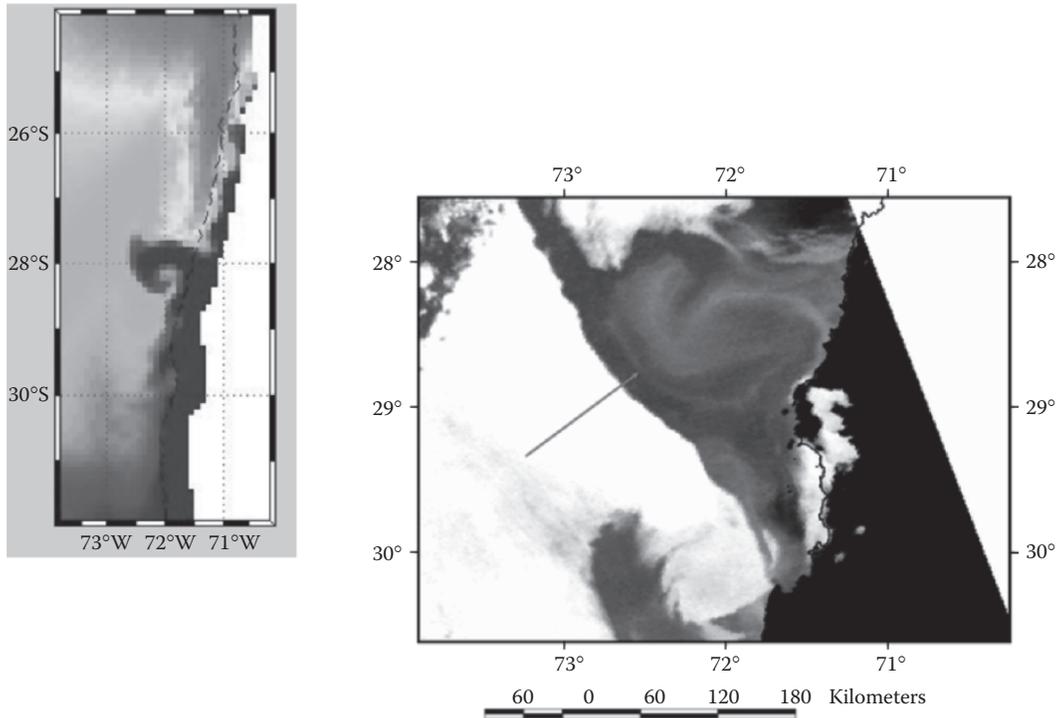


Figure 3 (See also Colour Figure 3 in the insert following page 344.) Result of the squirt simulation by means of the Regional Oceanic Modeling System (coloured image) for 17 January in comparison to the thermal squirt (NOAA satellite, black-and-white image) observed on 15 January 2005. Temperature coding of the coloured image goes from blue (lower temperature) to red (higher temperature) while for the NOAA image it goes from lighter to darker tones of grey. White areas in the NOAA image correspond to clouds. The study area in the model was defined by longitudinal boundaries set at 74°W and 70°W and latitudinal boundaries at 32°S and 24°S. The resolution was $1/10^\circ$, approximately 10 km, with 20 vertical levels, a minimum depth of 50 m and a smoothed bathymetry. The baroclinic time step was set to 900 s. Surface forcing (wind stress, heat fluxes, freshwater flux, SST, sea-surface salinity, and short-wave radiation) was derived from the monthly climatology found in the COADS dataset (Da Silva et al. 1994) and interpolated into the model grid. The temperature and salinity initial conditions for the model were obtained for the month of January from the 'World Ocean Atlas 2001' (Conkright et al. 2002). The Ekman and geostrophic velocities at the boundary were obtained combining these data with COADS winds, following Marchesiello et al. (2001), with level of no motion defined at 500 m (Marchesiello et al. 2003).

The water column chemistry

The northern Chilean ocean margin ($\sim 18\text{--}30^\circ\text{S}$) presents distinctive characteristics in topography, climatic and oceanographic conditions, which modulate PP and water column chemistry. It features a comparatively low PP (for the HCS), and despite semi-permanent wind-driven upwelling some areas are considered as high-nutrient low-chlorophyll (HNLC) environments (Torres 1995, Daneri et al. 2000). These observations are in contrast to the localised prominent upwelling cells with relatively high PP, such as off Iquique (21°S), Antofagasta (23°S) and Coquimbo (30°S) ($0.5\text{--}9.3\text{ g C m}^{-2}\text{ d}^{-1}$; González et al. 1998, Daneri et al. 2000, Thomas et al. 2001a).

Studies carried out in the main upwelling centres indicate that highest PP foci occur close to the coast over the narrow continental shelf and fuel major fisheries, with catches that represent

40% of the annual landings of the HCS (Escribano et al. 2003 and references therein). This production also constitutes an important way of sequestering CO₂ and supports a high rate of particulate organic matter (POM) exported to depth (González et al. 2000a, Pantoja et al. 2004). This material, which is partly remineralised in the water column, strengthens the oxygen-minimum zone (OMZ) and promotes biogeochemical anaerobic processes. In this sense, a sequence of mechanisms that are determined by the oceanographic conditions is regulating the chemistry of the water column and the sea bottom. These processes gain relevance in several aspects of material exchange (i.e., gas fluxes as CO₂ and N₂O), implying that this area could play a key role in the main global cycles (i.e., oceanic productivity, global warming, authigenic carbonatic and phosphorite mineral formation, etc.).

Oxygen distribution and relevance in organic carbon remineralisation

Most research efforts have focused on specific areas where high productivity cells are recognised, but the interactions with biogeochemical processes are still poorly understood. Along the northern margin of Chile, a well-developed OMZ is observed between 100 and 500 m water depth (Blanco et al. 2001). This zone is basically a mid-water feature since the topography of the margin precludes the OMZ to impinge on a large area of the bottom, except off Antofagasta (Mejillones) where it touches the bottom from 50 m to 300 m depth. Normally the shelf is extremely narrow from southern Peru to northern Chile (10–15 km) in comparison with central Peru and southern-central Chile (40–60 km; Strub et al. 1998), where the OMZ extends over a wide area of the shelf, promoting distinct biogeochemical processes (Gutiérrez 2000, Neira et al. 2001). This characteristic of northern areas could thus affect pathways (i.e., aerobic or anaerobic) associated with organic matter (OM) degradation in the sediments, which is an important source of regenerated nutrients to the water column. Off Mejillones, a high percentage (86%) of photosynthetically produced particulated protein is being degraded within the upper 30 m of the water column (Pantoja et al. 2004), coinciding with oxygenated waters. In consequence, OM reaching the sediments at greater depths is depleted of proteins. Over the shallower shelf sediments, where also preserved fish debris and bones are found (Milessi et al. 2005), high pigment concentrations have been reported (42–100 µg g⁻¹ of chloroplastic pigment equivalents in surface sediments; P. Muñoz et al. 2004a, 2005). Thus, there is a narrow band of inshore sediments that are enriched in fresh OM coming from the water column. The remineralisation of this material could generate an important flux of nutrients contributing to fertilisation of the water column. Similar predictions can be made for other areas of high PP along the coast of northern Chile, where upwelled waters containing preformed nutrients are enriched with recycled nutrients derived from the OM degradation in shelf sediments. The relevance of the sea floor in water column fertilisation and biological productivity as well as its relevance in the global carbon cycle has not been well examined. Some information is available for the role of sediments near the main upwelling centres, but nothing is known about the biogeochemical processes along the large extent of the margin between the main upwelling centres mentioned here.

The high OM degradation rates result in CO₂ supersaturated waters that, in combination with the CO₂ input from upwelled waters, favour the CO₂ flux from the ocean to the atmosphere. Some studies off Antofagasta (23–24°S) and Coquimbo (30°S) have measured a saturation of >200% in upwelled waters, an *f*CO₂ up to 1000 µatm and CO₂ flux ~3.9–4.0 mol C m⁻² yr⁻¹ (Torres et al. 2003 and references therein). These authors concluded that CO₂ outflux is a highly variable short-term process, depending on the intensity of the wind-driven upwelling, the depth of the upwelled waters, the OM degradation (positively correlated with the apparent oxygen utilisation, AOU) and the biological uptake. Furthermore, the high degradation rates of organic carbon by the microplankton community (dissolved organic carbon-, DOC; 1.1–21.6 µM h⁻¹; G. Daneri unpublished data) and high respiration rates (81–481 mmol O₂ m⁻² d⁻¹; R.A. Quiñones unpublished data) indicate

that nutrient recycling in the water column is an important process in the CO₂ production, resulting in high concentrations of CO₂ and outgassing when upwelled waters are warming up at the sea surface. A substantial proportion of the carbon assimilated by primary producers is reaching the bottoms via biogenic CaCO₃ flux, as has been observed off Coquimbo (30°S) where sediment traps located at 2300 m water depth (~180 km off the coast) revealed that almost 40–90% of carbonate flux is associated with some species of foraminiferans characteristic of upwelling areas (H.E. González et al. 2004a, Marchant et al. 2004). These authors suggest that biogenic CaCO₃ is the main pathway by which carbon is removed from the upper ocean, controlled by autochthonous and allochthonous foraminiferans, that is, large-size organisms with high sinking rates (1.5 days) and smaller organisms that are laterally advected. Therefore, part of this carbon is exported offshore, sequestered from the water column and preserved in the sediments (Hebbeln et al. 2000a,b), but it has not been clearly established what percentage of the total CO₂ assimilated by primary producers this CaCO₃ flux represents.

Macro- and micronutrient distribution

The distribution of nutrients shows a high variability in the water column associated with upwelling pulses and mixing. High concentrations occur inshore and usually decrease in the offshore direction, followed by decreasing pigment concentrations (Escribano et al. 2003, Marín et al. 2003a, 2004a, Peñalver 2004). Off 30°S, high surface concentrations of nitrate, phosphate and silicate have been reported (~5–15, 0.5–1 and 5–8 μM, respectively; Peñalver 2004). The nutrient distribution at this latitude is also affected by the topography of the area, where several islands reduce the circulation and mixing of the water column (Peñalver 2004). In northern Chile, between 20°S and 22°S, high concentrations of nitrate were also observed near shore at <100 m water depth (0–20 μM; Escribano et al. 2004b, Pantoja et al. 2004, Herrera & Escribano 2006). In general, the distribution of nitrate showed low subsurface concentrations (Pantoja et al. 2004, Peñalver 2004) associated with high nitrite concentrations (>2 μM; Morales et al. 1996) and coincident with low oxygen concentrations (<0.5 ml L⁻¹). This implies that denitrification is an important process in the nitrogen recycling, as has been recognised for other OMZ regions (Codispoti & Christensen 1985, Codispoti et al. 1986, Cornejo et al. 2006).

Another important aspect that controls the biogeochemistry of the water column is the hydrological regime. Northern Chile, with the Atacama Desert, is an extremely arid zone without relevant fluvial inputs into the ocean. The maximum amount of precipitation is ~0.5–78 mm yr⁻¹, which is significantly lower than in central and southern Chile (300 to >1000 mm yr⁻¹; www.meteochile.cl). In general, rivers play an important role in the fluxes of trace metals, nutrient and particulate matter to coastal waters, and some of these components are considered to be important factors determining PP in the water column. For example, Fe has been proposed as a factor limiting PP in waters enriched with other macronutrients but low in pigment concentrations (Martin & Gordon 1988, Martin et al. 1993, Coale et al. 1998). Some recent studies suggest that this element should be relevant in PP off northern Chile, where low dissolved Fe concentrations have been measured (0.6–1.4 nM; R. Torres unpublished data). Additionally, other elements such as Cd and Co may also play an important role in biological processes. The concentration of dissolved Co in the water column shows a similar vertical distribution as macronutrients in an upwelling region off Peru (8–10°S), apparently controlled by biological uptake and remineralisation (Saito 2005). In the same sense, dissolved Cd in the water column for Mejillones Bay shows a typical micronutrient-like distribution (23°S; J. Valdés unpublished data). Low values of dissolved Cd (~0.4–1.6 nM) were found in the water column, while very high concentrations were measured in surface sediments (~60 μg g⁻¹; Valdés et al. 2003). In other coastal waters of northern-central Chile, high Cd values in sediments are probably associated with biological uptake and subsequent deposition in the

sediments ($\sim 30^{\circ}\text{S}$; $< 6.6 \mu\text{g g}^{-1}$; P. Muñoz unpublished data). Therefore the uptake of trace elements by primary producers and subsequent export to sediments appears to be another important factor controlling the concentrations of metals and nutrients in the water column.

Dominant primary producers and their role in the pelagic food web

The HCS off Chile demonstrates high PP associated with wind-driven upwelling events of different intensities and frequencies along the South American coast (Strub et al. 1998). In northern Chile ($21\text{--}23^{\circ}\text{S}$, off Iquique and Antofagasta), a permanent upwelling sustains high PP throughout the entire year ($3\text{--}9 \text{ g C m}^{-2} \text{ d}^{-1}$; Daneri et al. 2000, Montecino & Quiroz 2000, Iriarte & González 2004) while in the central-southern area (i.e., Concepción at 36°S) the upwelling events are mainly concentrated in the spring–summer period (Strub et al. 1998). In the above coastal areas intense upwelling of nutrient-replete waters fertilise the euphotic zone (e.g., NO_3^- : $10\text{--}25 \mu\text{M}$) (Escribano et al. 2004b) creating suitable conditions for large-size primary producers, and in turn causing profound effects on the water column processes such as carbon flow through the pelagic food web and carbon export toward deeper layers of the ocean.

Off northern Chile a weak seasonality in chlorophyll-*a* (chl-*a*) concentration showed slightly higher values during the winter and early spring, whereas in central southern Chile ($30\text{--}40^{\circ}\text{S}$), the annual maximum in chl-*a* concentration occurred during the summer (Thomas et al. 2001a). In the northern coastal area off Chile ($18\text{--}24^{\circ}\text{S}$) the highest chl-*a* concentrations ($15\text{--}20 \text{ mg m}^{-3}$) were mostly restricted to a narrow inshore zone ($< 37 \text{ km}$) and were associated mostly with microphytoplankton ($> 20 \mu\text{m}$), whereas pico- and nanophytoplankton (pico: $0.7\text{--}2.0 \mu\text{m}$; nano: $2.0\text{--}20 \mu\text{m}$) predominate in the offshore, mostly oligotrophic zone (Morales et al. 1996, Iriarte & González 2004). Off central Chile ($33\text{--}37^{\circ}\text{S}$) upwelling-favourable south-southwest winds predominate during the austral spring and summer months when chl-*a* ranged between 3.8 and 26 mg m^{-3} compared with $1.0\text{--}2.5 \text{ mg m}^{-3}$ recorded during winter (González et al. 1989, Montecino et al. 2004).

The permanent and seasonal upwelling off Antofagasta (Mejillones Bay) and Concepción (Concepción Bay), respectively, produce a highly productive phytoplankton assemblage, dominated by no more than 10 species of chain-forming diatoms, such as *Chaetoceros* spp., *Thalassiosira* spp., *Guinardia delicatula*, *Rhizosolenia* spp., *Detonula pumila*, and *Eucampia cornuta* (Rodríguez et al. 1996). The cell sizes of the phytoplankton species along the northern coast of Chile generally are $> 20 \mu\text{m}$ (Morales et al. 1996, Iriarte & González 2004), and high microphytoplankton abundances in the sediment record correlate positively with intense/more frequent upwelling events (higher PP) in waters of Mejillones Bay (Ortlieb et al. 2000). In contrast, small-size phytoplankton ($< 20 \mu\text{m}$) predominate in oligotrophic regimes, associated with the intrusion of subtropical, nutrient-depleted, warmer subtropical waters (STW) (Iriarte et al. 2000, Iriarte & González 2004). In such cases, small dinoflagellates (*Gymnodinium* spp., $5\text{--}25 \mu\text{m}$) and autotrophic flagellates dominated the phytoplankton assemblages (Iriarte et al. 2000). In Concepción Bay (37°S), few numerically dominant diatom species represented $> 80\%$ of the total diatom abundance during upwelling events (González et al. 1987), and in correspondence with this, the highest biomass was concentrated in the microphytoplankton fraction ($> 20 \mu\text{m}$) from winter through spring (González et al. 1989).

The first studies that considered several trophic levels of the pelagic system (Peterson et al. 1988) and trophic models of carbon flux (Bernal et al. 1989) were conducted in the coastal area off Concepción during the late 1980s. These original studies supported the classical view that the upwelling areas are characterised by short food chains dominated by large chain-forming diatoms and few small clupeiform fish species or the ‘traditional food chain’ (Ryther 1969). This view has recently been challenged, highlighting the relevance of the microbial loop (Troncoso et al. 2003,

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Vargas & González 2004) and gelatinous food web (H.E. González et al. 2004b). These trophic flows are important throughout the whole year in oceanic areas and are highly relevant during the non-productive periods (including EN events) in coastal upwelling areas.

The carbon budget of the photosynthetically generated OM in the coastal areas of the HCS has been under debate for many years (Bernal et al. 1989, González et al. 1998). It is accepted nowadays that the fraction of the PP removed from the photic zone, which is highly variable on an annual basis (Hebbeln et al. 2000a), strongly depends on the various biological (internal metabolism), physical (stratification/mixing), and chemical (nutrient rich/poor waters) processes involved as well as the time of year. However, the sources of this variability, both in space and time, have been poorly analysed until recently (Morales & Lange 2004), mainly because of the lack of long-term time-series studies. In Figure 4 the main pathways of the photosynthetically generated organic carbon are depicted. Very high bacterial secondary production (BSP) has been reported in the coastal area of northern-central Chile (Troncoso et al. 2003, Cuevas et al. 2004), suggesting a tight coupling between PP and BSP. The pivotal role of bacteria is supported by the exceptionally high

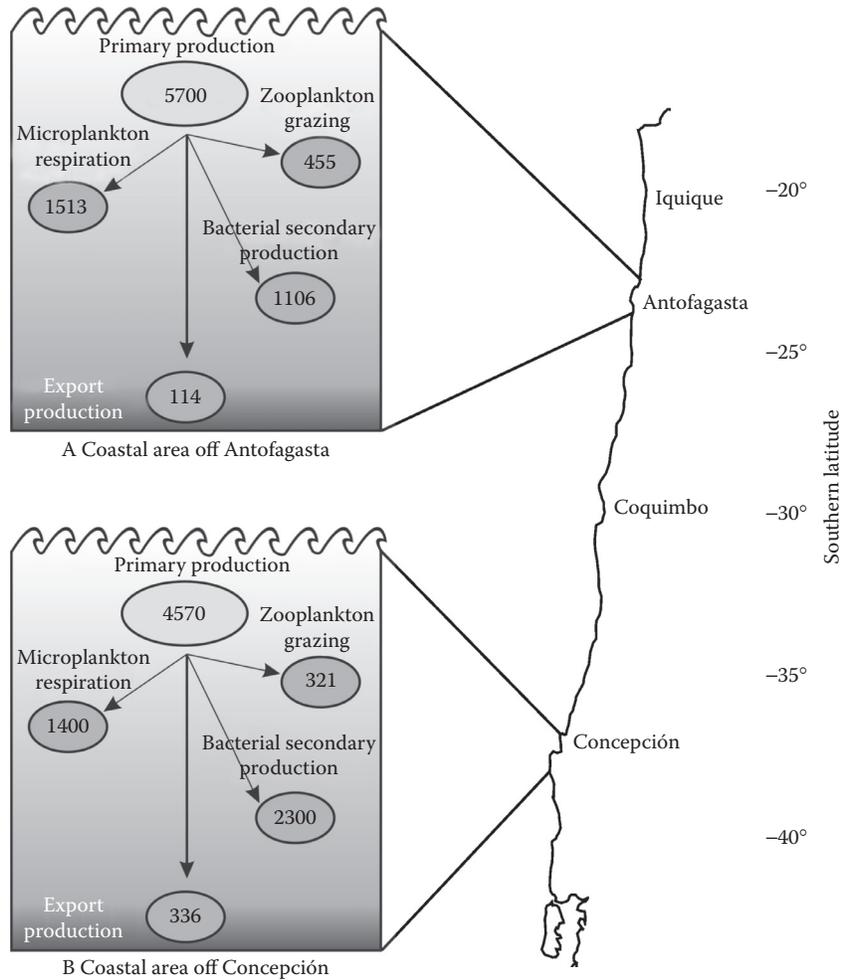


Figure 4 Photosynthetically generated carbon and its flows (rate estimates in $\text{mgC m}^{-2} \text{d}^{-1}$) through the more relevant biological processes in the upwelling system off Antofagasta (23°S) and Concepción (37°S).

degradation rates of dissolved organic carbon in Concepción Bay ($1\text{--}21 \mu\text{M h}^{-1}$; G. Daneri unpublished data) and the high BSP rates (range of $1100\text{--}2300 \text{ mg C m}^{-2} \text{ d}^{-1}$ or $19\text{--}50\%$ of PP). Microbial community respiration rates (Eissler & Quiñones 1999) are also very high along the HCS, reaching average values of $1450 \text{ mg C m}^{-2} \text{ d}^{-1}$ ($\sim 28\%$ of PP). Finally, both zooplankton grazing and export production (González et al. 2000b, Grünewald et al. 2002) gave values between 100 and $500 \text{ mg C m}^{-2} \text{ d}^{-1}$ (or mean values between 2% and 10% of PP). These carbon flows are more representative of the coastal upwelling systems of Antofagasta and Concepción because they are the most studied areas (from an oceanographic point of view) along the Chilean coast. Estimations of PP for the HCS along the Chilean coast are similar to those of the Peru ($4000 \text{ mg C m}^{-2} \text{ d}^{-1}$; Walsh 1981) and about 2-fold higher than those of the California ($1000\text{--}2500 \text{ mg C m}^{-2} \text{ d}^{-1}$; Olivieri & Chavez 2000) upwelling systems. In addition, typical upwelling values for the flow of OM through bacteria in the HCS ($19\text{--}50\%$ of PP) are well within the range ($3\text{--}55\%$ of PP) of those described for other upwelling systems in the world oceans (Ducklow 2000).

Processes affecting primary production and export processes

In coastal areas of central and southern Chile there is a distinctive seasonal pattern involving the development of maxima (spring) and minima (winter) in phytoplankton biomass and PP during an annual cycle (Ahumada 1989, González et al. 1989). In contrast, high and more constant phytoplanktonic biomass and PP has been observed during an annual cycle along the northern coast off Chile (Marín et al. 1993, Rodríguez et al. 1996, Marín & Olivares 1999). Among the factors that might control the PP, light limitation (P. Montero & G. Daneri unpublished data) and Fe availability (Hutchins et al. 2002, R. Torres unpublished data) have been suggested for the Concepción and Coquimbo upwelling systems, respectively. In addition, high microzooplankton grazing might control the PP during non-upwelling conditions (i.e., winter) in Concepción Bay upwelling (Böttjer & Morales 2005).

The understanding of the factors that regulate the magnitude and the variability of phytoplankton PP is quite complex in the HCS due to the geographically distinctive upwelling areas (wind stress, topography), seasonal changes (winter vs. spring) and coastal–oceanic gradients. Integrated values in Table 1 indicate that the variation in chlorophyll concentration is coherent with changes in PP; that is, estimates are lowest in the Coquimbo upwelling system and highest in Antofagasta and Concepción coastal upwelling areas. Higher chlorophyll-specific productivity at Coquimbo and Antofagasta during EN 1997–1998 ($2.5\text{--}2.8$ vs. $1.0\text{--}2.0$) indicates that the increase in specific productivity did not result solely from a biomass decrease, but from a change in the phytoplankton size distribution (therefore in species composition), from the larger size class (microphytoplankton) to smaller size classes (pico- and nanoplankton). The intrusion of oligotrophic oceanic waters into the coastal area off Coquimbo (Shaffer et al. 1995) and Antofagasta (Iriarte & González 2004) during an EN could be a possible explanation for the low productivity and the dominance of smaller phytoplankton size fractions and their large contribution to total PP. This feature suggests that biological and physiological shifts occur at the phytoplankton species level in order to counteract the change in prevailing physical and chemical conditions in those areas (Montecino & Quiroz 2000, Pizarro et al. 2002). On the other hand, in the permanent/seasonal coastal upwelling of cold nutrient-rich waters in enclosed areas like Concepción Bay and Mejillones Bay, PP estimates increase up to $12 \text{ g C m}^{-2} \text{ d}^{-1}$. In the above-mentioned areas, the microphytoplankton fraction accounted for $>50\%$ for the total autotrophic biomass and PP. In general, the range of specific rate of productivity in the three upwelling areas could indicate that physiological factors such as nutrient supply and/or light availability may regulate the seasonal signal of productivity in those areas, whereas top-down processes such as grazing and production export might be important in removing a fraction of the generated photosynthetic carbon (Figure 4, Table 1). Furthermore, high biological

Table 1 Range of primary productivity, chlorophyll, chlorophyll specific primary productivity rate and main phytoplankton taxa between the 22° to 37°S Humboldt Current System. Primary productivity and chlorophyll estimates are integrated to the 1% light penetration depth

Study area	PP (mg C m ⁻² d ⁻¹)	Chl. <i>a</i> (mg m ⁻²)	P ^B (mmol C mg Chl. a ⁻¹ d ⁻¹)	Dominant size class (as % of the total Chl. <i>a</i>)	Main phytoplankton taxa	Reference
Antofagasta (22–2°S) El Niño 1997-1998	338–6063	11.7–175.4	2.8	48–68% nanoplankton	<i>Gymnodinium</i> sp., <i>Pseudo-nitzschia</i> cf. <i>delicatissima</i> Autotrophic flagellates	Pizarro et al. 2002 Iriarte et al. 2000 Ulloa et al. 2001 Troncoso et al. 2003
Antofagasta (22–23°S) Non El Niño 2000–2002	1100–8100	47–695	1.0	60–86% micro- phytoplankton	<i>Chaetoceros</i> spp., <i>Thalassiosira</i> spp., <i>Rhizosolenia</i> spp., <i>Detonula pumila</i> , <i>Guinardia delicatula</i> , <i>Eucampia cornuta</i>	Iriarte & González 2004
Coquimbo-Valparaíso (30–33°S) 1992–1994, 1995	Total: 140–2955 Summer: 605–2224 Winter: 602–1012	8.0–92.5	2.5	Winter: 59% nanoplankton	<i>Detonula pumila</i> , <i>Leptocylindrus danicus</i> , <i>Pseudo-nitzschia pseudoseriata</i> , <i>Prorocentrum micans</i>	Montecino et al. 1996 Montecino & Pizarro 1995 Avaria & Muñoz 1982 Montecino & Quiroz 2000 Troncoso et al. 2003
Humboldt Current System (19–22°S)		53–141		Winter: >50%	Coast: <i>Pseudo-nitzschia pseudoseriata</i> , <i>Chaetoceros</i> <i>compressus</i> , <i>Leptocylindrus danicus</i> , <i>Rhizosolenia</i> <i>imbricata</i> , <i>Ceratium tripos</i> , <i>Diplopsalis lenticula</i> Oceanic: <i>Chaetoceros coarctatus</i> , <i>Ch. dadayi</i> , <i>Ceratium contortum</i> , <i>C. gibberum</i> , <i>C. macroceros</i> , <i>Dinophysis rapa</i> , <i>Ornithocercus magnificus</i>	Morales et al. 1996 Avaria et al. 1982
Las Cruces (33°S) 1999–2000		1–13.5 (mg m ⁻³)		Spring: 65% micro- phytoplankton		Narvaez et al. 2004
Concepción Bay and Gulf of Arauco (36–37°S)	Total: 200–21,000 Winter: 481–1600 Spring: 1770–16,670	Spring: 208–544	Spring: 2.0	Winter: 48% nanoplankton Spring: 84% micro- phytoplankton	<i>Thalassiosira</i> spp., <i>Detonula pumila</i> , <i>Chaetoceros socialis</i> , <i>Chaetoceros curvisetus</i> , <i>Skeletonema costatum</i> , <i>Leptocylindrus danicus</i> , <i>Guinardia delicatula</i>	González et al. 1989 Iriarte & Bernal 1990 Ahumada 1989 Daneri et al. 2000 Troncoso et al. 2003 Montecino et al. 2004 Cuevas et al. 2004

productivity observed along the northern and central coast of the HCS (23–37°S) is probably fertilising oceanic and oligotrophic areas through the formation of eddies and filaments that transport coastal water offshore (Marín et al. 2003a, Hormazábal et al. 2004, Letelier et al. 2004). Finally, much of what is known about upwelling dynamics, phytoplankton ecology and their role in biogeochemical cycles along the Chilean coast has been mainly gathered from selected upwelling areas (i.e., Antofagasta, Coquimbo, Concepción, Valparaíso) with scarce or no information from areas in-between.

Zooplankton consumers

Zooplankton consumers are considered the link between primary producers and higher trophic levels in the pelagic realm of the world ocean. This function also implies a role to regulate the rate at which phytoplankton-C can be transferred through the food web or retained as zooplankton biomass. This rate greatly depends on population turnover rates, which vary widely among zooplankton taxa. Thus, the knowledge of the population biology of dominant species, the community structure and its variation, become key issues in understanding the ecological and biogeochemical role of zooplankton. In the HCS substantial progress has been made in the last decades about some of these issues. In the following sections we summarise the major advances in understanding population, community and ecosystem processes involving zooplankton in the upwelling region off northern Chile. Much less progress is being made in molecular, genomic and genetic biology of zooplankton in this region. However, the need for a better understanding of zooplankton ecology in the region will most likely motivate the use of molecular tools in the near future.

Biogeographic and biodiversity issues

In the upwelling region off northern Chile most species or species assemblages are considered to be part of the subantarctic fauna. This fauna originates in the Austral region, but it is then advected northward. In northern Chile and off Peru, it mixes with some species of tropical and equatorial origin. The most studied taxa are Copepoda (Heinrich 1973, Vidal 1976, Hidalgo & Escribano 2001) and Euphausiacea (Antezana 1978, D. Fernández et al. 2002). Nearly 60 species of copepods have been identified, of which the dominant in the coastal zone are *Calanus chilensis*, *Centropages brachiatus*, *Paracalanus parvus*, *Acartia tonsa*, *Eucalanus inermis*, *Oithona similis*, *Oncaea conifera* and *Corycaeus typicus*. *Calanus chilensis* is an endemic species of the HCS (Marín et al. 1994), whereas *Centropages brachiatus*, *Paracalanus parvus*, *Acartia tonsa* and *Oithona similis* are cosmopolites and widely distributed along the Chilean coast. *Eucalanus inermis* is a typical tropical species, although the genus *Eucalanus* may contain about six species, which have not yet been clearly defined. Among euphausiids, the most abundant and endemic species of the HCS is *Euphausia mucronata* (Antezana 1978). This species is closely associated with upwelling centres off northern Chile (Escribano et al. 2000) and performs an extensive vertical migration into the OMZ. *Euphausia eximia* is another abundant species, which increases in number during EN (Antezana 1978, González et al. 2000b). Gelatinous zooplankton, on the other hand, has received much less attention, although it may form dense aggregations at times of the year in the coastal upwelling zone (Pagès et al. 2001), and it can exert a strong predation pressure on copepods (Giesecke & González 2004, H.E. González et al. 2004b, Pavez et al. 2006) and possibly on fish larvae.

Species replacements seem to occur in the zooplankton associated with EN versus LN regimes (Hidalgo & Escribano 2001). Dominant species alternate between copepods (mainly *Calanus* and *Eucalanus* genera) and euphausiids during upwelling conditions and cyclopoid copepods, *Paracalanus*

and *Acartia* during EN events (González et al. 2002). Warm conditions during an EN may also cause reduced size of copepods at maturity (Ulloa et al. 2001). All these changes in structure of the pelagic system may have profound implications on the functioning and productivity of this region (see, e.g., Alheit & Niquen 2004) and should also be considered in future ecosystem studies.

Zooplankton and coastal upwelling in northern Chile

In the coastal zone off northern Chile, wind-driven upwelling is the principal driver of biological productivity. Pelagic organisms benefit by high productivity in upwelling sites. However, upwelling zones comprise strongly variable environments and zooplankton must cope with changing conditions in this zone. The understanding of these physical and biological interactions in the water column of upwelling systems may give much insight into the key processes that control production and biological diversity of pelagic assemblages. In northern Chile, examples of physical–biological interactions taking place during coastal upwelling are restricted to particular conditions and sites (e.g., Escribano & Hidalgo 2000a, Escribano et al. 2001, 2002, Giraldo et al. 2002). Other studies (Marín et al. 2001) have shown some relevant findings that may help understanding mechanisms through which pelagic populations are able to maintain their populations in the food-rich coastal zone. Off Mejillones Peninsula (23°S), the interaction between a poleward flow and cold upwelling plumes may generate large eddies by which non-migrant plankton can be maintained nearshore. This type of circulation may act as a retention mechanism to avoid offshore advection of zooplankton (Giraldo et al. 2002). Thus, most species maintain their population in the food-rich upwelling centres being recirculated by near-surface currents. In other upwelling systems, such as the Benguela Current, zooplankton is maintained nearshore by vertical migration behaviour (Verheye et al. 1992, Roy 1998). Organisms advected offshore migrate to deep water and then are returned to shore by a compensatory flow. In northern Chile, however, vertical migration does not seem to be an important or widely used behaviour. In fact, most dominant species appear strongly constrained to the upper layer (<100 m) (Escribano & Hidalgo 2000a) because of oxygen-depleted waters in the OMZ, which come close to the surface (<50 m) during upwelling (Morales et al. 1999).

Upwelling in the coastal zone off northern Chile may exhibit much spatial variation characterised by discrete upwelling centres, such as those usually observed off Iquique (20°S), the river Loa (21°S), Mejillones (23°S) and Coquimbo (30°S) (Fonseca & Farías 1987). Zooplankton populations tend to aggregate in these upwelling centres and hence they are also very patchily distributed (González & Marín 1998, Escribano & Hidalgo 2000a). Spatial heterogeneity in plankton distribution linked to variability in oceanographic conditions, such as temperature and food quantity and quality, may be one of the major causes of variability in population growth and secondary production along the coast off northern Chile (Giraldo et al. 2002).

Zooplankton and the oxygen minimum zone

The OMZ system is a prominent feature in northern Chile closely related to the ESSW. This oxygen-depleted water mass is also strongly linked to wind-driven upwelling in the coastal area. The ESSW, which normally occupies the intermediate (200- to 500-m) layer (Blanco et al. 2001), may ascend to shallow waters (<50 m) near the coast due to upwelling (Morales et al. 1999). The influence of this low-oxygen water on pelagic communities of the coastal zone is not well understood. Dominant zooplankton, which usually aggregates near the upwelling centres in this region (Escribano & Hidalgo 2000b), must cope with such low-oxygen conditions. The options are either avoiding the OMZ and restricting the population to the upper oxygenated layer, as earlier reported for some dominant copepods (e.g., Escribano 1998), or evolving some metabolic adaptations to withstand

poor oxygen conditions, such as those described in González & Quiñones (2002). It has been observed that several abundant epipelagic species concentrate in the upper 50 m without exhibiting diel vertical migration (DVM) (Escribano 1998, Escribano & Hidalgo 2000a), although some euphausiids, such as *Euphausia mucronata*, may temporarily enter the OMZ (Antezana 2002), or some others like the copepod *Eucalanus inermis* may even reside in it (Hidalgo et al. 2005a). Thus, the OMZ cannot be considered as just a constraint for vertical distribution because several species may use it as their habitat, either temporarily or permanently. The ecological and biogeochemical consequences of entering and living within the OMZ should be considered as relevant issues. Future studies of species life cycles and behavioural or metabolic adaptations may provide novel findings for life under low oxygen, as described for benthic organisms inhabiting these systems (Helly & Levin 2004). Cycling and vertical fluxes of C and N mediated by zooplankton migration and vertical distribution may be substantially modified by the low-oxygen and highly reduced environment. These issues have received little attention for marine zooplankton associated with OMZ systems (e.g., Wishner et al. 1998).

In the upwelling region off northern Chile, the most abundant species are usually closely related to coastal upwelling plumes (Escribano et al. 2000, Giraldo et al. 2002). These species have been well identified (Heinrich 1973, Hidalgo & Escribano 2001). Among dominant ones, the studies of horizontal and vertical distribution have been focused on the calanoids *Calanus chilensis* (Escribano 1998), *Centropages brachiatus* (González & Marín 1998) and *Eucalanus inermis* (Hidalgo et al. 2005a) and on the euphausiid *Euphausia mucronata* (Escribano et al. 2000, Antezana 2002). The available information indicates that *Calanus chilensis* and *Centropages brachiatus* are mostly restricted to the upper layer without performing substantial DVM (Escribano 1998, Escribano & Hidalgo 2000a). By contrast, *Eucalanus inermis*, the dominant species among a complex of four to five species of the genus *Eucalanus* that coexist in this region, may remain in the upper boundary of the OMZ with limited excursion into surface waters (Hidalgo et al. 2005a). Meantime, *Euphausia mucronata* has been suggested as actively and daily migrating into the OMZ (Antezana 2002). A summary of the vertical extent of species habitats for zooplankton in this region has been recently constructed from several cruises (Escribano et al. accepted) and is illustrated in Figure 5. Zooplankton can indeed occupy the entire water column despite the presence of an intense OMZ. Occurrence and vertical movements of various species may ensure a substantial contribution of zooplankton to the vertical export of OM.

Zooplankton life cycles and population dynamics

Life cycles and population dynamics are certainly important issues for understanding the biogeochemical and ecological role of zooplankton in this region. When examining annual life cycles there are some important factors to consider. Since the entire upwelling region is subjected to interannual variability due to the ENSO cycle, different years might induce changes in populations. Water column warming, an abrupt thermocline and oxycline deepening characterises the EN conditions in northern Chile (Ulloa et al. 2001, Escribano et al. 2004a), in contrast to a typically shallow thermocline and OMZ indicating a 'normal' (LN condition) upwelling situation. However, despite oceanographic variability some species, such as *Calanus chilensis*, seem to have a rather stable annual cycle from year to year independent of ENSO variation (Escribano & Hidalgo 2000b). Dominant zooplankton species have been suggested to be strongly associated with upwelling centres (González & Marín 1998, Escribano & Hidalgo 2000b), and they can thus complete their life cycles within the upwelling zone, growing at temperature-dependent rates under non-limiting conditions of food (Escribano & McLaren 1999, Giraldo et al. 2002). Lack of food shortage has even been suggested during EN conditions (Ulloa et al. 2001). Continuous reproduction and multiple generations throughout seasons characterise life cycles of copepods in this region (Escribano & Rodríguez

THE HUMBOLDT CURRENT SYSTEM OF NORTHERN AND CENTRAL CHILE

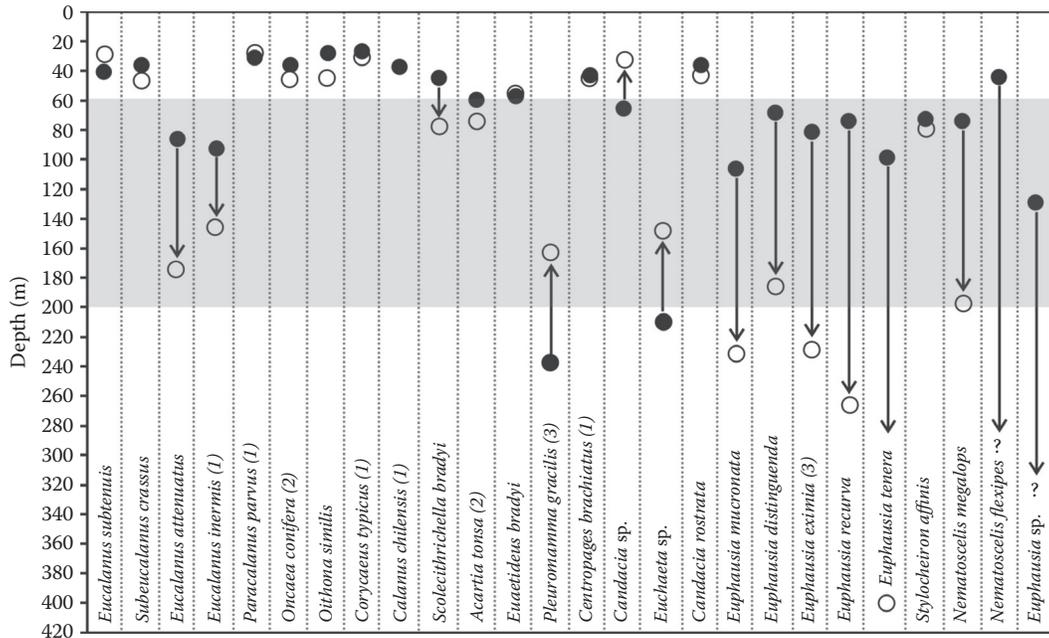


Figure 5 Dominant habitat and daily movements of zooplankton species in and out of the main core of the oxygen minimum zone (OMZ) (shaded area) during coastal upwelling at northern Chile. Day (white dots) and night (black dots) positions represent the depth distribution of each one of the species listed and the arrow the extent of their vertical movement. These positions were estimated from depth-weighted averages of abundances. Data are from *MinOx* cruise carried out in March 2000 (modified from Escribano et al. accepted). (1) Dominant species found in upwelling centers, (2) inshore species, (3) species associated with El Niño events.

1994, Hidalgo et al. 2005b). However, strong variation in population size can be observed at some times of the year (Escribano 1998, Ulloa et al. 2001, Hidalgo et al. 2005b). The populations of annual species typically show a sudden collapse that tends to occur by the end of the summer. This pattern has been described for *Eucalanus inermis* (Hidalgo et al. 2005b), *Calanus chilensis* and *Centropages brachiatus* (Hidalgo & Escribano submitted) and *Euphausia mucronata* (Escribano et al. accepted). The conceptual model of population dynamics for these species (Figure 6) considers a two-stage population, which may grow exponentially during the spring and early summer at low mortality rate and then exhibit an abrupt decay at high mortality rate due to increased predation. In this model the increase in predation pressure coincides with the rise of the OMZ, which produces a habitat that is vertically constrained to surface waters by low oxygen concentrations, thereby resulting in increased interactions among prey and predators. This model does not preclude the possibility that changing food quality associated with the rise of the OMZ, either through deleterious effects of diatoms on copepods (Ianora et al. 2004) or by low nutrition, might negatively impact the population. Indeed, a recent study (Vargas et al. 2006b) has shown that available food resources may strongly affect reproduction and recruitment of zooplankton in the coastal zone of the HCS.

Future perspectives in zooplankton research

Much of the current research devoted to understanding the ecological and biogeochemical role of zooplankton consumers in the upwelling region off northern Chile is focused on establishing

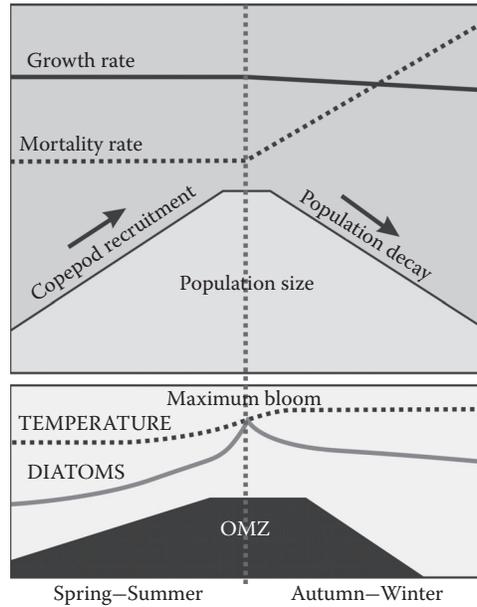


Figure 6 A conceptual model to describe the annual cycle of dominant zooplankton species at the coastal upwelling off Chile. The model proposes a life cycle in two phases. The first phase (left side) shows a positive growth of the population (growth rate is stable as well as mortality rate: bottom-up control). The population reaches a maximum size coinciding with the maximal diatom bloom and then it suddenly collapses. The second phase (right side) describes the population decay under increased mortality rate of early stages (top-down control) and a slight decrease of growth rate. The panel below describes the environmental conditions upon which both phases take place. Temperature has a weak signal, diatoms reach a maximum, but remain stable, and a key feature is the rise of the oxygen minimum zone (OMZ) coinciding with the population collapse.

quantitative relationships between species and trophic levels or functional groups (e.g., H.E. González et al. 2004b). It is expected that trophic relationships may provide insights on the functional role of zooplankton for recycling C and N in the ocean (Morales 1999, Hidalgo et al. 2005a, Vargas et al. 2007). This should be considered as baseline information for zooplankton modelling in the region. At population level, modelling approaches have rarely been applied to zooplankton in this area (Marín 1997). Nevertheless, biogeochemical modelling incorporating zooplankton is an expected issue for coming years. At any level, however, key oceanographic processes interacting with zooplankton populations need to be identified and understood. Among such processes coastal upwelling, OMZ distribution, ENSO variability and changing food quantity and quality are to be considered crucial.

Fish consumers

The pelagic food webs in the HCS, as in other upwelling systems, feature relatively short trophic pathways. In general, besides zooplankton (mainly copepods and euphausiids) three trophic levels of consumers can be distinguished: small-size planktivorous fish, larger fish predators and top predators (Neira et al. 2004). The dominant species among the small-size fish consumers are anchovy (*Engraulis ringens*) and Pacific sardine (*Sardinops sagax*); large predators include the jack

mackerel (*Trachurus murphyi*), hake (*Merluccius gayi*) and cephalopods (Neira & Arancibia 2004). Top predators in the HCS are large pelagic fish such as tuna (*Thunnus orientalis*) and swordfish (*Xiphias gladius*), southern sea lions (*Otaria flavescens*) and seabirds.

Most fish predators in the HCS appear to be non-specialists, which feed opportunistically on a wide range of different prey items. Sardines and anchovy consume small food particles (mainly phytoplankton and copepods), with the anchovy able to consume larger food items than sardines (Balbontín et al. 1979). Anchovy are more specialised on large zooplankton, while sardines consume a wide range of food items from phytoplankton to small zooplankton (Alheit & Niquen 2004). Jack mackerel prey on copepods, euphausiids, sardines and anchovies and benthic resources (Medina & Arancibia 2002). Jumbo squids (*Dosidicus gigas*) feed cannibalistically and on fish, including jack mackerel and anchovy (Chong et al. 2005). Some of the main fish consumers themselves are prey to larger predators, for example, swordfish (Ibáñez et al. 2004) and sea lions (Sielfeld 1999). A generalised scheme of the pelagic food web off central Chile shows the short trophic pathways and the predominance of relatively few main fish consumers (Figure 7A). While the food spectra of most pelagic consumers are relatively well known, information about consumption rates, intra- and interspecific competition or intraguild predation is limited. Similarly, relatively little is known about prey preferences and feeding strategies of the pelagic fish consumers in the HCS. This knowledge is particularly important in light of variable oceanographic conditions, which may modify availability of preferred food items or produce a spatial segregation of predators and prey (e.g., Bakun 2001, Alheit & Niquen 2004).

A review by Cury et al. (2000) suggested that the availability of small pelagic fish in the HCS off Peru determines the population size of higher trophic levels. Bakun (2001) pointed out that the interaction between small pelagic fish and their predators is highly dynamic, depending on multiple environmental (oceanic fronts, climate-driven changes in oceanography), biological (reproductive strategies) and behavioural (schooling behaviour) factors. Small fish consumers may temporarily escape from predation in this dynamic system, and if their reproductive and behavioural strategies permit them to find a refuge from predation these species may build up and maintain huge populations (Bakun 2001). Once this dynamic balance is interrupted (e.g., by climatic factors), regime shifts may occur (Alheit & Niquen 2004).

It has been proposed that the regime shift from a sardine-dominated system to an anchovy-dominated system (or vice-versa), which is related to long-term variations in oceanographic conditions (Chavez et al. 2003), may ultimately be mediated by trophic feedbacks (Alheit & Niquen 2004). During warm periods, the preferred prey items of anchovy (large copepods and euphausiids) become less available (see also Zooplankton consumers, p. 214ff.) while predation pressure on adult anchovies increases, due to invasions of jack mackerel into coastal waters (Alheit & Niquen 2004). Simultaneously, sardines, which are also important predators on anchovy eggs (Alheit 1987), may be favoured because they have a wide prey spectrum including phytoplankton. The consequences of these regime shifts, which have been analysed for Peru and northern Chile (Alheit & Niquen 2004), also extend to central Chile. Future studies need to examine to which degree bottom-up or top-down mechanisms are involved, and whether EN impacts and fisheries may accelerate these regime shifts.

Both prey and predator behaviour also affects trophic interactions in the HCS. In a recent study, Bertrand et al. (2006) suggested that the feeding behaviour of jack mackerel is closely linked to the OMZ and DVM of their prey. These authors discussed that during the day, when prey are hiding in deeper waters, jack mackerel rest near the upper limit of the OMZ. At night, when prey migrate into upper oxygenated waters, jack mackerel become active (Figure 7B). If this model is confirmed in future studies, interannual variation in oceanographic conditions (e.g., the intensity and depth of the OMZ) may also affect the trophic efficiency of jack mackerel. This hypothetical scenario underscores the importance of better knowledge of predator-prey behaviour and interactions in order to better understand the pelagic food webs in the HCS.

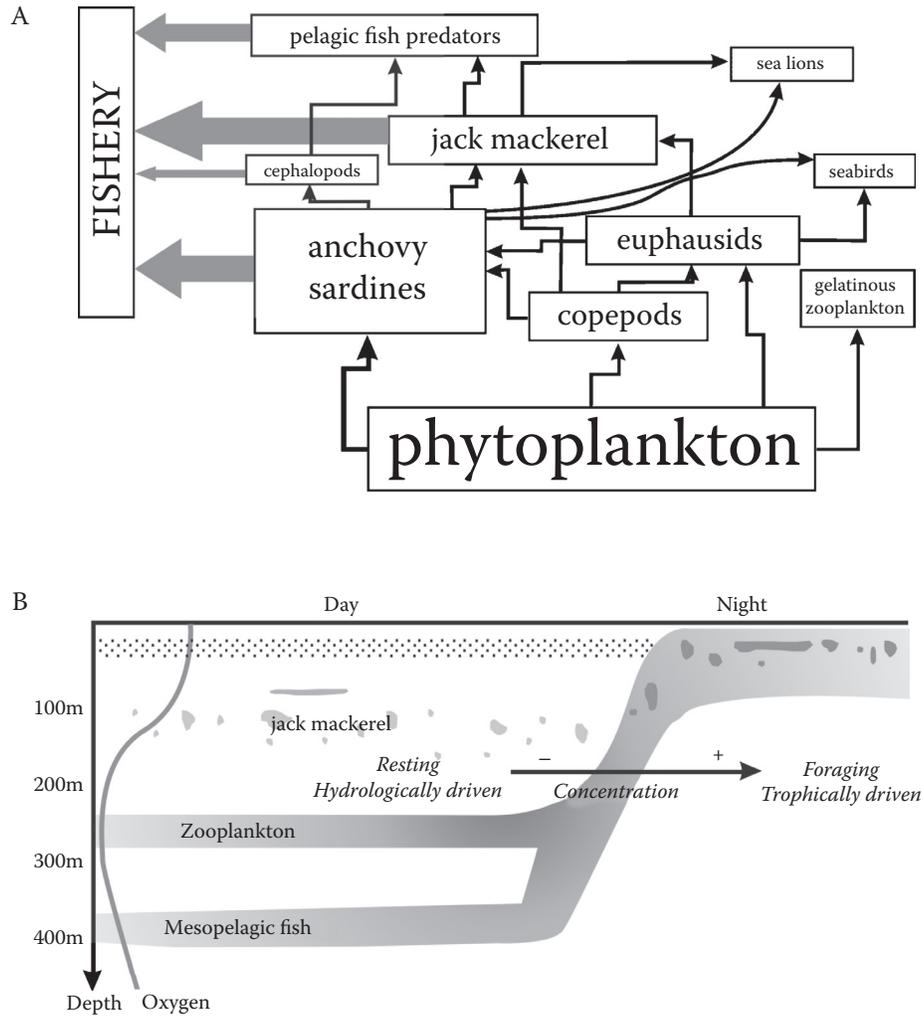


Figure 7 (A) Simplified pelagic food web in the HCS off northern and central Chile; size of boxes indicates relative proportions; grey arrows show mortality due to fishing. (B) Conceptual model of feeding behaviour of jack mackerel (*Trachurus murphyi*) in response to diel vertical migration of prey into the OMZ; position of jack mackerel shown as grey patches, position of prey organisms shown as continuous grey band. (Modified after Bertrand et al. 2006)

Interannual fluctuations in fish stocks do not seem to affect the general characteristics of the food web off central Chile (Neira et al. 2004). However, fisheries appear to have a long-term impact on the pelagic food web in this area. Fisheries are acting on several trophic levels of the pelagic food web (Figure 7A). Off central Chile, a decrease in the trophic level of the principal fisheries resources has been observed during recent decades (Arancibia & Neira 2005). It needs to be taken into account, however, that populations of some top predators that have experienced severe exploitation in the past (whales) may still be at very low levels, which may be reflected in the structure of present-day food webs. The interpretation of trophic relationships in the different parts of the

HCS (and in other EBCs) requires detailed understanding of the different components of the respective system (Moloney et al. 2005).

Seabirds and marine mammals

In marine environments seabirds and partially marine mammals are highly visible wide-ranging, upper trophic-level consumers. Upwelling systems are generally characterised by high production and relatively short food chains/webs, enabling massive energy transfer to the higher trophic levels (Cushing 1971, Arntz & Fahrbach 1991). The upwelling system of the Humboldt Current is particularly well suited for studying the effects of the marine environment on the biology and ecology of seabirds and marine mammals.

Seabirds

In the HCS there is a rich diversity of seabirds, comprising at least 14 breeding species, 9 of which are endemic (Table 2). According to available information, along the coast of Chile the most important breeding colonies are found on islands of northern-central Chile, near upwelling areas. The grey gull (*Larus modestus*), which nests inland in the Atacama Desert, travels to the coast on a daily basis to forage in the upwelling zones off Antofagasta (~23°S). Although proximity to a feeding ground is relevant in endemic seabirds, it seems that inaccessibility to predators and human intrusion strongly determines the distribution of breeding populations. Despite some protective status, most islands in the HCS are subject to human disturbance. In the past, this was caused mainly by guano harvesting and egg collecting. At present, introduced mammals and unregulated tourism (Ellenberg et al. 2006) are a major problem.

The majority of the endemic seabirds breed once a year. However, in their northernmost breeding areas (Peru), species such as the Humboldt penguin (*Spheniscus humboldti*) nest throughout the year. Apparently, the two-peak breeding strategy has evolved in response to more favourable oceanographic and climatic conditions off Peru, and this behaviour is preserved in northern-central Chile providing additional offspring to those produced during the spring event (Simeone et al. 2002). Furthermore, differences in food availability along its breeding range (~4000 km) might induce lower breeding performance in southern colonies of this species (Hennicke & Culik 2005). These birds feed on the main pelagic fish species from the HCS, mainly anchovy and jack mackerel. The proportion of fish stocks taken by endemic seabirds is not well known, but most likely does not exceed 10%. Incidental mortality of endemic seabirds due to fisheries is mainly caused by gill nets (Simeone et al. 1999, see also Majluf et al. 2002).

The HCS is visited regularly by a number of migrant species. Among the Procelariiformes, white-chinned petrels (*Procellaria aequinoctialis*), Buller's albatrosses (*Thalassarche bulleri*), Antarctic prions (*Pachyptila desolata*) and Juan-Fernández petrels (*Pterodroma externa*) are the most abundant species during austral summer (Weichler et al. 2004). There is evidence that the HCS is also frequented by other remarkable visitors such as the Chatham, wandering and royal albatrosses (*Thalassarche eremita*, *Diomedea exulans*, and *D. epomophora*, respectively). Apparently the presence of these species at such a distance from their colonies is related to the food abundance in the HCS, which in summer also attracts species like the black-browed albatross (*Thalassarche melanophris*) from southern islands (56°S) (Arata & Xavier 2003) and during winter species like the white-chinned petrels from South Georgia (Phillips et al. 2006). The abundances of some of these visitors during austral summer may reach 2.5–5 birds km⁻², but at present it is not known which proportion of the entire population of these visitors may at times use the HCS as a feeding ground. The large albatrosses mainly feed on cephalopods and pelagic fishes (resulting in deadly interactions with long-line fisheries),

Table 2 Breeding abundance and conservation status of seabirds (number of pairs) and mammals (individuals) on the coast of northern-central Chile. The geographic divisions correspond approximately to the limit of political division of Chile. Data for cetaceans (ψ) correspond to systematic counts during oceanographic trips conducted every January (1999, 2002, 2003 and 2004) surveying an area of ~420 km². The other data for cetaceans are mainly from sightings made from the land.

Species	18–21°59'S	22–26°59'S	27–29°59'S	30–32°59'S	33–34°S	Total	CS*
Seabirds							
Order Sphenisciformes							
Humboldt penguin <i>Spheniscus humboldti</i> ϕ			8120		810	8930	V
Magellanic penguin <i>Spheniscus magellanicus</i>					5	5	NT
Order Procellariiformes							
Peruvian diving-petrel <i>Pelecanoides garnotii</i> ϕ			4170			4170	E
Wedge rumped storm petrel <i>Oceanodroma tethys</i>			9			9	LC
Order Pelecaniformes							
Peruvian booby <i>Sula variegata</i> ϕ			15,560			15,560	LC
Peruvian pelican <i>Pelecanus thagus</i> ϕ			400	1000		1400	LC
Neotropic cormorant <i>Hypoleucos brasiliensis</i>			200	50	55	305	—
Guanay cormorant <i>Leucocarbo bougainvillii</i> ϕ			12	150		162	NT
Red legged cormorant <i>Stictocarbo gaimardi</i> ϕ	122	85	60	23	150	440	NT
Order Charadriiformes							
Band tailed gull <i>Larus belcheri</i> ϕ			1			1	LC
Grey gull <i>Larus modestus</i> ϕ		10,000				10,000	LC
Kelp gull <i>Larus dominicanus</i>			2700	100	450	3250	LC
Inca tern <i>Larosterna inca</i> ϕ				10		10	NT
Peruvian tern <i>Sterna lorata</i> ϕ						2499	E
Marine mammals							
Order Carnivora							
Family Otariidae							
South american fur seal <i>Arctocephalus australis</i>	655	1205				1860	LR
South american sea lion <i>Otaria flavescens</i>	13,797	6132	129	1598		21,656	LR
Family Mustelidae							
Marine otter <i>Lontra felina</i> (ind./km of coast)	1.5		1.0–2.5				E
Order Cetacea (numbers come from sightings)							
Family Balaenidae							
Southern right whale <i>Eubalaena australis</i>		21				21	LR

THE HUMBOLDT CURRENT SYSTEM OF NORTHERN AND CENTRAL CHILE

Table 2 (continued) Breeding abundance and conservation status of seabirds (number of pairs) and mammals (individuals) on the coast of northern-central Chile. The geographic divisions correspond approximately to the limit of political division of Chile. Data for cetaceans (ψ) correspond to systematic counts during oceanographic trips conducted every January (1999, 2002, 2003 and 2004) surveying an area of ~420 km². The other data for cetaceans are mainly from sightings made from the land.

Species	18–21°59'S	22–26°59'S	27–29°59'S	30–32°59'S	33–34°S	Total	CS*
Family Balaenopteridae							
Humpback whale <i>Megaptera novaeangliae</i>		1	17 ψ			18	V
Balaenoptera sp.		25	9 ψ			34	
Fin whale <i>Balaenoptera physalus</i>			63 ψ			63	E
Minke whale <i>Balaenoptera acutorostrata</i>		1	4 ψ			5	LR
Blue whale <i>Balaenoptera musculus</i>			1 ψ			1	E
Family Kogiidae							
Dwarf sperm whale <i>Kogia simus</i>			3 ψ			3	
Family Physeteridae							
Sperm whale <i>Physeter macrocephalus</i>	1	1	19 ψ			20	V
Family Ziphiidae							
Cuvier's beaked whale <i>Ziphius cavirostris</i>			5			5	—
Family Delphinidae							
Bottlenose dolphin <i>Tursiops truncatus</i>			301 ψ			301	DD
Short-finned pilot w. <i>Globicephala macrorhynchus</i>		n.d.					LR
Long finned pilot whale <i>Globicephala melas</i>			101			101	LR
<i>Globicephala</i> sp.			11 ψ			11	
Killed whale <i>Orcinus orca</i>			11 ψ			11	LR
False killer whale <i>Pseudorca crassidens</i>			5 ψ			5	LR
Common dolphin <i>Delphinus delphis</i>		200				200	LR
Southern rightwhale dolphin <i>Lissodelphis peronii</i>		450				450	DD
Risso's dolphin <i>Grampus griseus</i>			30 ψ			30	DD
Dusky dolphin <i>Lagenorhynchus obscurus</i>		456	1404 ψ			1860	DD
Family Phocoenidae							
Harbour porpoise <i>Phocoena spinipinnis</i>		72	10 ψ			82	DD

Notes: *CS: Conservation status was extracted from IUCN (2006). E: Endangered, V: vulnerable, NT: near threatened, LC: least concern, DD: data deficient, LR: lower risk. ϕ Endemic species of the Humboldt Current System. Data from Guerra et al. 1987, 1988, Sielfeld et al. 1997, van Waerebeek et al. 1998, Capella et al. 1999, Sielfeld & Castilla 1999, Rendell et al. 2004, Simeone et al. 2003, Frere et al. 2004, Jiménez 2005, Bernal et al. 2006, and G. Luna-Jorquera unpublished data.

while the smaller petrels consume mainly planktonic crustaceans (e.g., *Euphausia mucronata*). Although available information shows that incidental mortality in the artisanal Patagonian toothfish (*Dissostichus eleginoides*) fisheries in southern Chile is low (0.047 birds per 1000 hooks; C.A. Moreno et al. 2006), incidental mortality of petrels and albatrosses in industrial long-line fisheries has not yet been assessed for northern Chile, where most of the Chilean swordfish vessels are based.

Marine mammals

Species of mammals listed in Table 2 are those that mainly occur over the continental shelf in the HCS. Although there are no endemic species, the total species richness reaches at least 22 species, most of them being cetaceans. The number of species and abundance of individual sightings in Table 2 suggest that the upwelling regions between 18°S and 30°S are important feeding stations on the migration routes of whales (see also Rendell et al. 2004).

For the sea otter (*Lontra felina*), available information shows that this species feeds mainly in areas dominated by macroalgae (Ebensperger & Castilla 1992, Ebensperger & Botto-Mahan 1997, Villegas 2002), where refuges on land are available (Sielfeld & Castilla 1999). The diet of this species is principally composed of coastal fishes, crabs and seabirds (Sielfeld & Castilla 1999, Mattern et al. 2002) and foraging success is higher at wave-protected sites than at exposed sites (Villegas et al. 2007).

The biology and ecology of otariids at both sea and land has been investigated in Peru (Majluf et al. 2002) and Ecuador (e.g., Dellinger & Trillmich 1999), but studies from northern-central Chile mostly focus on population size or demography (e.g., Guerra et al. 1987). Interaction between sea lions (*Otaria flavescens*) and fisheries is an important issue in Chile (Hückstädt & Krautz 2003). Their traditional foraging behaviour (search and pursuit of prey) has changed to one of 'sit and wait' for food captured by fishing vessels (Hückstädt & Antezana 2003), a strategy that appears to be exploited by killer whales (*Orcinus orca*) preying on sea lions near fishing vessels (Hückstädt & Antezana 2004). While it is well known that sea lions destroy nets and consume pelagic fish, the extent of this problem has not yet been systematically examined in northern Chile.

Although there is a lack of information, it appears that there exists an inverse relationship between the breeding distribution of sea lions and endemic seabirds in northern-central Chile (Table 2). Sea lions are most abundant between 18°S and 26°S, while seabirds seem to be more abundant between 27°S and 33°S. The reasons for this spatial separation are not well known, but one possibility might be that sea lions are common in northern Chile where they can successfully breed on small rocky outcrops, while seabirds may be most abundant between 27°S and 33°S, where they form huge breeding colonies on undisturbed islands. Additionally, maternal care might impose higher restrictions (duration and distance of foraging trips) on female sea lions (e.g., Trillmich 1990) than on female seabirds, which share parental care with their male partners and thus can afford longer absence from the nest and farther foraging trips during breeding. The apparent lower productivity of pelagic fish between 27°S and 33°S (see also Pelagic fisheries and fisheries management 1980–2005, p. 288ff.) might affect female sea lions (which usually forage close to the breeding sites; e.g., Trillmich 1986) to a higher degree than seabirds (which may travel >30 km from breeding colonies during individual foraging trips, as observed in Humboldt penguins; Luna-Jorquera & Culik 1999). Future studies should examine the causes for the inverse abundance patterns of sea lions and seabirds along the coast of northern Chile.

Effects of ENSO on seabirds

In the upwelling area of Coquimbo (Region IV), the species composition of seabirds at sea fluctuates among different sites, and distribution patterns are linked to variation in SST and chlorophyll

concentration. Dense swarms of pelagic fishes attract high numbers of piscivorous birds, which is the most important factor to explain their distribution patterns. Usually, only 3% of all birds recorded in a given area are seen directly attending fishing vessels (Weichler et al. 2004). Life-history theory predicts that seabirds will respond to reduction in food availability by changing their behaviour and/or breeding effort, thus buffering adult survival. Data of Peruvian boobies (*Sula variegata*) are in agreement with this prediction (G. Luna-Jorquera unpublished data). In January 2002, about 3000 breeding pairs of this species were registered in a colony off Coquimbo, but 1 month later there were only 10 pairs, coinciding with a positive SST anomaly (Figure 8). Counts of birds at sea conducted in ~420 km² around the colony showed that the numbers of boobies were lower than in a 'normal' year, indicating that boobies left the area probably due to a reduction in food availability. This caused both a reduction in the total numbers of all seabirds foraging in feeding flocks and a simultaneous increase of seabirds attending fishing vessels. During cooler LN years, large concentrations of seabirds were seen in feeding flocks and few birds followed fishing boats (Figure 8). The apparent change in food availability is also reflected in the high number of breeding pairs of boobies during LN years (Figure 8).

Endemic seabirds have evolved in the upwelling area of the HCS, where historically their populations are subjected to large fluctuations, ENSO being an important selective force for the evolution of their breeding biology and life-history patterns. During EN, some species abruptly leave their eggs and young to undertake eruptive movements away from the usual breeding and feeding sites in apparent search for food; total or partial breeding failure then often occurs (Simeone et al. 2002). Seabirds are generally characterised by longevity, high age of first breeding, slow reproductive rate and intense offspring care and are thus typical K-strategists. However, it has been hypothesised that, compared with related species, Peruvian boobies and Guanay cormorants (*Leucocarbo bougainvilli*) have larger clutches, may attempt to breed more than once within 1 yr and reach sexual maturity at an unusually early age (Luna-Jorquera et al. 2003). This enables them to build up populations rapidly in the years after EN events because even young, unexperienced adults are able to raise large broods because the food supply per bird is much greater than it would be in a population in equilibrium with the environment (Furness & Monaghan 1987). However, since the establishment of the anchovy fishery, the dynamics of the seabird populations have changed (Duffy et al. 1984). Instead of rapidly increasing populations by raising large broods at least once per year, endemic seabirds failed to respond to the reduced competition brought about by their reduction in numbers. It seems that the anchovy fishery has taken up the superabundance of food, which in the past permitted the seabirds from the HCS to cope with the recurring crashes induced by oceanographic perturbations (Jahncke et al. 2004). In fact, data available for Peruvian seabird colonies (Tovar & Cabrera 1985) show that the EN 1957–1958 caused a mortality of 39% of the estimated populations of 28 million adult birds. Mortality increased to 57% (of 6.54 million adult birds) due to EN 1972–1973, after 1970 when anchovy landings had reached 12 million t (metric tons). The extreme EN 1982–1983 caused a decrease from 6 million birds to only 0.3 million birds in Peru. After that, the populations showed an increase in numbers, reaching ~6 million birds, but the EN 1997–1998 reduced it again to less than 0.4 million birds. In 2000, the size of the Peruvian seabird population was estimated to be 1.93 million adult birds, showing a slight recovery (IMARPE 2006). No comparable datasets are available for the coast of northern-central Chile, where only infrequent surveys of breeding colonies have been conducted so far (e.g., Simeone et al. 2003).

Food resources or breeding sites?

Seabirds and sea lions feed on fish and population crashes during EN years have been explained with the disappearance of fish stocks. Which proportion of the fish stocks do seabirds and seals consume? And how are they affected by variable food supply? Bioenergetic modelling provides

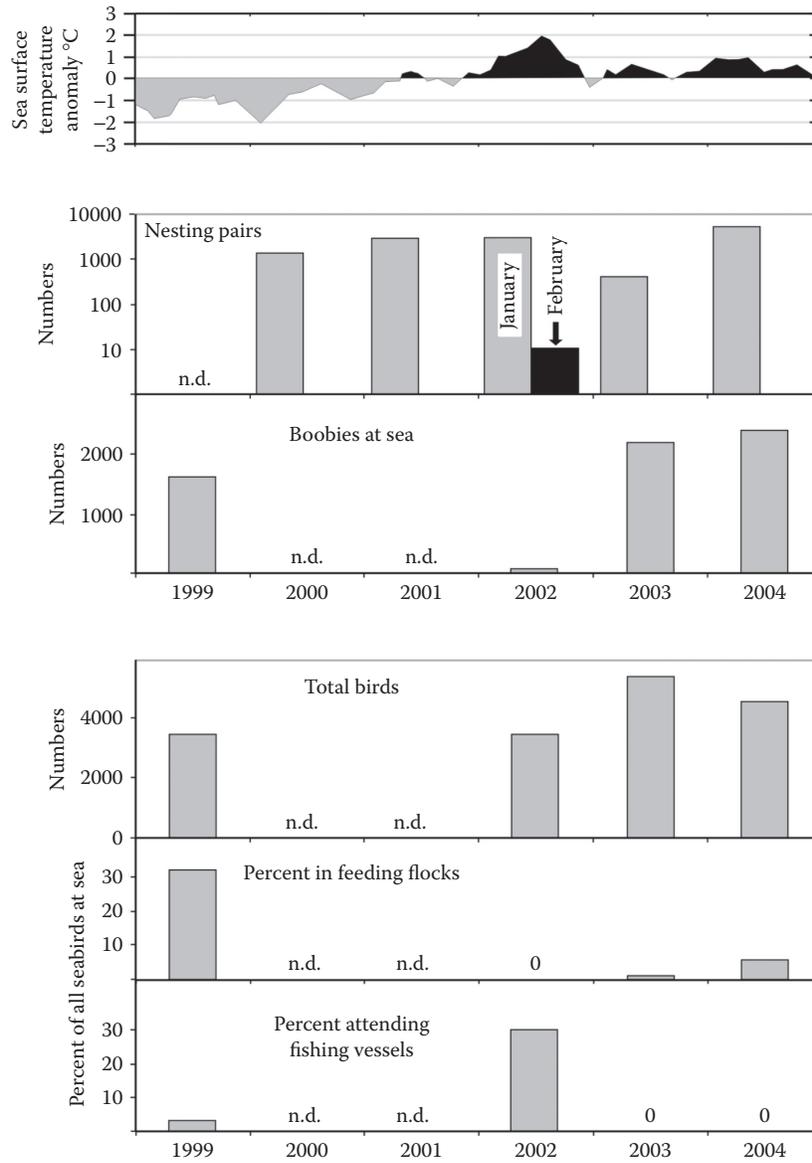


Figure 8 Abundance of breeding and foraging seabirds in the vicinity of Coquimbo, Chile (30°S), and the relationship with sea-surface temperature (SST) anomalies in the southeast Pacific. Upper panel shows SST anomalies during the study period; middle panel shows nesting pairs of Peruvian boobies in a breeding colony on Pájaros Island (29°35'S), and boobies counted during censuses at sea in the Upwelling system of Coquimbo, between 29°08' and 30°11' (see Weichler et al. 2004 for more details); lower panel shows total number of all seabirds counted in the study area in January of each year, and the percentage of birds foraging in feeding flocks or attending fishing vessels in search of food.

useful quantitative assessment of the impact of marine vertebrates on fish stocks and may serve to predict changes in fishery practices or effects of fish stock sizes on seabird and seal numbers. Simple predictions would be that species with specialised feeding methods and a high dependence on specific diets, which have been reduced in availability (due to fisheries or oceanographic

conditions), would be most likely to decline in numbers. In order to develop the models to test these predictions, a long-term research programme is necessary to assess (1) breeding populations, (2) feeding ecology, (3) reproductive biology and (4) energy budgets, under different environmental conditions. In particular, it appears to be important to examine the breeding biology of seabirds. There is an indication that populations of seabirds in northern and central Chile may be limited by the availability of undisturbed breeding islands (see Schlatter 1984, 1987, Schlatter & Simeone 1999). While additional research is necessary, present knowledge already identifies the protection of undisturbed breeding sites as one of the highest priorities for seabird conservation in the HCS of northern and central Chile.

Sandy beaches

Sandy beaches are a common feature of the Chilean coast between 18°S and 41°S (Figure 9), where they offer breeding habitats and important food resources for migrating shorebirds. The extent and distribution of sandy beaches offers unique opportunities for studying the factors driving the population dynamics of invertebrate consumers along the coast of northern and central Chile. Beaches are found along exposed shorelines, sheltered bays and coastal islands and their total extent and average length show a clear latitudinal trend, increasing toward southern-central Chile (Figure 9). Sandy beaches of the coast of Chile show a general zonation pattern of three zones that differ both in their physical characteristics and biological communities (Figure 10) (Jaramillo 1987,

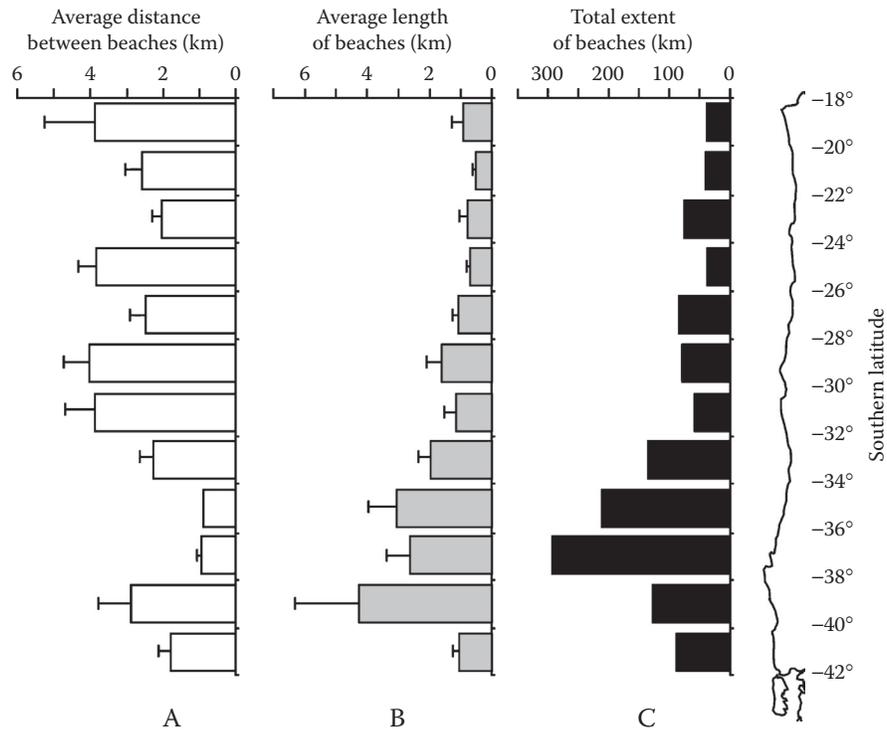


Figure 9 (A) Average distance (mean \pm standard error) between beaches, (B) average length of individual beaches, and (C) total extent of sandy beaches within each sector; individual sectors correspond to the coastline between two subsequent degrees of latitude (information extracted from GOOGLE-EARTH, a total of 810 sandy beaches were measured between 18°S and 42°S).

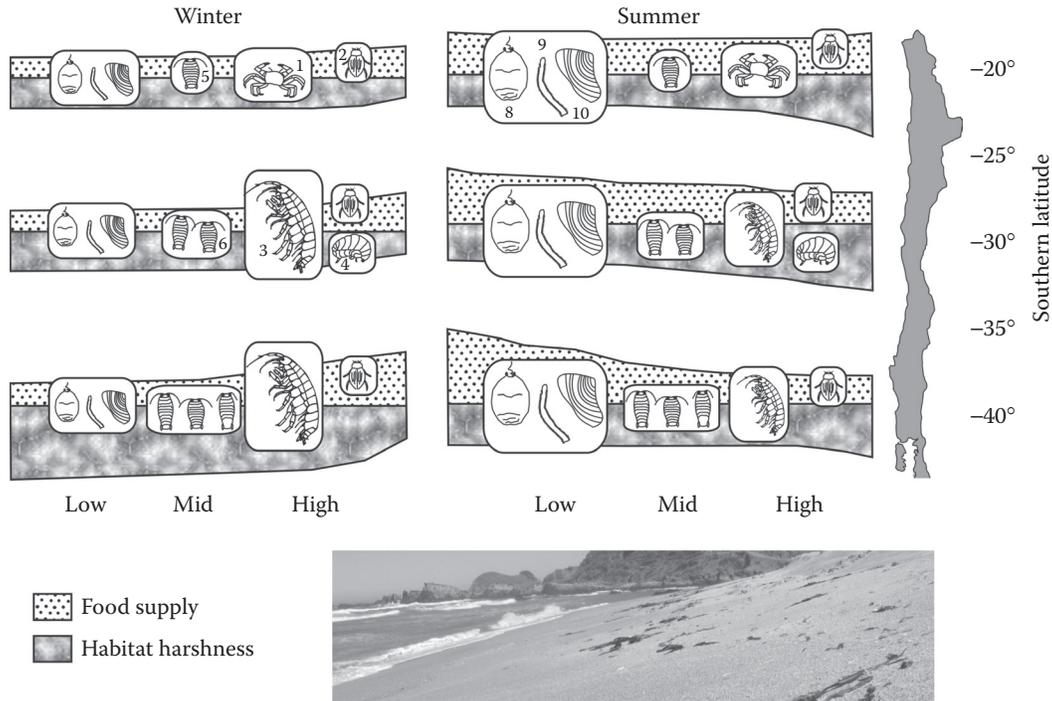


Figure 10 Zonation scheme of sandy beach community along the coast of Chile during winter and summer; shaded background areas represent intertidal gradients in food supply (FS, dotted area) and habitat harshness (HH, grey area), showing both latitudinal and seasonal variation in these physical factors; size of boxes with animal sketches represents proportional abundances of the respective species; note the latitudinal difference in species composition in the upper intertidal zone; species shown are 1, *Ocypode gaudichaudii*; 2, *Phalerisida maculata*; 3, *Orchestoidea tuberculata*; 4, *Tylos spinulosus*; 5, *Excireolana braziliensis*; 6, *E. hirsuticauda*; 7, *E. monodi*; 8, *Emerita analoga*; 9, *Nephtys impressa*; 10, *Mesodesma donacium*. (Figure inspired by a drawing from Jaramillo 1987.)

McLachlan & Jaramillo 1995, Jaramillo et al. 2001). The lower and middle shore have similar species composition (i.e., *Emerita analoga*, *Mesodesma donacium*, *Nephtys impressa*, *Excireolana braziliensis*, *E. hirsuticauda* and *E. monodi*) along the continental coast of Chile, while the upper shore has species-composition differences between northern, central and southern Chile (Jaramillo 1987) (Figure 10). The upper zone, extending from the drift line up to the dunes, is a very dry environment, occasionally moistened by sea mist. Inhabitants of this zone, such as tenebrionid beetles (*Phalerisida maculata*), talitrid amphipods (*Orchestoidea tuberculata*) and oniscoid isopods (*Tylos spinulosus*) feed on plant and animal remains washed up on the beach (Jaramillo 1987). In the northern zone (18–25°S) and off Peru, the amphipod and isopod species are replaced by the ghost crab *Ocypode gaudichaudii* (Quijón et al. 2001), which together with *Phalerisida maculata* inhabits the upper shore (Figure 10). To which degree species replacement is due to physical factors or to species interactions is not well known at present. However, the fact that these faunal changes in the supralittoral zone are accompanied by a gradient in burrowing depth and proximity to the drift line of the main organisms suggests that physical factors (in particular desiccation risk) may play an important role. Guppy (1906) expressed that “the beaches are of dry loose sand in which the hand fails to find on scooping below the surface that refreshing coolness which is the character of beaches in all latitudes where the land is vegetated”.

Within the beach, there are differences not only in the interspecific but also in the intraspecific zonation patterns, which may be accompanied by behavioural differences. In particular, locomotor activity and position on the beach varies depending on the developmental stage and on the time of the day. For example, juvenile *Orchestoidea tuberculata* and *Phalerisida maculata* are most active during the day, while adults show highest activities at night (Jaramillo et al. 1980, 2000). This has been suggested as a strategy to avoid intraspecific competition for food and additionally the risk of intraspecific predation. Furthermore, *Orchestoidea tuberculata* shows an aggregated distribution on kelp patches stranded in the supralittoral zone (Duarte et al. 2004), which is related mainly to feeding behaviours. For *Emerita analoga* and *Mesodesma donacium*, similar ontogenetic differences in activity or habitat use have been reported. Juvenile *Emerita analoga* typically occur in highest abundances in the low intertidal zone slightly above the adults (Contreras et al. 2000). Similarly, juvenile *Mesodesma donacium* inhabit the lowest intertidal zone of the beach (in the swash zone), while adults live in permanently water-covered sediments of the subtidal zone (mainly in the surf zone) (Jaramillo 1994).

Most sandy beach studies have centred on the effect of physical factors, in particular wave exposure, grain size and tides, on the community structure. Species richness, biomass and abundance decrease from dissipative to reflective beaches (Jaramillo 1994, McLachlan & Jaramillo 1995). Biological interactions are more intense on dissipative beaches than on reflective beaches, where the population dynamics are mainly controlled by physical factors (Defeo & McLachlan 2005). Strong competition between mole crabs *Emerita* and surf clams *Donax* has been suggested as the cause for the aggregated distribution of the surf clams (Leber 1982), and negative interactions between *Emerita analoga* and *Mesodesma donacium* were observed along the Chilean coast (Dugan et al. 2004), but aggregations may also be a response to sediment characteristics (i.e., grain size). On the other hand, organisms inhabiting the upper shore (i.e., talitrid amphipods) are not associated to one particular beach type (Defeo & McLachlan 2005), which suggests that their populations are not influenced by beach morphodynamics but rather by other physical factors or food availability. To which degree resource or interference competition (or direct predation) is responsible for the latitudinal changes in the species composition of this zone remains to be explored.

The species that inhabit sandy beaches have diverse reproductive strategies, which can be related to the habitat characteristics. For example, most of the species of the upper and middle shore (i.e., *Orchestoidea tuberculata*, *Tylos spinulosus* and *Excirolana* spp.) have direct development, which might suggest that the connectivity between populations is low. In northern-central Chile (29°S) the reproductive peak of *Excirolana hirsuticauda* is in spring–summer (Contreras & Jaramillo 2003), and it is suggested that the other species from the upper/middle shore follow a similar pattern. The lower intertidal and subtidal zone is inhabited by organisms with indirect development (*Emerita analoga*, *Mesodesma donacium*, *Nephtys impressa*), which have planktonic larvae possibly permitting higher connectivity between local populations. For *Emerita analoga*, distinct recruitment peaks (see also Arntz et al. 1987 for Peru) have been reported for autumn, spring or early summer in northern (22°S) and southern-central Chile (39°S), but ovigerous females are usually found throughout the year (Contreras et al. 1999, Contreras et al. 2000). In northern-central Chile (30°S) the surf clam *Mesodesma donacium* has two spawning peaks during the year (usually during the early summer and autumn), but females with mature gonads have been observed throughout most of the year (Alarcón & Navea 1992, Stotz et al. 1999). These observations suggest continuous reproductive activity, but spawning or successful recruitment seems to occur only infrequently, possibly depending on particular environmental factors (triggering gamete release) and oceanographic conditions (affecting larval survival and supply).

There is also a high temporal variability of faunal abundance throughout the year. For example, *Orchestoidea tuberculata* reach highest abundances during the winter months, both in central (30°S) and southern Chile (40°S) (Sánchez et al. 1982, McLachlan & Jaramillo 1995). Furthermore, during

the winter, these amphipods live higher up on the beach, mainly to avoid being washed out by higher wave activity. During summer, the abundances of *O. tuberculata* decrease and they are found closer to the flotsam (Sánchez et al. 1982, McLachlan & Jaramillo 1995), possibly to avoid desiccation risk in the supralittoral zone or to get close to their food. The cirrolanid isopods (*Excirolana* spp.) have similar abundances in summer and winter, but they shift their position in the intertidal zone, moving higher during the winter months (Sánchez et al. 1982). On the other hand, *Emerita analoga* in the northern (22°S) and *Mesodesma donacium* in northern-central Chile (30°S) reach highest abundances in summer (Sánchez et al. 1982, Contreras et al. 2000). At present, the reasons for the apparent inverse population dynamics of species from the upper versus those from the lower intertidal zone are speculative, and seasonally varying offspring (larval) survival or food supply could be invoked. One very interesting species from the supralittoral zone, *Tylos spinulosus*, which has a restricted distribution in northern-central Chile (17°–30°S) (Schmalfluss & Vergara 2000), is little known aside from a few data on its population density (Sánchez et al. 1982, Jaramillo et al. 2003), and it appears a promising enterprise to examine its population dynamics.

The vicinity to upwelling centres plays an important role in the succession and structure of hard-bottom communities (Broitman et al. 2001, Narváez et al. 2006), but there is no clear indication that the macrofauna composition of sandy beaches is influenced by their proximity to upwelling areas (Jaramillo et al. 1998). Contreras et al. (2000) concluded that growth rates of *Emerita analoga* from a beach near the upwelling centre of Mejillones (22°S) were within values reported for other areas, suggesting only limited or no direct effects of upwelling on sandy beach inhabitants. Community dynamics of sandy beaches may be influenced by upwelling to a lesser degree than those pertaining to hard-bottom communities. For example, higher nutrient availability near upwelling areas positively influences growth rates of seaweeds on hard bottoms (Camus & Andrade 1999, Wieters 2005) and thereby the community succession (Nielsen & Navarrete 2004), which clearly is of no importance on exposed sandy beaches where algae are usually imported from neighbouring (or distant) hard-bottom habitats. Furthermore, the interplay between upwelling and subsequent relaxation events strongly affects the recruitment of hard-bottom organisms with planktonic larvae (Narváez et al. 2006), but seems to be of minor importance on sandy beaches, where the most common organisms feature direct development.

The effect of ENSO has been intensively studied in hard-bottom environments, but its role in the dynamics of sandy beach communities is not well known (Arntz et al. 1987). EN events may have deleterious effects on the organisms from the lower intertidal zone of sandy beaches (e.g., *Mesodesma donacium*; see also Artisanal benthic fisheries, p. 278ff.). On the other hand, it is known that EN provokes mass mortalities of seaweeds and animals, many of which eventually will strand on sandy beaches (Arntz 1986). This high supply of OM may represent an important food source for scavenging animals of the supralittoral zone of sandy beaches (e.g., *Orchestoidea tuberculata*). In this way, it can be suggested that intertidal organisms are distinctly affected by EN: species from the lower shore (suspension feeders with planktonic larvae) may be negatively affected by EN, while those from the supralittoral zone (scavenging animals with direct development) might benefit from the higher food supply and more benign climate (lower desiccation risk) during EN.

Subtidal soft-bottom communities

Zonation patterns

Recent studies suggest that the bathymetric distribution of subtidal benthic communities off the Chilean margin seems to be controlled mainly by bottom water oxygen conditions and sediment organic loading. OMZs are significant mid-water features in the eastern Pacific Ocean (Wyrski 1973, Kamykowski & Zentara 1990) that strongly influence the distribution and diversity of

planktonic and benthic marine communities. Where OMZs intercept the continental margin (bottom-water dissolved oxygen $< 0.5 \text{ ml L}^{-1}$), strong gradients are formed in both bottom-water oxygen concentration and OM input (Levin et al. 1991, Levin et al. 2000). These gradients influence the biogeochemical properties of sediments (Cowie et al. 1999) and the distribution and diversity of bacteria, meio-, macro- and megabenthic organisms (Sanders 1969, Mullins et al. 1985, Wishner et al. 1990, Tyson & Pearson 1991). Off Chile, oxygen-deficient waters are in general associated with the ESSW, which partially covers the continental shelf and upper bathyal area. The intensity and vertical extent of the OMZ suggest a latitudinal gradient, the effect disappearing at about 41°S (Brandhorst 1971). Off northern Chile, sediments affected by the OMZ extend from a few tens of metres below the surface to 300–400 m water depth. Between Huasco and Valparaíso ($\sim 28\text{--}32^\circ\text{S}$), the OMZ seems to intercept the sea floor deeper than 100 m (D. Lancellotti & W. Stotz unpublished data), and due to the narrowness of the shelf and steepness of the slope, there are zones that probably are not severely affected. This is also corroborated by the presence of a fauna atypical for oxygen-deficient areas (e.g., diverse species of gastropods) and the absence of bacterial mats (Lancellotti & Stotz 2004). The shelf widens southward and when upwelling prevails, during spring–summer, the OMZ again can be found only a few metres from the surface even in southern-central Chile ($\sim 36^\circ\text{S}$), within Concepción Bay (Ahumada et al. 1983), and extending down to 200–300 m (see also Arntz et al. 2006). However, the OMZ intensity here is probably the result of many local factors (e.g., the high PP that leads to high remineralisation rates in the water column and sea floor, consuming oxygen and generating sulphidic conditions within the sediment) (P. Muñoz et al. 2004b). In this way, it is probably possible to visualise the OMZ impinged sea floor, from northern to central Chile, as a wedge-shaped band, getting narrower southward, but with two foci of most intense oxygen-deficient conditions, one off northern Chile and the other at the shelf off Concepción. The continuity between these two foci may be interrupted by better-oxygenated sediments, at comparable depths, off central Chile. Reports of low bivalve abundances between 80 and 120 m depth in Valparaíso Bay (31°S) are suggestive of OMZ effects (Ramorino 1968), but additional data are required to resolve the intensity and extent of the OMZ and its effect on benthic communities between 25°S and 35°S .

Considering the general effect of the OMZ on benthic communities, and based on the limited amount of biological sampling available at that time, Gallardo (1963) proposed the existence of basically three main benthic zones for the local eukaryotic communities: (1) an upper sublittoral zone, up to 50 m depth, with favourable conditions for the development of ‘normal’ benthic communities, (2) a lower sublittoral zone, from 50 to 300–400 m (varying with latitude and coinciding with the extent of the OMZ), in which only those organisms highly adapted to cope with oxygen deficiency and high organic loadings are able to thrive (basically small polychaetes, oligochaetes, nematodes and a few molluscs), and (3) a bathyal area, associated mainly with Antarctic Intermediate Waters, with a diverse and rich fauna (dominated by annelids, crustaceans, molluscs and echinoderms) that benefits from enhanced oxygen and good quality and quantity of sediment OM. How this general pattern differs in southern areas ($>41^\circ\text{S}$) where the OMZ dissipates is still poorly known.

One of the most distinguishing features of benthic shelf communities within OMZ-impinged sediments is the presence of extensive mats of the filamentous, sulphide-oxidising bacteria *Thioploca* and *Beggiatoa* (Gallardo 1963, 1977, Schulz et al. 2000, Arntz et al. 2006). These bacteria are the most conspicuous component of the benthos also in the central and southern Peruvian shelf (Rosenberg et al. 1983). Bacterial biomasses of up to 1 kg m^{-2} wet wt have been reported from shelf sediments off Iquique ($\sim 21^\circ\text{S}$) (Gallardo 1963) and off Concepción ($\sim 37^\circ\text{S}$) (Gallardo 1977) at depths between 50 and 100 m. On the other hand, within the OMZ eukaryotes are in general small-size forms, like meiofauna, calcareous foraminiferans and nematodes (Gooday et al. 2000, Neira et al. 2001, Levin 2003). Very high densities, on the order of 10,000 individuals (ind.) 10 cm^{-2} ,

of meiobenthic organisms, mostly nematodes, have been recorded on the shelf off Concepción (Neira et al. 2001, Sellanes et al. 2003). OMZ macrofaunal assemblages thus have low diversity and are typically composed of organisms with morphological and metabolic adaptations and feeding strategies suited to these conditions. A good example is the locally abundant polychaete *Paraprionospio pinnata*, an interface feeder organism, which is also able to switch to suspension feeding (Gutiérrez et al. 2000), with a complete set of enzymes for anaerobic metabolism (González & Quiñones 2002), and also bearing a set of highly branched and complex gills. *Paraprionospio pinnata* comprises about half of the ~14,000 macrofauna individuals m⁻² reported from off Concepción within the OMZ (Palma et al. 2005).

Below the OMZ, the total abundance of macrobenthos decreases while biomass and diversity increase in parallel with increases in oxygen and decreases in organic carbon (Levin 2003). In the bathyal area off Chile, important crustacean assemblages, mainly of commercially valuable galatheid decapods (e.g., *Pleuroncodes monodon* and *Cervimunida johni*), thrive at the slope within and below the lower boundary of the OMZ. Below the OMZ, groups that are favoured by increased oxygen concentrations are decapod crustaceans, gastropods and at greater depths echinoderms (mainly ophiuroids, asteroids and irregular echinoids). The large tubicolous onuphid polychaete *Hyalinoecia* sp. (tubes 10–20 cm in length) is particularly abundant at mid-slope depths off Concepción and Chiloé (J. Sellanes personal observations). Scleractinian corals and many species of gorgonarians are common on the slope off Chiloé, below 500 m water depth.

Finally, though the three-layer scheme for benthic zonation is the general rule, another type of chemosynthetic community, methane seep areas, has been reported from off Concepción at 700–1400 m water depth (Stuardo & Valdovinos 1988, Sellanes et al. 2004, Sellanes & Krylova 2005). In these reducing systems, C is fixed locally by both free-living and symbiotic chemosynthetic bacteria. Seepage areas thus provide a suitable environment for the development of singular communities consisting of sulphide oxidising bacteria (e.g., *Beggiatoa*), highly endemic endosymbiont-bearing clams (e.g., Vesicomidae, Lucinidae, Thyasiridae and Solemyidae) and tubeworms (e.g., *Lamelli-brachia* sp.). In addition, non-chemosymbiotic megafauna (e.g., crustaceans, gastropods, cephalopods, fish) are massively attracted to these deep-sea hot spots of biological activity. The attraction of these areas is due to both the abundance of locally produced organic material and the presence of authigenic carbonate reefs (generated by microbial and chemical processes), which are avidly colonised by a diverse benthic fauna (J. Sellanes unpublished data).

Latitudinal and bathymetric patterns

In general, for the available data of macrofaunal species richness on the Chilean shelf, no clear latitudinal pattern emerges. Published reports of species numbers range from 18 to 56 species at northern Chile (~23°S, 15–65 m water depth) (Jaramillo et al. 1998), 42 to 85 species at Huasco (~28°S, 20–50 m water depth) (Lancellotti & Stotz 2004), 10 to 41 species at Concepción (~36°S, 15–65 m water depth) (Carrasco et al. 1988), and 24 to 34 species further south (~45°S) (D. Lancellotti & W. Stotz unpublished data). Highest abundances reported are for the shelf off Concepción (36,290–38,590 ind. m⁻²; Carrasco et al. 1988) and biomass values of almost 900 g wet wt m⁻² are reported for south of Chiloé (D. Lancellotti & W. Stotz unpublished data).

A crude comparison among the few available deeper studies (>100 m water depth) suggests higher macrofaunal standing stocks and abundances also at the shelf off central and southern areas, both for macro- (body size 0.3–2 cm) and megafauna (body size >2 cm), compared with northern Chile (Figure 11). Palma et al. (2005) reported macrofaunal biomass values for three transects covering a depth range from about 100 m to 2000 m at Antofagasta, Concepción and Chiloé (about 22°S, 36°S and 42°S, respectively). Though biomass trends with depth, beyond the OMZ, are in general unimodal at all transects, with higher values at intermediate depths and lowest within the

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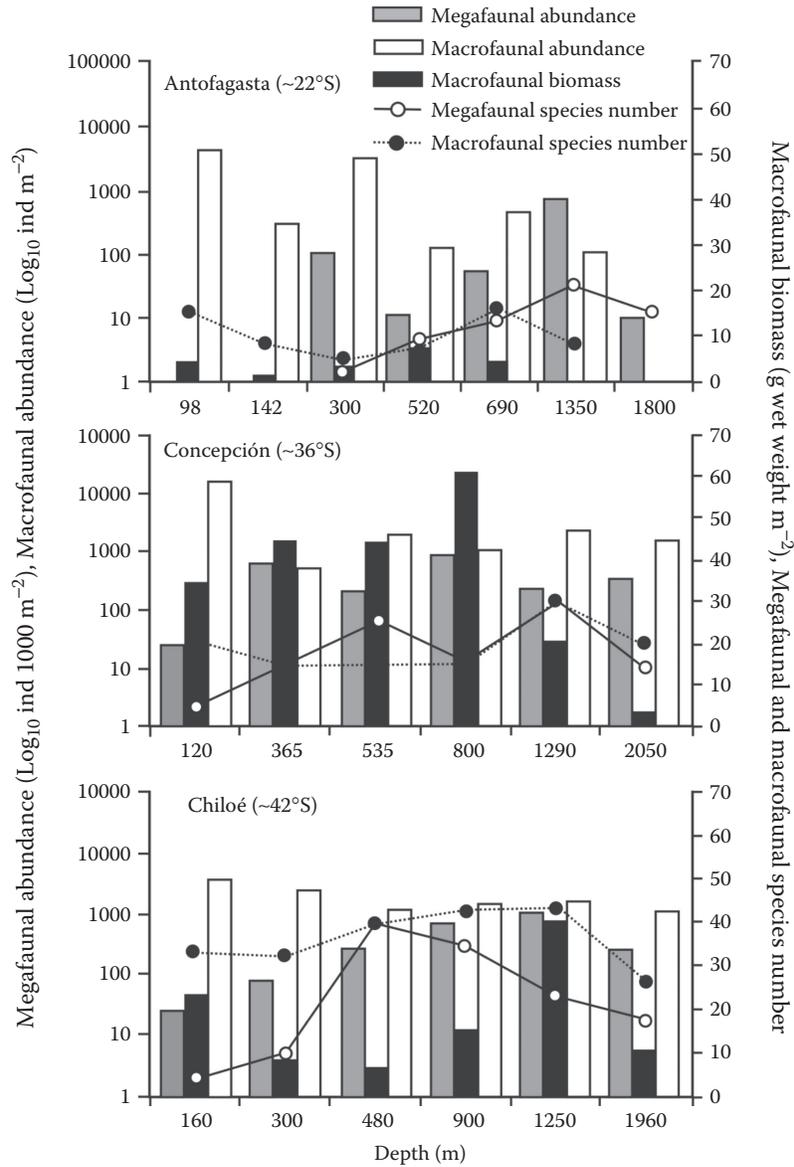


Figure 11 Macro- and megafauna depth-related patterns for three transects (22°S, 36°S and 42°S) across the shelf and upper bathyal zone of the Chilean margin. Data for macrofaunal abundance, biomass and species number from Palma et al. (2005) and for megafaunal abundance and species number from E. Quiroga unpublished data).

OMZ and beyond 1350 m, average biomasses are lower off Antofagasta. Maximum values for this transect (6.9 g wet wt m⁻²) are reported at 518 m water depth, while values about an order of magnitude higher (60.7 g wet wt m⁻²) are reported off Concepción at 784 m depth. For southern Chile (~42°S) intermediate values (39.2 g wet wt m⁻²) are reported for a station located at 1250 m depth. This also indicates a deepening of macrofaunal biomass maxima with latitude (Figure 11). For the megafauna observed at the same three transects, though biomass values are not available, abundances in general exhibited a similar pattern to that previously explained for macrofaunal

biomass (Palma et al. 2005). On average, pooling the data for the three transects, abundance (~500 ind. m⁻²) and species number (~25) peaks were located between 1000 and 1500 m depth.

Temporal patterns of variability in shelf communities

As explained in previous sections of this review, the coastal zone off northern and central Chile is strongly influenced by seasonal wind-driven upwelling, giving rise to one of the areas with the highest PP rates known worldwide (Fossing et al. 1995, Daneri et al. 2000). Since water column oxygen conditions and sediment organic loadings fluctuate at both intra- (i.e., seasonal) and interannual scales (i.e., ENSO cycle), some degree of coupling with the dynamics of benthic communities is expected (Tomicic 1985, Arntz & Fahrback 1991). This has been demonstrated for southern-central Chile (~36°S), where seasonal and interannual changes in upwelling intensity can lead to changes in bottom-water dissolved oxygen concentration, in the amount of OM reaching the bottom (Gutiérrez et al. 2000), in the quality and lability of deposited OM (Neira et al. 2001, Sellanes & Neira 2006) and in the sediment nitrogen fluxes (P. Muñoz et al. 2004b). During the last strong EN event (1997–1998), important insights were gained by examining the effects of changing environmental conditions on local bacterial, meiofaunal (Neira et al. 2001, Sellanes et al. 2003) and macrofaunal (Gutiérrez et al. 2000) communities off central Chile. The largest biomasses of the bacterial component have been observed after several years of upwelling-favourable conditions, which are associated with cold LN phases of the ENSO (V.A. Gallardo et al. unpublished data), while the bacterial biomass is effectively depressed during warm EN phases. A decreasing trend in macrofaunal density, as well as the presence of deeper-burrowing infauna, evolved toward the end of EN 1997–1998, mainly due to the decrease of the polychaete *Paraprionospio pinnata* (Gutiérrez et al. 2000). It appears that more oxygenated bottom waters and oxidised sediment during EN caused *P. pinnata* to fail in its summer recruitment. In addition, it is probable that increased competition and predation by other species have contributed to its decline. Indeed, it has been reported that during EN, many subtropical predators invade the coastal areas (Arntz et al. 1991), negatively affecting the surface-feeding polychaetes (Tarazona et al. 1996). In central Chile, *P. pinnata* recovered its numerical dominance only in summer 2003, i.e., 5 yr after the end of EN. Severe hypoxic and sulphidic conditions that developed during summer 2003 probably eliminated or precluded possible competitors and/or predators, triggering the explosive increase of the *P. pinnata* population during this period (Sellanes et al. 2007).

In northern Chile (20–30°S) few datasets extending over at least 12 months are available from shallow benthic communities (20–80 m). For the time period 1990–1995, relatively high abundances of polychaetes have been reported from several stations in northern Chile (23°50'S) at water depths of 50–60 m (Carrasco 1997). This author remarked on the absence of a clear seasonal signal in abundance changes of the main polychaete species, and he suggested that the observed variations rather reflected long-term patterns. At a long-term monitoring station near 28°S, abundances of polychaetes were high in 1995 (Figure 12), comparable to those found by Carrasco (1997). High abundance, biomass and species diversity at 28°S were associated with the warm period 1993–1995 and followed by a strong decline in 1996, coincident with LN conditions, which continued during the EN 1997–1998 (Lancellotti 2002, D. Lancellotti & W. Stotz unpublished data). Gradual disappearance of spionids, as observed in Huasco in 1996 during LN (Figure 12), was also observed during the same time period in Iquique (20°S) between 9 and 30 m depth (Quiroga et al. 1999). In northern-central Chile, during EN events, increased wave activity and freshwater runoff are frequent, in contrast to calmer periods recorded during LN events. Turbulence and runoff, in a zone where rains and strong storms are uncommon, probably oxygenate the water column, resuspend OM and/or provide terrigenous material, thus favouring reproduction and settlement of macrobenthic species living below the zone of direct wave and sediment deposition impact (>20 m

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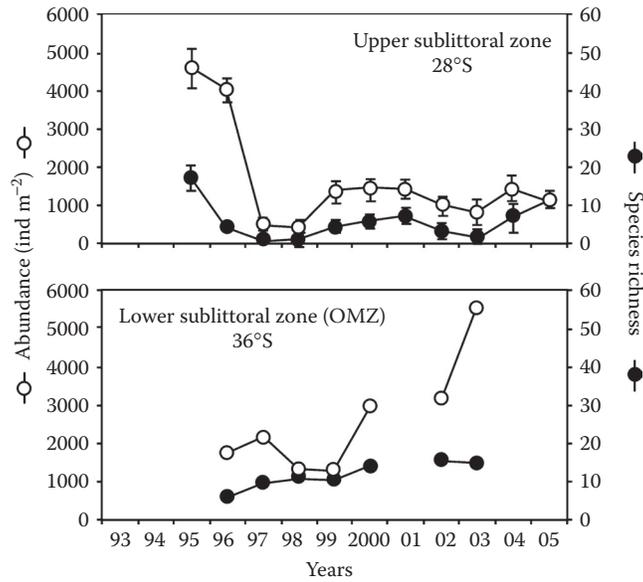


Figure 12 Temporal variations in the abundance of soft-bottom macrofauna in the upper sublittoral zone (northern Chile, 28°S) and the lower sublittoral zone (central Chile, 36°S); average abundance and species richness (S) are given; data from the upper littoral zone are taken by Smith-MacIntyre grab (1995–1996) or with sediment cores by divers (1997–2005) (D.A. Lancellotti & W. Stotz unpublished data); data from the lower sublittoral zone are taken with a multicorer, and several samples from each year were pooled, thus not allowing intra-annual variation to be seen (J. Sellanes unpublished data).

water depths). Effects of EN (and other) events on the temporal variability of benthic soft-bottom communities at present are difficult to evaluate because very few long-term datasets from benthic habitats are available from the HCS along the Chilean coast. It is herein suggested that long-term monitoring programmes should be implemented, sampling on a seasonal or bimontly basis, following examples in Peru (Tarazona et al. 2003, Arntz et al. 2006, Peña et al. 2006) and the Northern Hemisphere (Frid et al. 1996, Kroencke et al. 1998, Salen-Picard et al. 2002).

Intertidal and subtidal hard-bottom communities

Hard bottoms along the coast of northern-central Chile are generally restricted to a narrow fringe extending from the intertidal zone to shallow sublittoral waters. The rock substratum is composed of rock of volcanic, granitic or sedimentary origin (Fariña et al. in press). The extensive rocky shores between 18°S and 40°S are mostly exposed to strong wave action, and they are only interrupted by short stretches of sandy beaches, which increase in extent toward the south (see Sandy beaches, p. 227, Figure 9), thereby leading to a wider separation of neighbouring hard-bottom environments. Communities on intertidal and subtidal hard bottoms are dominated by macroalgae and suspension-feeding animals that form large patches (occasionally extending over to neighbouring soft bottoms) or belt-like stretches (running parallel to the shore at a certain tidal level). Most intertidal and subtidal hard bottoms are covered by one or a few dominating habitat-forming organisms. Patches may persist for many years at a given location (Durán & Castilla 1989, Fernández et al. 2000, Vega et al. 2005), and they offer abundant microhabitat and food for associated organisms (Moreno & Jara 1984, Vásquez et al. 1984, Núñez & Vásquez 1987, Buschmann 1990, Vásquez 1993a, López & Stotz 1997, Sepúlveda et al. 2003a,b). Here these habitat-forming

species, their spatial and geographic extent, their temporal dynamics and their role as ecosystem engineers (EEs) will be described. Further, it will be briefly discussed how the spatiotemporal distribution of these EEs may influence local biodiversity, population dynamics and trophic interactions in hard-bottom communities along the HCS.

Habitat-forming species on hard bottoms

Large kelps (*Lessonia nigrescens*, *L. trabeculata*, *Macrocystis integrifolia*, *M. pyrifera* and *Durvillaea antarctica*), which grow abundantly in the low intertidal and shallow subtidal zone of the HCS, have compact and complex holdfasts that offer abundant and diverse microhabitats on the rock substratum itself. Their stipes and blades reach lengths of 2.5 m (*Lessonia trabeculata*) up to 30 m (*Macrocystis pyrifera*), and they have an important effect on local hydrodynamics because they act as wave breakers and slow down currents (Graham 2004). Smaller macroalgae with shorter thalli of 5–50 cm (such as *Halopteris funicularis*, *Glossophora kunthii*, *Asparagopsis armata*, *Corallina officinalis* and *Gelidium chilense*) form dense carpets (turfs) that offer primary and secondary microhabitats because they act as sediment traps retaining sand and shell fragments between their thalli and stolons (López & Stotz 1997, Kelaher & Castilla 2005).

A diverse group of suspension-feeding EEs on hard bottoms include polychaetes (*Phragmatopoma moerchi*), barnacles (*Austromegabalanus psittacus*), bivalves (*Perumytilus purpuratus*, *Semimytilus algosus*, *Choromytilus chorus* and *Aulacomya ater*), and ascidians (*Pyura chilensis* and *P. praeputialis*). Their matrices reach heights of 2–40 cm, offering abundant space between living individuals (Cerdeña & Castilla 2001) or in remaining tubes or shells of dead individuals. Matrices of these suspension feeders may also retain considerable amounts of sediments (Prado & Castilla 2006), thereby providing secondary substratum for associated organisms.

Habitat-forming species compete among themselves for space on hard-bottom substrata. Several studies indicate that mussels are competitively superior over barnacles (Navarrete & Castilla 1990, 2003, Tokeshi & Romero 1995a) and can also overgrow turf algae (Wieters 2005), ascidians may outcompete mussels (Castilla et al. 2004a) or barnacles (Valdivia et al. 2005), and large kelp may recruit in and then overgrow turf algae (Camus 1994a). Superior competitors themselves may be suppressed by predators (e.g., mussels and ascidians by gastropod and seastar predators; Paine et al. 1985, Castilla 1999, Castilla et al. 2004b) and grazers (Vásquez & Buschmann 1997, Buschmann et al. 2004a). Humans, acting as top predators by removing intermediate consumers, also strongly influence the structure of hard-bottom communities in northern and central Chile (Moreno et al. 1986, Castilla 1999). Furthermore, recruitment and growth of habitat-forming species are controlled by a variety of processes (e.g., upwelling) that drive larval and food supply (Navarrete et al. 2002, Nielsen & Navarrete 2004, Wieters 2005). Following disturbances and detachment, open space on hard bottoms is quickly recolonised, starting with ephemeral algae, which subsequently are replaced by large and long-lived turf or kelp algae and suspension feeders (Durán & Castilla 1989; Valdivia et al. 2005).

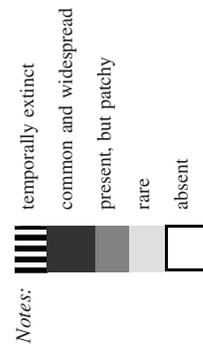
Spatial and temporal dynamics of ecosystem engineers

The geographic range of most macroalgae and suspension-feeding EEs extends throughout northern-central Chile (into Peru), but not all of them have a continuous latitudinal distribution (Table 3). All EEs from hard bottoms have pelagic dispersal stages, but in the case of the macroalgae the planktonic phase is of short duration (minutes to hours).

Kelps of the genera *Lessonia* and *Macrocystis* extend from southern Chile to north of 18°S, but EN events may provoke large-scale extinctions in northern Chile (see also Kelp forests,

Table 3 Main ecosystem engineer species from intertidal and subtidal hard bottoms along the Humboldt Current System of northern and central Chile

Ecosystem engineer	Zonation (m)	Wave-exp.	Height of patches (m)	Size of patches (m ²)				Latitudinal extent (°)				Distance between patches (km)				Patch persistence (years)				
				< 1000	10 to 1000	> 1000	> 10000	18,19	20,21	22,23	24,25	26,27	28,29	30,31	32,33	34,35	36,37	38,39	< 1	> 1
<i>Lessonia trabeculata</i>	0-30	E,S,P	2.5	x	x												x	x	x	x
<i>Lessonia nigrescens</i>	0	E,S	6	x	x												x	x	x	x
<i>Macrocystis integrifolia</i>	0-15	S,P	10	x	x															
<i>Macrocystis pyrifera</i>	0-30	S,P	30	x	x															
<i>Durvillaea antarctica</i>	0	E	15	x	x															
<i>Glossophora kanzhii</i>	0-8	E,S,P	0.25			x	x													
<i>Halopteris funicularis</i>	0-8	E,S,P	0.1			x	x													
<i>Asparagopsis armata</i>	0-8	S,P	0.12			x	x													
<i>Corallina officinalis</i>	0-8	E,S,P	0.15			x	x													
<i>Gelidium chilense</i>	0-2	E,S,P	0.06			x	x													
<i>Phragmatopoma moerchi</i>	0	E	0.2			x	x													
<i>Perumytilus purpuratus</i>	0	E	0.05			x	x													
<i>Semimytilus algosus</i>	0	E	0.1			x	x													
<i>Aulacomya ater</i>	10-20	E	0.2			x	x													
<i>Austroragabalanus psittacus</i>	0-20	E,S	0.2			x	x													
<i>Pyura chilensis</i>	1-20	E,S,P	0.2			x	x													
<i>Pyura praeputialis</i>	0-10	E,S,P	0.6			x	x													



Information obtained from Hoffmann & Santelices 1997, Santelices 1989, Santelices 2001, Sepúlveda et al. 2003a,b and Hernández et al. 2001.

p. 240ff.). *Durvillaea antarctica* does not extend further north than 32°S. Patches or belts formed in the low intertidal zone by *Lessonia nigrescens* and *Durvillaea antarctica* generally have extents of several square metres up to >100 m². Subtidal kelp forests of *Lessonia trabeculata* and *Macrocystis* spp. may extend over >1000 m², comprising some of the largest habitat patches formed by EEs. Distances between neighbouring patches are small in the case of *Lessonia* spp. and *Durvillaea antarctica* but individual forests of *Macrocystis* spp. can be separated by several hundred kilometres (see also Kelp forests, p. 240ff.). Persistence of patches over time may be favoured by recruitment of new sporophytes into existing kelp patches (Santelices & Ojeda 1984).

Turf algae generally form smaller patches, with individual patches rarely exceeding an area of a few square metres. *Corallina officinalis* and *Gelidium chilense* (and other turf algae, e.g., *Montemaria horridula*, *Rhodymenia skottsbergii*) form long-lived patches in the intertidal zone (López & Stotz 1997, Vásquez & Vega 2004a, Wieters 2005), and distances between neighbouring patches are relatively small (Table 3). *Glossophora kunthii*, *Halopteris funicularis*, *Asparagopsis armata* (and others, including *Corallina officinalis*) occur mainly on shallow subtidal hard bottoms where they form patches of several square metres and, while thalli may disappear during the winter, the stolons persist over several years (Vásquez et al. 2001a). Patches may extend their size or renew thalli via asexual proliferation.

The polychaete *Phragmatopoma moerchi* forms patches of several square metres in extent in the low intertidal and shallow subtidal zone in areas with a high supply of sand and shell fragments (Sepúlveda et al. 2003b). These patches persist over several years, but disappear if renewal is reduced, either due to low larval supply or high postsettlement mortality (Zamorano et al. 1995). The barnacle *Austromegabalanus psittacus* forms aggregations in the low intertidal and shallow subtidal zone; patches generally are small, rarely exceeding more than a few square metres in area. This species occurs all along the coast of northern and central Chile and little is known about the temporal dynamics of individual patches. Bivalves form extensive patches of a few square metres up to >1000 m² in area in the mid-intertidal (*Perumytilus purpuratus*), low intertidal (*Semimytilus algosus*) and subtidal zones (*Choromytilus chorus*, *Aulacomya ater*). In the absence of predators patches can persist over many years (Durán & Castilla 1989), facilitated by regular recruitment into adult patches (Alvarado & Castilla 1996). Most bivalve species have a wide latitudinal distribution, but *Perumytilus purpuratus* and *Aulacomya ater* are almost entirely absent over an extensive area in northern Chile between 23°S and 32°S (Fernández et al. 2000, personal observations), which appears to be mainly due to limited larval supply in that region (for *Perumytilus purpuratus* see Navarrete et al. 2005). The ascidian *Pyura chilensis* occurs in small patches in the shallow subtidal zone (e.g., Vásquez & Vega 2004b), while the congener *P. praeputialis* forms extensive belts in the low intertidal zone (Table 3). Patches of *P. chilensis* persist over many years at the same location (personal observations), but little is known about the population dynamics within patches. In *P. praeputialis*, recruitment may be most successful in the vicinity of adults (Clarke et al. 1999), thereby favouring the long-term persistence of patches. While *P. chilensis* has a wide geographic distribution, *P. praeputialis* is restricted to a small range of 70 km along the Bay of Antofagasta (23°S) in northern Chile (Castilla et al. 2000).

Macrofauna associated with ecosystem engineers on hard bottoms

A wide diversity of organisms is associated with habitat-forming species on hard bottoms of northern and central Chile. Highest species richness is found in the kelp holdfasts, intermediate numbers of associated species are reported from ascidian and bivalve reefs, and turf algae harbour fewest species of associated macrofauna (Figure 13A). This relationship appears to be related to

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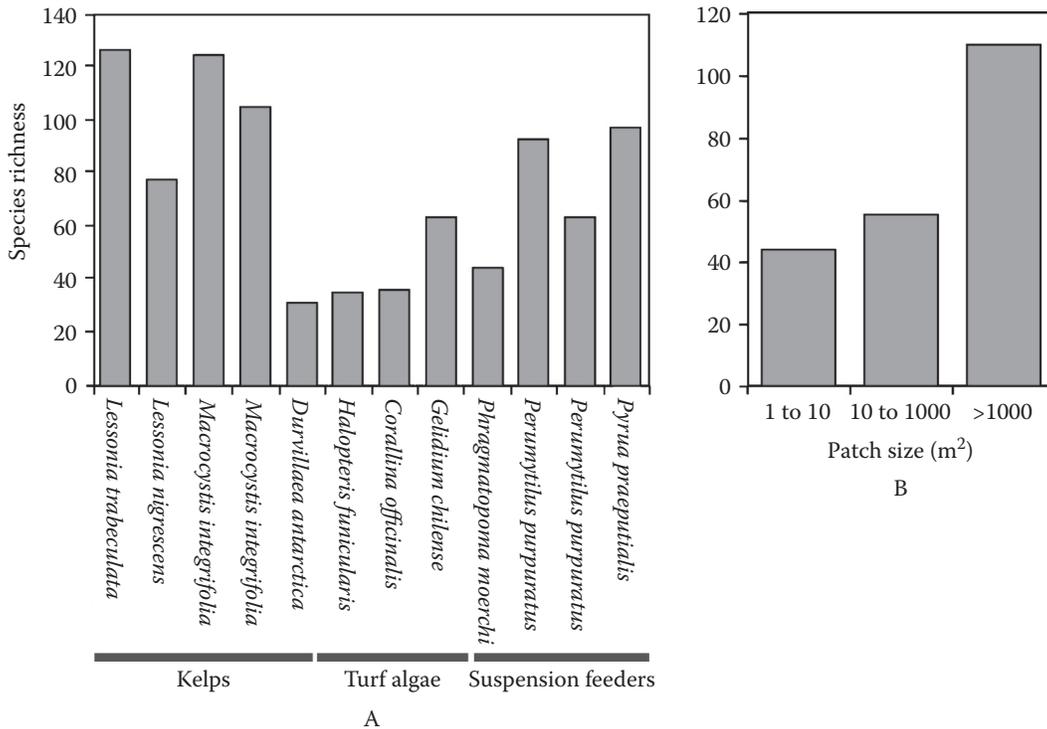


Figure 13 (A) Species richness of macroinvertebrates associated with habitat-forming macroalgae or suspension feeders from intertidal and subtidal hard bottoms of the northern and central coast of Chile; for reasons of comparability only studies that reported at least seven phyla of associated macrofauna were considered. (B) Average species richness in biotic habitats of different patch sizes; information obtained from López & Stotz 1997, Gelcich 1999, Godoy 2000, Thiel & Vásquez 2000, Cáceres 2001, Cerda & Castilla 2001, Hernández et al. 2001, Vásquez et al. 2001b, Thiel & Ullrich 2002, Sepúlveda et al. 2003a,b, Prado & Castilla 2006.

the fact that kelp beds and ascidian and bivalve reefs have a comparatively large spatial extent while patches of turf algae rarely cover more than a few square metres (Figure 13B). A positive relationship between patch size and number of associated species has been revealed for most habitat-forming species (Vásquez & Santelices 1984, Villouta & Santelices 1984, Thiel & Vásquez 2000, Hernández et al. 2001, Sepúlveda et al. 2003a,b).

Several macrofauna species have been reported from a variety of different biotic habitats. Of 251 species identified from biotic substrata (see references in Figure 13), 11.6% have been found in all three types of main biotic habitats (kelps, turf algae and suspension feeder reefs), 23.5% have been found in two types and 64.9% are only reported from one type of habitat. It must be emphasised that so far no single study has compared the associated fauna among the three main types of EEs, and there is little indication that there are habitat specialists that only occur in one type of biotic substratum. For example, Hernández et al. (2001) emphasise that several of the polychaetes found in patches of the barnacle *Austromegabalanus psittacus* also occur in other habitats. Similarly, Sepúlveda et al. (2003b) mention that many species from surrounding habitats associate with the reef-building polychaetes *Phragmatopoma moerchi*. They also emphasise that these biotic substrata may serve as recruitment habitat for some organisms. Similar observations led López & Stotz (1997), who found juvenile stages of many crustaceans and molluscs in *Corallina officinalis*, to

speak of a ‘transitory fauna’ in biotic substrata (see also Vásquez & Santelices 1984, Cerda & Castilla 2001). EEs may thus favour many mobile organisms that temporarily find shelter in these habitats (e.g., Vásquez et al. 2001b). In this context, Castilla et al. (2004b) reported that the intertidal ascidian *Pyura praeputialis* facilitates the extension of mobile macrofauna from the subtidal into the mid-intertidal zone, thereby enhancing local species richness.

The main functional groups of the organisms associated with biotic habitats are suspension feeders (32.4% of all species), grazers (25.2%) and predators (23.4%) (H. Bastias & M. Thiel unpublished data). Vásquez et al. (2001b) found very similar proportions of functional groups both in kelp holdfasts and on the surrounding hard bottoms. By offering structural protection, EEs are considered to mediate species interactions and buffer the effect of physical stress, often favouring suspension feeders (Wieters 2005, Valdivia & Thiel 2006). While the role of EEs in sustaining and promoting local biodiversity on intertidal and subtidal hard bottoms has been elucidated in numerous studies during the past decades (Vásquez & Santelices 1984, Villouta & Santelices 1984, Cerda & Castilla 2001, Sepúlveda et al. 2003a,b, Castilla et al. 2004b, Prado & Castilla 2006), relatively little is known about their trophic role on exposed rocky shores of northern-central Chile. Several studies have underlined the role of kelp forests as contributors of algal biomass to neighbouring habitats (Rodríguez 2003) and as feeding grounds for fish predators that consume understory algae and kelps (Angel & Ojeda 2001) or associated fauna (Núñez & Vásquez 1987, Palma & Ojeda 2002). Fish consumers are known to play an important role in kelp food webs of northern-central Chile (Angel & Ojeda 2001, Fariña et al. in press) but little is known about the food webs in other EEs. While most studies acknowledge the importance of EEs as habitat for associated organisms, their trophic efficiency (uptake of nutrients and suspended matter, release of dissolved and particulate organic matter) and the role of associated macrofauna in the tropho-dynamics of communities on intertidal and subtidal hard bottoms have not been thoroughly studied (see also Graham et al. 2007). The high biomass and diverse assemblage of associated consumers suggest that EEs are energetic power plants that concentrate and convert food resources in a similar way to kelp, seagrass or suspension feeder reefs in other parts of the world (e.g., Asmus & Asmus 1991, Lemmens et al. 1996, Wild et al. 2004).

Kelp forests

Giant kelp dominate shallow, subtidal rocky-bottom areas in temperate and cold seas down to a depth of ~40 m (Dayton et al. 1984, Harrold & Pearse 1987, Vásquez 1992, Graham et al. 2007). Kelp distribution from south Peru to central Chile is as follows: (1) intertidal rocky areas are dominated by *Lessonia nigrescens*, which forms belts along exposed coasts; (2) rocky subtidal environments are dominated by *Lessonia trabeculata* until 40 m in depth; (3) *Macrocystis integrifolia* forms shallow kelp beds from the intertidal zone to depths of about 15 m. In southern-central Chile, these species are gradually replaced by *Durvillaea antarctica*, which dominates the intertidal zone in wave-exposed areas (Hoffmann & Santelices 1997), and in subtidal areas by *Macrocystis pyrifera*, which occurs in both wave-exposed and –protected habitats (Buschmann et al. 2006a). While the two species from the genus *Lessonia* have an almost-continuous distribution along the entire Chilean continental coast, *Macrocystis integrifolia* has a fragmented distribution, forming patchy populations in northern Chile. In this zone *Lessonia trabeculata* and *Macrocystis integrifolia* coexist, but mixed kelp populations have segregated patterns of bathymetric distribution, *M. integrifolia* being more abundant in shallow areas (Vega et al. 2005). Local populations may vary from hundreds of metres to hundreds of kilometres in extent. The observed distribution patterns are the result of complex life-history strategies that interact with environmental factors such as spatial and temporal variation in water movement, nutrient availability and temperature (Buschmann et al. 2004b, V. Muñoz et al. 2004, Vega et al. 2005).

The kelp forest community

Kelp communities are highly productive (Dayton 1985), and they harbour a high diversity and abundance of invertebrates and fishes. Kelps, especially their holdfasts, constitute feeding areas, refuges against predation and bottom currents, spawning, settlement areas and nursery sites (Vásquez & Santelices 1984, Vásquez et al. 2001c, Vásquez & Vega 2005). Below the kelp canopy a wide diversity of turf algae exists, including several Corallinales, *Asparagopsis armata*, *Halopteris paniculata* and *Gelidium* spp.; several species of barnacles and other sessile invertebrates (*Pyura chilensis*, *Phragmatopoma moerchi*, *Aulacomya ater*) are also part of the associated species sheltered by the kelp canopy (Vásquez et al. 2001b,c, Vásquez & Vega 2004a). In contrast to the Northern Hemisphere, no large predators have been reported for southeastern Pacific kelp beds (Graham et al. 2007). Instead, invertebrate predators such as the muricid snail *Concholepas concholepas*, seastars (*Meyenaster gelatinosus*, *Stichaster striatus*, *Heliaster helianthus* and *Luidia magellanica*), and intermediate-size coastal fishes (*Cheilodactylus variegatus*, *Semicossyphus maculatus* and *Pinguipes chilensis*) dominate the predator guild in kelp forests from northern-central Chile (Vásquez 1993b, Vásquez et al. 1998, 2006). These predators feed on a diverse guild of herbivores, including sea urchins (*Tetrapygus niger* and *Loxechinus albus*), gastropods (*Tegula* spp. and *Fissurella* spp.), as well as fishes (*Aplodactylus punctatus*, *Girella laevis* and *Kyphosus analogus*) (e.g., Medina et al. 2004). These herbivore species graze on kelp and associated algae, regulating their abundance and distribution (Vásquez & Buschmann 1997, Vega et al. 2005, Vásquez et al. 2006). Marine mammals widely distributed in the coastal zone of the HCS, such as sea lions *Otaria flavescens* and sea otters *Lontra felina*, also use kelp beds as feeding areas.

Population dynamics and spatial distribution of kelps in northern-central Chile

The kelp species from northern and central Chile belong to the Laminariales, which have a complex life cycle with two morphologically different stages: one conspicuous stage, recognisable as kelp that produces spores (the sporophytes), and a microscopic stage comprising independent female and male plants (the gametophytes) that lead a hidden life in the benthos. Sporophytes are the product of gametic reproduction, which is triggered by environmental factors (temperature, irradiance, photoperiod, and nutrient concentrations).

The sporophytes themselves are reproductive year-round, but peak spore release has been observed during winter. Since spore survival in Laminariales is short, the dispersal range of kelps is generally assumed to be quite reduced (Graham et al. 2007); if spores do not settle within a relatively short period they die (Santelices 1990a). However, spores may survive in the guts of different herbivores (Santelices & Correa 1985, Santelices & Payá 1989) or as filaments in darkness (Santelices et al. 2002). Furthermore, fertile floating plants may act as spore carriers and thereby contribute to dispersal (Macaya et al. 2005).

Juvenile sporophytes of *Lessonia* recruit onto hard-bottom substrata during late winter–spring, and in the field are capable of producing spores after 6–8 months (Santelices & Ojeda 1984; see review by Edding et al. 1994). Interference by adult plants inhibits the intertidal recruitment of juvenile *L. nigrescens* in exposed habitats. Nevertheless, water movements produce whiplash effects (*sensu* Dayton et al. 1984) that gives protection against grazers, thereby promoting successful recruitment of sporophytes (Santelices & Ojeda 1984). In subtidal habitats abundance of grazers, currents and reproductive behaviour of two species of elasmobranchs (*Schroederichthys chilensis* and *Psammobatis scobina*) affect *Lessonia trabeculata* populations. Grazing modifies algal morphology, producing two morphotypes: shrub-like and tree-like morphs. Water movement affects these differentially and generates higher mortality on tree-like morphs (Vásquez 1992). Short distances between plants (or high densities) reduce the access of grazers to the holdfasts. The

whiplash effect of fronds and stipes pushes herbivores away from the plants, reducing grazing pressure. On the other hand, spawning of egg cases of elasmobranchs on *L. trabeculata* ties the stipes together, thereby reducing the whiplash effect and thus permitting grazers to approach kelp plants. Additionally, this 'tie effect' modifies plant shape toward the tree-like morph, and plants are more easily dislodged by water movement (Vásquez 1992).

Longevity of kelps from northern Chile in the field is not well known since they do not show any evident age-related structure. Nevertheless, individual *Lessonia* plants can survive in the field for as long as 5 yr (J.A. Vásquez personal observations), and *Macrocystis integrifolia* has been reported as a perennial species in northern Chile (Buschmann et al. 2004b). Several factors generate significant biomass loss in the field: grazing pressure, wave impact, and spore release, which takes place mainly during summer (Santelices & Ojeda 1984, Edding et al. 1994).

Lessonia and *Macrocystis* populations in northern-central Chile grow throughout the year but exhibit growth peaks during spring–summer (Buschmann et al. 2004b, Tala et al. 2004). Growth patterns are modified by wave impact, quantity and quality of light, water temperature and nutrient concentration (Buschmann et al. 2004b, Vega 2005). Local factors such as intraspecific interactions (Santelices & Ojeda 1984), herbivory (Vásquez & Buschmann 1997, Vásquez et al. 2006) and coastal upwelling events (González et al. 1998, Vásquez et al. 1998) can modify seasonal patterns of abundance and distribution (see also Graham et al. 2007). Large-scale phenomena such as ENSO produce interannual variability in abundance and could eventually generate local extinctions, as observed after the EN events of 1982–1983 and 1997–1998 (Soto 1985, Tomicic 1985, Vega 2005, Vásquez et al. 2006). Major impacts of EN were observed in kelp beds from lower latitudes (18–21°S). For example, a kelp bed occupying an area of ~40 ha at 18°S during the 1970s (IFOP 1977) disappeared as a consequence of EN 1982–1983 (Soto 1985) and has not recovered since. Similarly, during EN 1997–1998, the density of adult sporophytes on subtidal hard bottoms at 21°S decreased rapidly and linearly with increasing positive thermal anomalies (Figure 14). Six months later the site remained completely devoid of adult sporophytes, and no recolonisation occurred in the subtidal zone during the study period. In areas south of 23°S positive thermal anomalies registered during EN 1997–1998 had only limited effects on kelp beds (Figure 14). As a result, the spatiotemporal abundance patterns of *M. integrifolia* sporophytes in northern-central Chile is highly variable (Figure 14).

Kelp conservation and human activities

Many of the diverse kelp-associated species have significant socioeconomic importance for human populations along the coast in north-central Chile and have been subject to harvesting by local human communities since pre-Columbian times (Jerardino et al. 1992, Vásquez et al. 1996). Spatial and temporal dynamics of kelp beds are significantly affected by anthropogenic impacts produced by both intense harvesting and severe pollution with organic as well as mining waste (Faugeron et al. 2005; Vásquez & Vega 2005). *Lessonia nigrescens*, *L. trabeculata* and *Macrocystis integrifolia* are commercially exploited between 18°S and 32°S. These species account for >95% of landings of macroalgae and basically are used for alginic acid extraction. Until 2002, collected biomass in dry weight (dry wt) amounted to ~200,000 t, almost exclusively based on stranded kelps, resulting from natural mortality of plants with holdfasts that are weakened by grazing and then detached by strong bottom currents and waves. Since 2003, however, due to international needs for raw (dry) materials and also due to increasing demands for fresh algae (to sustain aquaculture of herbivorous invertebrates in northern Chile), harvesting of natural kelp increased to ~300,000 t dry wt per year. This has led to the recent implementation of new administrative rules in order to mitigate the impact on natural kelp populations. Regulations aim at the establishment of a sustainable kelp fishery, applying the following strategies: (1) harvest management (Vásquez 1995, 1999, 2006), (2) stock

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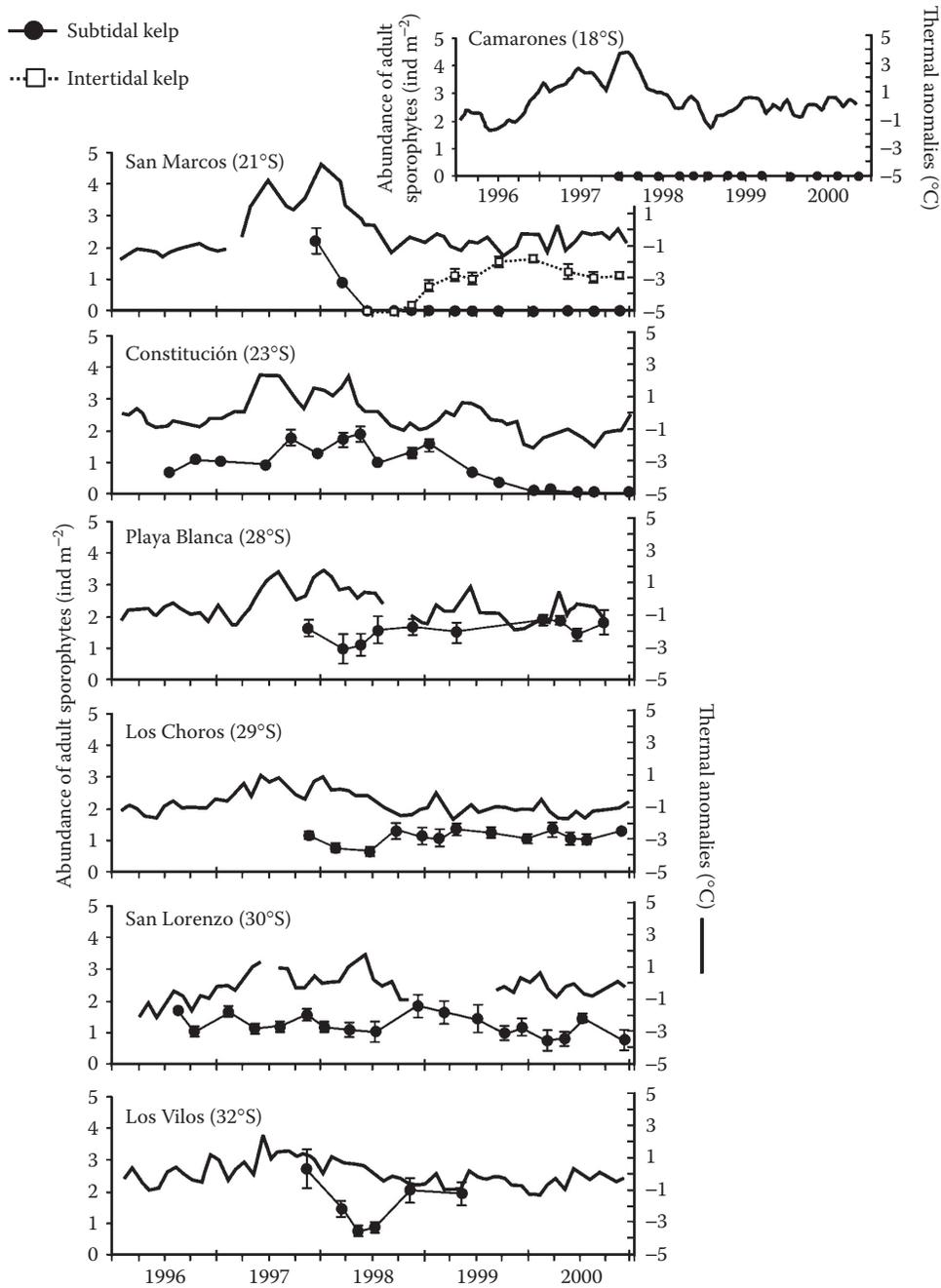


Figure 14 Temporal variation (between 1996 and 2000) of abundances of adult sporophytes of *M. integrifolia* (●) and thermal anomalies estimated *in situ* (line) over a latitudinal gradient in northern Chile. Note: At San Marcos, an intertidal kelp population appeared after the El Niño event (□), while the subtidal kelp bed did not recover. At Camarones (top) no sporophytes were observed during the study period. (Modified from Vega 2005)

enhancement (Vásquez & Tala 1995), (3) cultivation (Edding & Tala 2003, Westermeier et al. 2006, Gutierrez et al. 2006), and (4) conservation programmes including Marine Protected Areas (MPAs; CONAMA 2006). Considering the high variability of kelp populations in northern Chile, the limited dispersal capability of *Lessonia* species, and in particular the patchy distribution of beds of *Macrocystis integrifolia*, sustainable exploitation of natural kelp forests requires integrated management plans with continuous monitoring of standing stocks.

Export and import processes within the HCS

Kelp forests, as other EEs, strongly influence trophic fluxes in benthic environments (e.g., Graham et al. 2007). In the HCS, some of the most important trophic connections occur in the vertical direction, such as dissolved nutrients released from sediments into the water column, upwelling of nutrient-rich waters from subsurface layers to the sea surface, or POM sinking from the euphotic zone toward deeper water layers and finally to the sea floor. In addition, there exist numerous types of horizontal transfer of particulate or dissolved components between the marine and the terrestrial realm, between the benthic and the pelagic environment, or between benthic habitats. In the following section the importance, intensity and frequency of these exchange processes in the HCS of northern-central Chile are considered, with a focus on coastal habitats.

Exchange between realms

Exchange between the marine and the terrestrial environment occurs in both directions. Flux of materials toward the sea is via rivers, which (due to limited freshwater flow) is usually only of minor importance between 18°S and 30°S. In some areas in northern-central Chile, dissolved and solid components from human activities are continuously supplied to the marine environment, impacting local intertidal and subtidal communities (Vásquez et al. 1999, Gutiérrez et al. 2000, Lancellotti & Stotz 2004). During certain time periods (EN events or summer rains in the Andes highlands), river flow increases dramatically, transporting mainly sediments but also large quantities of terrestrial vegetation to nearshore coastal waters (Vásquez et al. 2001a). Shallow subtidal habitats along the coast of northern-central Chile are infrequently impacted by these mud flows (Miranda 2001, Vásquez et al. 2001a, Lancellotti & Stotz 2004), and it is considered likely that these impacts occur in parallel over a large geographic range.

In the reverse direction, several natural exchange mechanisms are relevant in the HCS, namely, energy transfer by seabirds and marine mammals from offshore waters to coastal habitats, which occurs in a highly concentrated manner on breeding or roosting sites. Additionally, some terrestrial vertebrates (rodents, lizards, songbirds) from coastal environments forage along the drift line or in the intertidal zone (Navarrete & Castilla 1993, Fariña et al. 2003a, Sabat et al. 2003). Most of these organisms maintain relatively stable territories along the coastline, and thus material transfer from the intertidal to the upper supralittoral zone is dispersed in space, but relatively continuous in time. The same process has been reported from coastal habitats in California, where populations of insects, spiders, lizards, rodents and coyotes are mainly maintained and modulated by the food subsidy from the marine environment (Polis & Hurd 1995, 1996, Polis et al. 1997).

Under certain conditions, marine resources are also transported toward the shore without the aid of biotic agents (invertebrate or vertebrate consumers defecating on land). Mortality of seabirds and marine mammals during EN events results in large numbers of animal carcasses accumulating on local beaches (e.g., Guppy 1906, Arntz & Fahrbach 1991). Similarly, during storm events, algae or benthic invertebrates are detached and cast onto the shore (González et al. 2001). These food bounties attract large numbers of terrestrial vertebrate scavengers but since supply is highly infrequent (e.g., Moore 2002), no quantitative estimates of material transfer during these events are available.

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Fisheries also contribute to the transfer of OM from the marine toward the terrestrial realm. This not only includes direct (extraction) but also indirect forms of transfer, such as by scavenging seabirds around fishing vessels at sea (Weichler et al. 2004) or in fishing ports (Ludynia et al. 2005). Populations of kelp gulls (*Larus dominicanus*) near main population centres in northern-central Chile depend to a large extent on these human-derived food sources, and they then distribute remains in terrestrial environments (Ludynia et al. 2005).

Exchange between environments

There is a wide range of exchange processes between the pelagic and the benthic environments. This includes, for example, supply of POM from the water column to soft bottoms where micro- and macroorganisms remineralise this POM, returning dissolved materials to the water column (Graf 1989, Marcus & Boero 1998, Dunton et al. 2005). Suspension feeders are important agents, which aid in transfer of suspended material (e.g., phytoplankton and kelp detritus) from the water column to the benthic system (Wolff & Alarcón 1993). In some of the bays of northern-central Chile dense stocks of natural or culture beds may significantly affect these fluxes (Uribe & Blanco 2001, Avendaño & Cantillán 2005). The intensity and direction of transfer can be affected by regional discontinuities in the oceanographic conditions (e.g., distance from upwelling areas), which influence the transport and flux of POM and nutrients (Graco et al. 2006). These processes are also exposed to large-scale temporal variations in oceanographic conditions (e.g., ENSO cycles) (Farías et al. 2004, P. Muñoz et al. 2004b). Fisheries in small fishing ports contribute POM in the form of fish remains to soft bottoms (Sahli 2006).

On hard bottoms, macroalgae and suspension feeders take up nutrients and suspended POM from the water column, returning algal remains, repackaged faeces or dissolved excretions to the water column. Most large kelps are continuously shedding senescent parts (e.g., Tala & Edding 2005). These authors estimated that annual export of shed plant detritus from a kelp forest of *Lessonia trabeculata* may amount to 18 kg wet wt m⁻². What proportion of this detritus remains suspended in the water column or sinks immediately to the bottom is not known at present. Kelp productivity shows some seasonal variation, but kelp detritus is supplied throughout the year, at least in northern-central Chile (Tala & Edding 2005). This suspended kelp detritus may also sustain the large proportion of suspension-feeding organisms on intertidal and subtidal hard bottoms (see also Intertidal and subtidal hard-bottom communities, p. 235ff. and Bustamante & Branch 1996). Little is known about the role of DOC released by kelp forests. It enhances bacterial populations (Delille et al. 1997) and contributes to foam lines at the sea surface, which are thought to play a role in propagule dispersal and survival (Meneses 1993, Shanks et al. 2003a). Foam lines are frequently observed along the coast of northern-central Chile.

Fish consumers also have an important role in energy transfer from benthic toward pelagic environments (Angel & Ojeda 2001). This transfer includes all feeding guilds of fishes from herbivores to omnivores and carnivores (Angel & Ojeda 2001). Studies of trophic coupling between hard bottoms and the water column have mainly focused on kelp forests and little is known about these trophic interactions in other hard-bottom communities (see also Intertidal and subtidal hard-bottom communities, p. 235ff.).

Exchange between benthic habitats

Exchange between neighbouring communities (NCs) occurs throughout the shallow subtidal zone. The form of materials exchanged between NCs and the direction of transport can be highly variable. Algal detritus exported from kelp forests contributes an important food source for animal communities on intertidal hard bottoms (Bustamante et al. 1995, Bustamante & Branch 1996, Rodríguez-Graña

Table 4 Different types of material transfer between communities within the HCS of northern Chile. Distances of transport increase with increasing length of line, intensity of transfer increases with increasing size, and frequency augments with increasing number of dots.

Material type	Agent	Distance	Intensity	Frequency	Reference
Between Realms TERRESTRIAL (T) –MARINE (M)					
Particulate inorganic matter (mining discharge)	River (T to M)	—	•	•••••	Lancellotti & Stotz 2004
Dissolved metals (mining discharge)	River (T to M)	—	•	•••••	Vásquez et al. 1999 Vásquez et al. 2000
Particulate inorganic matter (river floods)	River (T to M)	—	●	•	Miranda 2001
Organic matter (carcasses and algae)	Currents	—	●	•	Guppy 1906 Arntz & Fahrbach 1991
Organic matter	Terrestrial vertebrates (M to T)	—	●	•••••	Navarrete & Castilla 1993 Fariña et al. 2003a Sabat et al. 2003
Nutrients and dead biomass (food)	Seabirds (M to T)	—	●	•••••	Sanchez-Pinero & Polis 2000 Ludynia et al. 2005
Between Environments PELAGIC-BENTHIC					
POM & phytoplankton	Suspension feeders	—	●	•••	Uribe & Blanco 2001
POM (algal detritus)	Currents	—	●	•••	Bustamante & Branch 1996 Tala & Edding 2005
Between Benthic Habitats NEIGHBOURING COMMUNITIES					
POM (detached algae)	Currents	—	●	•••••	Rodríguez 2003 Tala & Edding 2005
Shell remains	Waves and currents	—	•	•••••	Bomkamp et al. 2004 Personal observations

Note: POM = particulate organic matter.

& Castro 2003). The transfer of large amounts of algal fragments from subtidal kelp forests toward the shore has been considered as a principal food source, structuring and maintaining macrofauna communities on sandy beaches (Colombini et al. 2000, Dugan et al. 2003). Transport of detached kelp plants or parts to aggregations of sea urchins in tide pools is considered to be an important trophic subsidy for these grazers (Rodríguez 2003). Arrival of kelp in the intertidal zone of northern-central Chile continues throughout the year, but highest quantities arrive from late spring until early autumn, also depending on the proximity to source habitats (Rodríguez 2003). The importance of kelp transfer to deeper subtidal habitats (for the Californian coast see, e.g., Kim 1992, Harrold et al. 1998, Vetter & Dayton 1998, 1999) or to the rocky subtidal zone has not been evaluated in the HCS, but given that the main kelp species are non-buoyant (*Lessonia* spp.), it is assumed that large fractions of detached kelp may be accumulating on deeper or wave-sheltered subtidal bottoms.

In addition to kelp detritus, hard-bottom communities also export large quantities of shell remains to NCs (Bomkamp et al. 2004). Along the coast of northern-central Chile, shell gravel is relatively common near exposed headlands (Ramorino & Muñiz 1970). These sediments are mainly composed of shell fragments from barnacles, sea urchins and bivalves, but source habitats, fluxes of these materials from hard bottoms to sediments and the relevance of local hydrography have not been examined.

Frequency and intensity of exchange processes

Exchange of nutrients or particulate matter among marine communities in northern-central Chile varies in frequency and intensity (Table 4). Some of the most important and frequent exchange processes in northern Chile occur in the vertical direction (sedimentation of POM, release of nutrients into the water column, upwelling of nutrient-rich waters). Horizontal transfer processes appear to be most intense and frequent in coastal habitats, such as, for example, supply of kelp detritus to NCs. In contrast to this relatively continuous exchange of material, depositions of terrestrial sediments to coastal waters or of dead plants and animals to local beaches appear to be some of the least frequent and unpredictable transfer events. When these events occur, their intensity is often so high (e.g., Arntz 1986) that they exceed the escape or ingestion capacity of the organisms in the receiving habitats. This can result in the destruction of local communities and the incorporation of materials to deeper sediment layers. Transfer of marine-derived materials in colonies of seabirds and sea lions is also very intense (and frequent), but in northern-central Chile cannot be utilised by terrestrial organisms due to lack of water. A similar effect is observed in the water column and sediments of the OMZ where recycling processes are suppressed due to the lack of oxygen (Graco et al. 2006). Thus the intensity of the fluxes, which overcome the recycling capacity of receiving communities, may favour the long-term storage of POM not only in shelf sediments (H.E. González et al. 2004a), but also in terrestrial, intertidal and subtidal habitats of the HCS (islands with seabird and sea lion colonies, sandy beaches, subtidal kelp accumulations). It appears to be important to estimate carbon and nutrient export (and storage) not only to shelf sediments but also to terrestrial soils and intertidal and subtidal bottoms along the HCS.

Propagule supply, dispersal and recruitment variability

Exchange of biological information (i.e., gene flow) depends on the dispersal ability of the organisms in question. Dispersal of individuals determines the scale at which species interact with the physical environment, the nature and consequences of the interaction with other species, the way in which they respond to perturbations and ultimately the selective forces and rates to evolve, speciate or go extinct. Because in most benthic habitats there is a predominance of species with complex life cycles, which include a free-swimming larval stage (Thorson 1950, Strathmann 1990), high dispersal capabilities are intuitively associated with most marine organisms. However, this is not a rule since coexisting with species with planktonic larvae there always exists a myriad of species with very limited dispersal potential, such as most macroalgae and direct developers or brooding species (Reed et al. 1992, Kinlan & Gaines 2003, Shanks et al. 2003b). Moreover and to further complicate things, many species use rafting as an alternative method of long-distance dispersal (Santelices 1990a, Thiel & Gutow 2005). Despite the early realisation of the high diversity of life cycles found in every marine habitat, the ecological consequences of such diversity on species interactions and on the structure and dynamics of benthic communities are only beginning to be unveiled (Kinlan & Gaines 2003, Leibold et al. 2004, Velázquez et al. 2005).

Methodological approaches to the study of dispersal

The study of dispersal in the ocean is fraught with methodological problems imposed by the difficulty of following the usually microscopic propagules over extended time. Indirect methods to estimate aspects of dispersal have been developed. For instance, the use of highly variable neutral DNA markers offers an unprecedented opportunity to estimate realised dispersal distances (Palumbi

1995, Kinlan & Gaines 2003, Palumbi 2003, Sotka & Palumbi 2006). Similarly, trace element microchemistry (elemental fingerprinting) (Swearer et al. 1999, DiBacco & Levin 2000, Zacherl et al. 2003) or stable isotope ratios (Herzka et al. 2002, Levin 2006) hold promise for identifying larval origin under specific environmental conditions. However, these techniques do not yet provide a quantitative measure of the fate of all propagules released from a focal location (i.e., the ‘dispersal kernel’). Therefore, spatially explicit connectivity among local populations, the type of information needed regarding the location of MPAs (Botsford et al. 1994, Lockwood et al. 2002, Kaplan 2006), remains tractable only through the combination of biophysical models linking larval attributes with advection-diffusion physical processes (Marín & Moreno 2002, Largier 2003, Siegel et al. 2003, Guizien et al. 2006, Kaplan 2006, Levin 2006, Aiken et al. 2007).

Studies of dispersal in HCS

Studies of dispersal within the HCS are scarce at best. Santelices (1990a) provides a review of dispersal in marine seaweeds and points out that most information comes from laboratory studies conducted under idealised hydrographic conditions or from rather anecdotal evidence of colonisation of new habitats. Studies conducted by incubating seawater samples have demonstrated the existence of a multispecific ‘spore cloud’ which is present year-round in coastal waters of central Chile (Hoffmann & Ugarte 1985, Hoffmann 1987). These studies showed the patchy and temporally variable nature of the spore cloud, but the dispersal distances and mechanisms involved are unclear. Considering the small size of spores (5–150 µm) and their short duration (a few hours, but it can be up to few days; Santelices, 1990a), stochastic turbulence diffusion probably plays a major role in shaping the dispersal kernels in algal dispersal. Nearshore advective currents within the dispersal scale of spores (e.g., tidal currents, breaking waves, internal tidal bores) cannot be ruled out, however. Recent studies by Bobadilla & Santelices (2005) conducted by sampling the water column with a semi-automated sampling device (Bobadilla & Santelices 2004), illustrate the great temporal variability in multispecific dispersal kernels for major algal groups and dispersal distances exceeding 100 m.

The most direct studies of dispersal of invertebrates in the HCS are restricted to species with short larval duration, such as tunicates (Castilla et al. 2002a,b, 2004a). These studies sampled larval distribution at distances from a unique adult population source. Quantitative aspects of dispersal for species with long-lived larval stages are virtually unknown for any invertebrate or coastal fish species in the HCS. Several physical processes that can increase offshore and alongshore advection, or instead increase retention of larvae near shore, have been described for the coast of Chile, such as upwelling filaments, cyclonic circulation in embayments, topographically controlled eddies and upwelling shadows and traps (Vargas et al. 1997, Marín et al. 2001, Castilla et al. 2002a, Escribano et al. 2002, Wieters et al. 2003, Narváez et al. 2004). These features undoubtedly influence dispersal of coastal species, potentially increasing self-recruitment (Swearer et al. 2002), but their effect on connectivity among adult populations of any species is hard to demonstrate. A few high-resolution 3-dimensional numerical models of currents in the coastal ocean have been developed and tested against physical data for different sections of the coast of Chile (Mesías et al. 2001, Aiken et al. 2007). Coupled with Lagrangian larval-tracking techniques these biophysical models can generate testable hypotheses about dispersal and connectivity in real biological systems (e.g., Aiken et al. 2007).

There is an urgent requirement to develop highly variable, neutral molecular markers such as microsatellites for algal and invertebrate species inhabiting the HCS system to improve the ability to infer dispersal distances over ecological timescales and to test hypotheses about connectivity (see also Population connectivity, p. 252ff.) derived from theoretical models.

Settlement studies in the HSC

A more tractable and directly related problem is the settlement and recruitment of species to a given habitat. Settlement is the process through which a spore or larva makes permanent contact with the benthic habitat (Keough & Downes 1982). Since most adults of benthic organisms are sessile or have limited movement, settlement marks the end of the effective dispersal phase. For brooding organisms with mobile adults or those that use rafting as a secondary dispersal mechanism this is of course not the case (Thiel & Haye 2006). Recruitment is the input of new individuals to the benthic population measured at some arbitrary time after settlement. Therefore, while settlement is expected to reflect the arrival or supply of propagules, recruitment can be substantially modified by postsettlement mortality. Of the considerable number of studies of supply ecology conducted in the HCS over the past decades, very few have come close to measuring settlement (Hoffmann & Ugarte 1985, Hoffmann 1987, Moreno et al. 1993a, 1998, Martínez & Navarrete 2002, Vargas et al. 2004, Lagos et al. 2005, Narváez et al. 2006), and most have actually examined recruitment at varying time intervals after settlement. The paucity of studies of settlement of marine algae, due largely to the enormous difficulties of identifying sporelings to species level (Hoffmann 1987, Santelices 1990a), has not permitted the identification of mechanisms involved in algal settlement patterns. On the other hand, using intertidal barnacles, mussels and several gastropod species as model organisms, a few larval transport mechanisms have been demonstrated in the central and southern HCS. At the locality of Las Cruces in central Chile, which has been characterised as an upwelling shadow (Kaplan et al. 2003, Wieters et al. 2003, Narváez et al. 2004), the onshore daily settlement of several invertebrate species is associated with conditions that favour the occurrence of internal tidal bores, which appear to be common in the area when the water column is well stratified (Vargas et al. 2004). These results suggest that, for a number of intertidal invertebrates, internal tidal bores (Pineda 1991, 1994a) can be an important mechanism of onshore transport. In contrast with results at some sites in the California upwelling ecosystem (e.g., Farrell et al. 1991, Wing et al. 1995a), studies at Las Cruces showed that settlement of invertebrates was not directly associated with upwelling-relaxation events, which occur throughout spring and summer over synoptic timescales. The suggestion here is not that the upwelling-relaxation transport model (e.g., Roughgarden et al. 1988, 1991, Wing et al. 1995a,b) plays no role in settlement and recruitment in central Chile, but rather that at Las Cruces larval transport toward the shore does not seem to be dominated by these mechanisms. Indeed, spatially intensive studies over a region of about 120 km around Las Cruces showed a clear mesoscale spatial pattern in barnacle settlement, apparently imposed by the topographic variability in upwelling intensity (Lagos et al. 2005). Thus, the spatial variability in upwelling intensity typical of central Chile (Strub et al. 1998, Broitman et al. 2001, Halpin et al. 2004) might influence the spatial position of the larval pool and probably affects the scales of dispersal of invertebrates, as suggested also by the study of spatial synchrony in recruitment of species with contrasting dispersal potential (Lagos et al. in review). Topographic effects on patterns of settlement and recruitment have also been reported for a variety of brachyuran crab species (A.T. Palma et al. 2006). Buoyancy fronts produced by river plumes, common from about 30°S to the south in the HCS, in conjunction with wind stress can also play a role in delivering larvae to shore (Vargas et al. 2006c). Narváez et al. (2006) also report on the effect of what they called 'large warming events', which occurred a few times in spring–summer in association with downwelling-favourable (northerly) winds. During these specific large warming events these authors observed significant synchrony in recruitment of several invertebrate taxa (decapods, gastropods, polychaetes, mussels and sea urchins), suggesting that larvae could be entrained in these advective fronts and delivered onshore. A roughly similar phenomenon has been observed around Valdivia in southern Chile, where southward and onshore movement of warm waters produced by winter

storms delivered larvae of several gastropod species to the shore (Marín & Moreno 2002, C.A. Moreno in a personal communication to S.A. Navarrete).

Few studies have directly and simultaneously examined the distribution of larvae in the plankton, physical processes and settlement onshore in the HCS. Even fewer have examined larval behaviour under field or laboratory conditions (Poulin et al. 2002a,b, Manríquez et al. 2004, Vargas et al. 2006a).

Patterns of recruitment and benthic communities

Systematic studies of recruitment of species in the HCS have focused on (1) characterising spatial and temporal variation in the arrival of new individuals for intertidal and a few subtidal species (e.g., Jara & Moreno 1983, Hoffmann & Santelices 1991, Stotz et al. 1991a, Camus & Lagos 1996, Martínez & Navarrete 2002); (2) relating these patterns with large-scale oceanographic anomalies, such as El Niño events (e.g., Moreno et al. 1998, Navarrete et al. 2002); (3) examining the effects of recruitment variability on population dynamics and recovery of local populations from physical, biological or human-induced disturbance (e.g., Santelices & Ojeda 1984, Moreno et al. 1993b, Duarte et al. 1996, Alvarado et al. 2001); (4) determining the consequences of recruitment variation on the nature and intensity of species interactions in the adult habitat (e.g., Navarrete & Castilla 1990, Moreno 1995, Navarrete et al. 2005, Wieters 2005); and (5) characterising the effects on the processes that regulate the dynamics of entire intertidal communities over large spatial scales (Navarrete et al. 2005).

The far-reaching ramifications of persistent variation in recruitment have been most amply demonstrated in recent studies that quantify patterns of recruitment over large temporal (years) and spatial (tens to hundreds of kilometres) scales. These studies are starting to shed light on, and find recurrent patterns in, the causes of the typically large, baffling and usually ‘unpredictable’ variation in coastal ecosystems. Studies along the California coast have found large-scale regularities in patterns of recruitment of sessile species that can help reconcile odd experimental results (Menge et al. 1994, Connolly et al. 2001, Menge et al. 2003). Studies in the HCS conducted by Navarrete et al. (2002, 2005) have evaluated the effects of variation in wind-driven upwelling on community regulation along 900 km of coastline between 29°S and 35°S during 72 months. Sharp discontinuities in upwelling regimes around 30–32°S produced abrupt and persistent breaks in the dynamics of benthic and pelagic communities over hundreds of kilometres (regional scales) (Figure 15A,B). Rates of mussel and barnacle recruitment changed sharply at 32°S, determining a geographic break in adult abundance of these competitively dominant species. Analyses of satellite images also corroborate the existence of regional-scale discontinuities in dynamics and concentration of offshore surface chl-*a* that had been previously described at coarser resolution (Thomas 1999, Thomas et al. 2001b). Intertidal field experiments showed that the paradigm of top-down control of intertidal benthic communities (Castilla & Durán 1985, Paine et al. 1985, Castilla 1999, Navarrete & Castilla 2003) holds only south of this geographic discontinuity. To the north, populations seem recruitment limited, and predators have negligible effects, despite attaining similarly high abundances. Thus, geographically discontinuous oceanographic regimes set bounds to the strength of species interactions and define distinct regions for the design and implementation of sustainable management and conservation policies along the HCS. Further ecological studies using molecular markers are needed to define the consequences of this variation for the genetic population structure of mussels and barnacles, as well as for other components of intertidal communities, many of which do not experience such a discontinuity in recruitment, despite having similar life histories and general biology (Figure 15C,D).

THE HUMBOLDT CURRENT SYSTEM OF NORTHERN AND CENTRAL CHILE

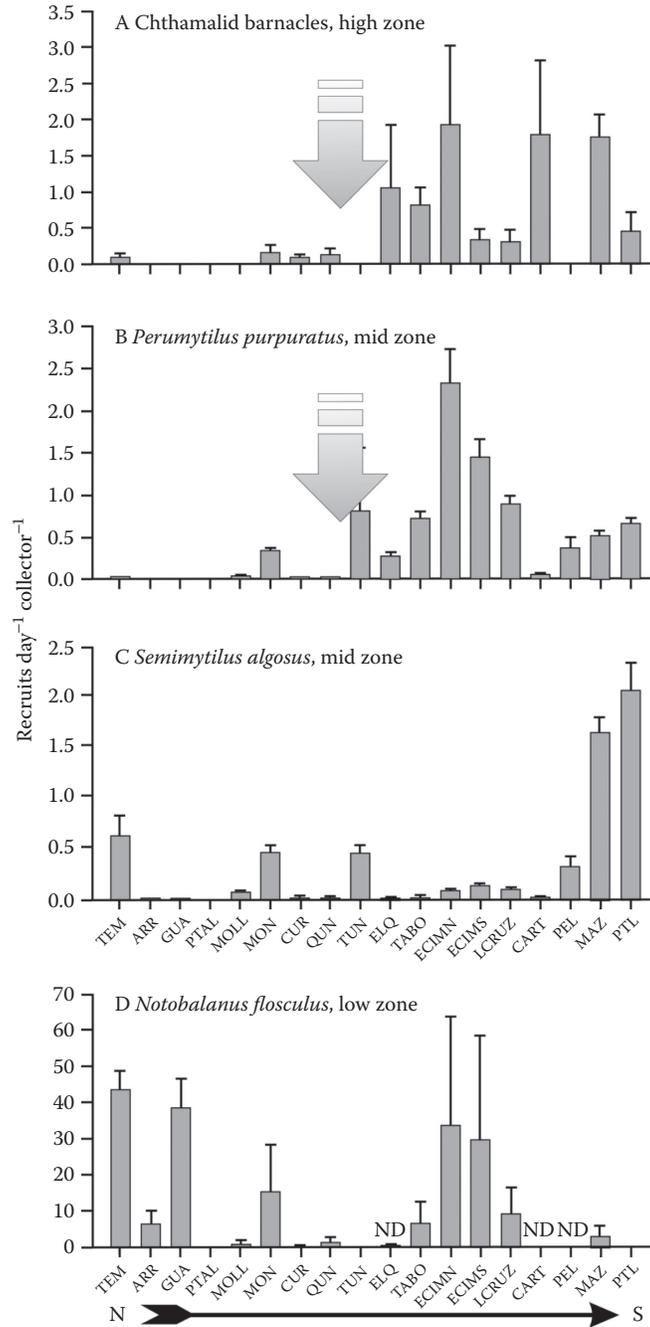


Figure 15 Average recruitment of intertidal invertebrates along the coast of central Chile at sites ordered from north to south, from ~29°S to 35°S. Data correspond to long-term (3–7 yr) averages per site of individuals found in replicated collectors that replaced monthly. The arrow in panels (A) and (B) indicates approximate position of regional discontinuity in intertidal chthamalid barnacles in the high intertidal zone and the dominant mussel *Perumytilus purpuratus* in the mid-zone. See Navarrete et al. (2005) for further details.

Population connectivity

Connectivity can be defined as the extent to which populations in different parts of a species' range are linked by exchange of larvae, recruits, juveniles or adults (Palumbi 2003) and determines the degree of cohesion of its genetic pool and the geographic structure of its genetic diversity. The intensity and geographical scale of connectivity within a species is given by the realised dispersal through active and passive mechanisms, which depend on species life-history traits and environmental characteristics. Among the numerous dispersal mechanisms reported in marine organisms, active swimming/crawling and planktonic larval transport, together with rafting and anthropogenic dispersal, are considered as the most relevant to achieve connectivity among local populations (Thiel & Haye 2006). Of particular relevance for connectivity of marine species are the temporal and spatial oceanographic characteristics such as currents, upwelling, water masses and gyres. For example, even though a species may have long-lived planktonic larvae, in a particular bay the larvae may not effectively disperse due to local larval retention (e.g., Swearer et al. 1999, Poulin et al. 2002a, Baums et al. 2005). In contrast, benthic species lacking dispersive larval stages can achieve long-distance dispersal by rafting or anthropogenic transport (Thiel & Haye 2006). Indeed, a recent study demonstrated that biogeographic patterns along the coast of South Africa are reflected in the genetic population structure of littoral organisms regardless of their dispersal stages (i.e., with or without planktonic larvae) (Teske et al. 2006). It seems particularly interesting to pursue this avenue in the HCS of northern-central Chile where no distinct biogeographic barriers but rather taxon-dependent breaks exist (see section on biogeography). Moreover, the unique characteristics of the HCS make it an interesting system to study the genetic connectivity of marine populations. Important characteristics of the system for genetic connectivity are its wide geographic extent and the oceanographic cyclic variations that lead to temporal and spatial changes in population size and distribution. It is expected that both life-history traits and oceanography play crucial roles in determining the realised dispersal of marine populations and thus their connectivity and the extent of their geographic ranges. Few population genetic studies have been published on marine species of the HCS, although there are several currently being developed on pelagic fishes, marine invertebrates and algae. Nevertheless, some predictions may be formulated and, where possible, validated through existing examples.

The pattern of genetic connectivity among local populations of a species determines the geographic structure of its genetic diversity (Figure 16). The frequency, intensity and geographical scale of dispersal within a species shape the resulting gene flow that counteracts the action of genetic drift and local selection. In this context, the intensity of genetic drift is principally determined by population dynamic processes such as population size variation, local extinction, recolonisation and founder effects, all intimately related to connectivity among populations. Therefore, acting both on gene flow and genetic drift, the different patterns of connectivity should result in different geographic structuring of the genetic diversity. Very high gene flow (at the scale of the geographic distribution of the species) leads to genetic homogeneity among local populations independently of the geographic distance. With lower levels of gene flow, different patterns of population genetic structure may result depending on the association between gene flow and geographic distance. If the magnitude of the gene flow is associated with geographic distance, which may be the case for many organisms with planktonic larvae, a genetic cline may form through the range of distribution, characterised by genetic differentiation being proportional to geographic distance, a pattern known as isolation by distance (IBD). This pattern will also be influenced by the direction and strength of the currents. If the magnitude of the gene flow is not strongly associated with geographic distance, which may be the case for organisms that disperse through passive mechanisms, the resulting pattern may be chaotic patchiness. So far two parameters have been

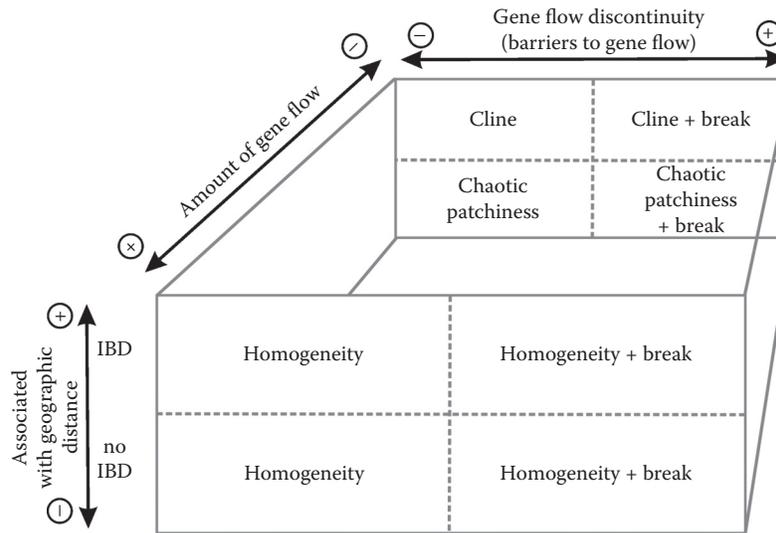


Figure 16 Summary of the patterns of genetic connectivity that may result from the interaction among intensity of the gene flow, its association with geographic distance and its geographic and temporal continuity.

considered: amount of gene flow and association with geographic distance. A third relevant parameter is the geographic and temporal continuity of the gene flow, from very continuous to a highly discontinuous gene flow that will lead to a break in the geographic structure of the genetic diversity. However, because the amount of time required to reach equilibrium between migration and drift is at least hundreds of times the generation time of a species, the genetic structuring may also reflect historic connectivity. Moreover, such equilibrium cannot be reached under high temporal variability in the pattern of connectivity.

Population connectivity studies in the HCS

A first and very general prediction for the HCS is associated with the long and continuous extent of the southeastern Pacific coast, without apparent geographic breaks. In this context, IBD and genetic homogeneity should be the prevalent patterns of geographic structure of the genetic diversity, particularly for organisms that achieve high gene flow through long-lived planktonic larvae or frequent rafting routes. The hairy edible crab *Cancer setosus*, which is of commercial interest, may represent an example of the above scenario. Gomez-Uchida et al. (2003), using allozymes and AFLPs (amplified fragment length polymorphisms), show genetic homogeneity over 2500 km of the Chilean coast for this species. The authors propose that this pattern may reflect the long-lived larvae (60 days) of *C. setosus*, the absence of geographic barriers and the oceanographic conditions (north and southward currents) of the area that allow effective mixing of larvae. A similar pattern of genetic homogeneity has been observed in pelagic fishes such as Chilean hake (*Merluccius gayi gayi*) between 29°S and 41°S (Galleguillos et al. 2000) and Chilean jack mackerel (*Trachurus murphyi*) between 20°S and 40°S (E. Poulin unpublished data). It is predicted that species with high connectivity and extensive geographic ranges may appear less affected by the oceanographic cyclic variations of the HCS, either because they suffer less population reduction or because they have a relatively rapid recovery after a disruptive event. Overall, these taxa may lose less genetic variability and show a faster ecological recovery after ENSO events.

Conversely, it is predicted that taxa with low dispersal potential will exhibit pronounced genetic structure and will be the most affected by the oceanographic variations. Genetic studies of the macroalga *Lessonia nigrescens* show that gene flow is limited among nearby populations (Martínez et al. 2003, Faugeron et al. 2005). Additionally, these authors found that 20 yr after the EN 1982–1983 event, which caused a massive mortality of *L. nigrescens* on 600 km of the coastline, northward recolonisation had only advanced 60 km (Martínez et al. 2003). *Lessonia nigrescens* is a good example of a species very vulnerable to oceanographic changes, specifically EN, and that may be continuously recovering from drastic population reductions and local extinction, never reaching migration–drift equilibrium. The genetic structure found for *L. nigrescens* corresponds to chaotic patchiness at a small geographical scale (tens of metres), reflecting recent population dynamic processes (years to tens of years) and life-history traits such as very low distance dispersal of propagules (Faugeron et al. 2005). Other species that show genetic differentiation at a small spatial scale are the alga *Mazzaella laminarioides* (Faugeron et al. 2001) and the edible and overexploited snail *Chorus giganteus* that has a low larval dispersal potential (Gajardo et al. 2002). For the edible and also overexploited scallop *Argopecten purpuratus*, Moragat et al. (2001) found both genetic and morphological differentiation between populations at the two protected sides of the Mejillones Peninsula (50 km apart) and discuss that it is probably due to currents that restrict the gene flow between the two localities.

It can further be predicted that biogeographic breaks will reflect strong barriers to dispersal and thus gene flow for species with low dispersal potential, leading to breaks in the geographic structure of the genetic diversity of species. It has been shown that along the northern Chilean coasts, habitat discontinuities can cause gene flow interruptions (e.g., Faugeron et al. 2001, 2005). Species with lower dispersal potential will be more vulnerable to breaks, while species with high potential of dispersal may not show evidence of a genetic break associated with a biogeographic break, as is the case of *Cancer setosus* (Gomez-Uchida et al. 2003). Even though for the HCS it has not yet been demonstrated that recognised biogeographic breaks correspond with the geographic distribution of the genetic diversity, it has been shown to be the case for other biogeographic regions such as Point Conception in the California Current System (e.g., Burton 1998, Wares et al. 2001).

Rafting may be a very advantageous dispersal mechanism for populations that suffer recurrent extinctions and recolonisations, mostly in the extent of the HCS where macroalgae with high floatability are very abundant. Once organisms are in a raft that has the potential to be in voyage for weeks or months, the rafting-mediated gene flow resulting may not be strictly associated with geographic distance and the resulting pattern of connectivity will depend on the intensity of gene flow, that is, if the rafting route is frequent, intermittent or episodic (see Thiel & Haye 2006). We predict that given the abundance of floating macroalgae, rafting routes along the Chilean coast may be intermittent or frequent, leading to patterns of genetic diversity ranging from chaotic patchiness to homogeneity. Ongoing studies of the isopod *Limnoria chilensis* may contribute to the validation of this prediction. These organisms have the potential to persist in rafts for long periods of time because they are brooders, have local recruitment and feed on the raft. It is interesting to mention that even though *Lessonia nigrescens* shows high genetic differentiation even at small spatial scales, the geographic distribution of the genetic diversity does not follow an IBD pattern, suggesting that some long-distance dispersal may occur, although it is not known whether it could be via free-living spores or on drifting fragments of mature thalli (Faugeron et al. 2005).

The HCS appears to be an interesting model for studying marine connectivity patterns in variable environments. Despite the general lack of such studies, recent and still unpublished results on pelagic fishes such as anchovies and sardines, and commercially exploited benthic marine invertebrates like the gastropod *Concholepas concholepas* and the bivalve *Mesodesma donacium*, support the existence of genetic homogeneity at large geographical scales as a consequence of the absence of contemporary biogeographical barriers along the HCS for species with high dispersal

potential. In general, it is expected that further studies of different biological systems will show that all the patterns of connectivity (Figure 16) are present along the HCS as a result of the interaction of present and past environmental conditions with species life-history traits.

Biogeography

Large-scale patterns in the HCS

The pioneer work by S.P. Woodward in 1856, which is probably the earliest biogeographical classification involving the southeast Pacific (Camus 2001, Harzhauser et al. 2002), was followed by a series of foundational studies (e.g., Dall 1909, Ekman 1953, Stuardo 1964, Viviani 1979, Santelices 1980, Brattström & Johanssen 1983, among others) that provided a consistent view of the major biogeographic features of the HCS temperate area (south of the tropical Panamian Province), based on physical gradients and patterns of endemism, richness and spatial turnover of species, and supported by subsequent studies (see reviews by Fernández et al. 2000 and Camus 2001). Overall, two main biotic replacements along the coast differentiate three biogeographical units (see Brattström & Johanssen 1983 and Camus 2001 for reviews on available classifications): (1) a warm-temperate biota extending from northern Peru (4–6°S) toward a variable, taxon-dependent limit in northern Chile (usually 30–36°S), often designated as Peruvian Province, and dominated by subtropical and temperate species; (2) a cold-temperate biota (also present in southern Argentina) extending along the fragmented coast of the Chilean archipelago from 54°S to about 41–43°S, corresponding to the Magellanic Province dominated by subantarctic and temperate species, exhibiting reduced wave exposure and an estuarine condition due to the dilution caused by high rainfall levels, glaciers and rivers (Ahumada et al. 2000); and (3) a transition zone between both provinces, characterised by strong numerical reduction of subtropical and subantarctic species at its southern and northern borders, respectively, rather than by diffusive overlap of biotas. However, many species occurring throughout this transition zone have a subantarctic affinity and a wide distribution in Chile (e.g., Menzies 1962, Castillo 1968, Alveal et al. 1973, Santelices 1980), probably facilitated by the HCS transporting cool water masses toward the north, which is also considered to be the main reason why the area lacks a definite biogeographic character.

Traditionally, the important physical changes around 42°S are considered to be external forcings that act as effective filters for dispersal, and with few exceptions, this zone represents the steepest induced transition along the HCS coast. Contrastingly, the northern limit of the transition zone is remarkably diffuse for the whole coastal biota (Figure 17) and highly variable depending on the taxon examined (Camus 2001), which has been attributed so far to the apparent absence of major physical discontinuities between northern Peru and Chiloé Island (e.g., Brattström & Johanssen 1983, Jaramillo 1987). Such variation mirrors a typical pattern of transitions (Brown & Lomolino 1998), due to differential attenuation rates among taxa related with their different dispersal ability and physiological tolerance. In fact, some particular taxa (e.g., peracarid crustaceans; Thiel 2002) show a well-defined overlap of northern and southern species with a gradual replacement pattern. On a wider taxonomic basis, however, the breaking points for different taxa do exhibit some latitudinal scattering throughout northern Chile, but they are significantly concentrated around 30°S and 33°S (see comparative analyses of animal and macroalgal taxa in Brattström & Johanssen 1983, Lancellotti & Vásquez 2000, Meneses & Santelices 2000, Santelices & Meneses 2000, Camus 2001). Notably, these multiphyletic breaks include southern and northern limits of species with very different life forms and ecological requirements, even involving pelagic groups (e.g., Antezana 1981, Hinojosa et al. 2006). This information strongly suggests that such breaks are not a passive outcome of dispersal and tracking of key environmental variables. For instance, recent work shows that latitudinal patterns of SST (the main causal factor invoked in most studies) fail to explain

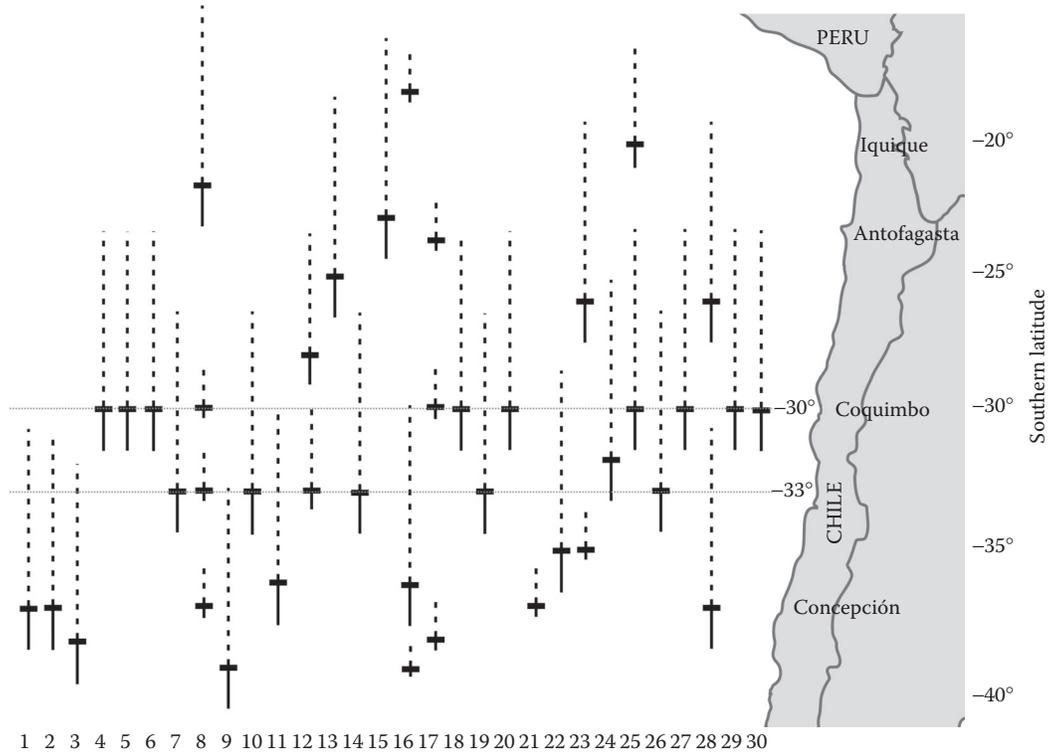


Figure 17 Break points of distribution along the north-central Chilean coast documented in 29 biogeographical classifications published between 1951 and 2006 (breaks outside the range 17–38°S are not shown). The figure includes a wide spectrum of animal and macroalgal taxa of varying hierarchical levels, life forms and habitats, and some classifications may partially overlap in one or more of these categories. Each classification is represented along an imaginary vertical axis in correspondence with the numbers at the bottom, where dashed lines denote the zones in which break points were found (each one marked by a thick horizontal dash), ranging from one to three break points per study. Horizontal lines highlight the latitudes 30°S and 33°S where break points tend to concentrate. Classifications (for numbers 1–10 and 11–22, see references in compilations by Brattström & Johanssen 1983 and Camus 2001, respectively): 1, Mollusca (Carcelles & Williamson 1951); 2, Foraminifera (Boltovskoy 1964); 3, Mollusca (Marincovich 1973); 4, several animal taxa (Knox 1960); 5, eulittoral organisms (Hartmann-Schröder & Hartmann 1962); 6, intertidal Mollusca (Dell 1971); 7, benthic animals (Semenov 1977); 8, several animal taxa (Viviani 1979); 9, Anthozoa (Sebens & Paine 1979); 10, several animal taxa (Brattström & Johanssen 1983); 11, benthic macroalgae (Santelices 1980); 12, Bryozoa (Moyano 1991); 13, fishes (Mann 1954); 14, Isopoda (Menzies 1962); 15, several animal taxa (Ekman 1953); 16, several animal taxa (Balech 1954); 17, planktonic Euphausiids (Antezana 1981); 18, Asteroidea (Madsen 1956); 19, macroalgae (Alveal et al. 1973); 20, sandy beach Isopoda (Jaramillo 1982); 21, Porifera Demospongiae (Desqueyroux & Moyano 1987); 22, several invertebrate taxa (Lancellotti & Vásquez 1999); 23, demersal fishes (Sielfeld & Vargas 1996); 24, littoral Teleostei (Ojeda et al. 2000); 25, Phaeophyta (Meneses & Santelices 2000); 26, Rhodophyta (Meneses & Santelices 2000); 27, several animal and algal taxa (Camus 2001); 28, Peracarid crustaceans (Thiel 2002); 29, benthic Polychaeta (Hernández et al. 2005); 30, pelagic barnacles (Hinojosa et al. 2006).

variations of mollusc diversity along the HCS, which would be determined by shelf area (Valdovinos et al. 2003), while the distribution of some littoral species appears more related to regional variations in temperature trends (Rivadeneira & Fernández 2005). Thus, the transitions in northern Chile are

not readily explained simply by the contact between warm and cold biotas, and proper explanations will require a multivariate, integrative approach and an exploration of possible external forcings.

The role of past and present processes in northern-central Chile (18–35°S)

Different lines of historical and ecological evidence suggest that northern-central Chile constitutes a very complex and dynamical biogeographic scenario. Clearly, present-day patterns are not divorced from physical changes related to the origin and installation of the cold HCS during the Tertiary or from subsequent Quaternary fluctuations (e.g., see Villagrán 1995, Hinojosa & Villagrán 1997, Villa-Martínez & Villagrán 1997, Maldonado & Villagrán 2002). The establishment of the HCS had involved both the northward advance of the subantarctic biota and the northward retraction of a former tropical/subtropical biota (Brattström & Johanssen 1983, Camus 2001), with consequences that may persist until the present, reflected in the heterogeneous character of the northern biota. For instance, 10 of the nowadays most common bivalves in northern Chile exhibit upper thermal tolerances exceeding the highest temperatures recorded during EN events in the past century (Urban 1994), which is unexpected for species evolving in a cold upwelling system. At least one of them (*Argopecten purpuratus*) is thought to be a relict of the Miocene tropical/subtropical fauna (Wolff 1987). Such physiological ‘anomalies’ suggest the presence of an inertial faunistic component within the modern northern biota (i.e., remnants of the former warm fauna that escaped the forced retraction to lower latitudes, and maintained their warm-water characteristics facilitated by recurrent post-Miocene warming events such as EN) (Wolff 1987). In comparison, the marine flora appears more homogeneous and dominated mainly by subantarctic species, while tropical/subtropical species are virtually absent (Santelices & Meneses 2000). For instance, some common and ecologically important kelp species are not only more sensitive to warming episodes but also their upper thermal tolerance varies in accordance with the thermal latitudinal gradient (Martínez 1999).

In this regard, the northern fauna underwent repeated distributional alterations in the past associated with climatic fluctuations. Some of them involved the simultaneous range retraction and expansion of different species (e.g., Ortlieb et al. 1994), but more often the occurrence of tropical/subtropical fauna related to warming (EN-like) events in the Pleistocene (e.g., Ortlieb 1995) and Holocene (e.g., Llagostera 1979). Moreover, Neogene processes related to the establishment of the modern upwelling system in the HCS (e.g., shallowing of the OMZ) provoked a mass extinction of bivalve molluscs (>75% of species), with lasting impacts on their current distribution patterns and biological characteristics (Rivadeneira 2005), and similar effects have been suggested for the polychaete fauna (R.A. Moreno et al. 2006a). Notwithstanding, the causal relationships between historical events and current distribution patterns in northern Chilean waters remain largely unexplored, although their importance may be overwhelming.

On the other hand, modern processes also have strong influences in northern Chile, particularly interannual fluctuations related to ENSO, which, however, should be looked at retrospectively, acknowledging the frequency and importance of EN-like events throughout the Holocene (e.g. see Maldonado & Villagrán 2002). Strong EN events can modify the taxonomic composition of littoral communities (e.g., Arntz 1986, Castilla & Camus 1992, Camus et al. 1994, Vega et al. 2005, Vásquez et al. 2006) and the geographical occurrence of many species including key structural components such as intertidal and subtidal kelps (e.g., *Lessonia nigrescens*, *L. trabeculata* and *Macrocystis pyrifera*). Short-term modifications of community composition during EN occur through local extinctions and invasions, depending also on local conditions, which either favour or prevent their occurrence (Arntz 1986, Camus et al. 1994, Martínez et al. 2003, Castilla et al. 2005a). Moreover, the impacts on key species may scale up to produce long-term biogeographic changes, as exemplified by the dramatic effects of the 1982–1983 EN event on the intertidal kelp *Lessonia*

nigrescens (for similar cases in subtidal kelp beds see Vega et al. 2005, Vásquez et al. 2006 and the discussion of EN effects here). *Lessonia nigrescens* plays a key role in Chilean rocky shores (e.g., Ojeda & Santelices 1984, Castilla 1988, Santelices 1990b), and its presence/absence has direct effects on community organisation and diversity. The kelp suffered a regionally correlated local extinction (also involving the loss of its rich holdfast fauna) along 600 km of coastline, which left a few and highly isolated patches, provoking a strong alteration of its geographical population structure (Camus 1994b, Martínez et al. 2003). The regional recovery process of *L. nigrescens* was slow, more effective toward higher latitudes, and only partial as it failed to re-establish populations in northernmost Chile (Castilla & Camus 1992). Twenty years later, northward recolonisation advanced less than 60 km, and some recovered populations lost >50% of their genetic diversity exhibiting significant IBD (Martínez et al. 2003). These extinctions also lead to transient changes in biotic interactions within the community (see El Niño section), which had negative effects on local kelp recruitment and contributed to its slow recovery (Camus 1994a). Additionally, *Scurria scurra*, a limpet living on the stipes and holdfasts of *Lessonia nigrescens* (Muñoz & Santelices 1989), suffered a concomitant extinction. In southernmost localities, *Scurria scurra* recolonised and re-established its association with the kelp within 1 yr following the EN event, but in some northernmost localities it failed to do so for at least 11 yr (Camus 1994b) (and remains absent in some places until now; P.A. Camus unpublished data). Overall, the ecological, biogeographical and evolutionary consequences derived from the recurrent extinction-recolonisation dynamics undergone by different species in northern Chile are not yet fully understood. However, it may be argued that they promote changes in spatial patterns of genetic diversity and gene flow, increase between-community diversity, and affect the dynamics of endpoints of distribution, leading to unstable biogeographical limits (Camus 2001, Thiel 2002). This last effect can be reinforced by the transient or permanent invasion of warm-water species favoured by EN episodes (e.g., Soto 1985, Tomicic 1985, Arntz 1986, Castilla et al. 2005a, Coloma et al. 2005, Arntz et al. 2006), thus contributing to the mixed biogeographic character of the northern Chilean biota. However, while some general conclusions can be drawn at this level, a proper understanding of large-scale patterns will need to distinguish their historical and ecological components and consider the physical-biological coupling generating differential responses among taxa. In this regard, the factors affecting dispersal and recruitment deserve special attention. Even though EN is known to be related in varied ways to the recruitment of coastal species (e.g., Soto 1985, Glynn 1988, Vega et al. 2005), in northern Chile its effects on dominant littoral species may be negligible or highly specific, with no clear association with interannual variations (Navarrete et al. 2002). Both mesoscale and regional factors related to the spatial structure of upwelling dynamics seem promising to explain such recruitment variations (e.g., Lagos et al. 2005, Navarrete et al. 2005). Additionally, the spatiotemporal dynamics of the OMZ (e.g., Morales et al. 1999, Palma et al. 2005) and the mesoscale eddy activity bounding coastal ecosystems (Hormazábal et al. 2004) may both play a significant role in understanding the dynamic connection between oceanographic processes and biogeographic patterns.

El Niño-La Niña in coastal marine communities

The El Niño Southern Oscillation (ENSO) is the largest modern source of interannual variability in the ocean-atmosphere system (e.g., Wang et al. 1999) and, even though its effects are stronger in the tropics, it significantly affects marine life in northern Chile. The ENSO cycle has been a crucial factor in the global climate for at least the past 130,000 yr (Cane 2005), showing continuous, although variable, activity during the last 12,000 yr (Moy et al. 2002); regionally, it has had a major influence on the Chilean coast since the Holocene (e.g., see Ortlieb et al. 2000, Maldonado & Villagrán 2002; see also Biogeography, p. 255ff.). This suggests that coastal communities in northern Chile have continuously been shaped by impacts of EN events (Camus 1990, 2001).

Properties of coastal waters in northern Chile are primarily driven by remote equatorial forcing, which can provoke strong changes in PP due to the availability of nutrients and essential trace elements, corresponding to ENSO cycles (Takesue et al. 2004). Such alterations can trigger a complex chain of biological effects derived from bottom-up controls and physiological constraints, which may involve several levels of biological organisation at different spatial scales, during and between EN.

The dramatic and widespread impacts of EN 1982–1983 on coastal communities of northern Chile allowed the identification of biological changes associated with ENSO such as bathymetric or latitudinal migrations, invasion by exotic species, behavioural alterations, reproductive and recruitment failures, increasing population abundance, population decrease due to mass mortality, and in the most severe cases local population extinctions (e.g., see Soto 1985, Tomicic 1985, Arntz 1986, Glynn 1988, Camus 1990, Castilla & Camus 1992, Sielfeld et al. 2002, Vega et al. 2005, Arntz et al. 2006, Vásquez et al. 2006). As a whole, these impacts affect all kinds of taxa and environments, although with clear species- or site-specific components (e.g., in northern Chile none of these effects involves either an entire taxonomic group or the whole suite of species from a given place; e.g., see Soto 1985, Tomicic 1985). Moreover, the type and magnitude of impacts, as well as the range of affected taxa, may vary from one event to another, depending both on the strength of the event and the type of physical-biological couplings that may take place (e.g., see Navarrete et al. 2005). On the other hand, some biotic modifications may occur, or have simultaneous effects, at both local and regional scales (Camus 1994a, 2001, Vega et al. 2005, Vásquez et al. 2006), as observed also in the northeast Pacific (Edwards 2004). Additionally, from a socio-economic perspective, the increase or decrease in abundance or diversity of fisheries resources at some places may be certainly interpreted as positive or negative effects, respectively (e.g., Arntz 1986). However, from an ecological point of view, it would be as yet uncertain to qualify such changes in the same terms, even for species with no recognisable importance with variations that may have unknown or unpredictable consequences for the community.

Thus, simple generalisations on the ecological impacts of EN in northern Chile may still be inappropriate, except at very specific levels. This situation is mainly because of (1) the lack of long-term and systematic biological observations encompassing several events, preventing robust comparisons before, during and after EN conditions, and (2) the irregularity of ENSO itself (e.g., Wang et al. 1999) and the lack of correlation between EN and LN in their strength and duration (e.g., Kerr 1999). Nonetheless, ENSO impacts are indisputably relevant in the ecology of coastal communities in northern Chile.

One of the key aspects needed to understand EN effects is its recurrent impact on ‘engineer species’ (*sensu* Jones et al. 1994) such as kelps, which play a crucial role for the diversity, complexity, structure and functioning of coastal communities along the southeast Pacific (Graham 2004, Vega et al. 2005, Vásquez et al. 2006). Local extinction of kelps is frequent during strong EN events (Camus 1994a,b) such as the 1982–1983 episode, when intertidal populations of *Lessonia nigrescens* and *Macrocystis integrifolia* disappeared from the area between 10°S and 21°S and so did the invertebrate community associated with their holdfasts (Soto 1985; see also Biogeography, p. 225 ff.). Concurrent and dramatic impacts were reported during the same event (Soto 1985), affecting ecologically important species of ascidians (e.g., *Pyura chilensis*), seastars (e.g., *Stichaster striatus*, *Heliaster helianthus*) and several fish species, most of them associated with kelp beds. However, the implications of these impacts, both at population and community levels, remain largely unknown.

A long-term series of subtidal community dynamics during variable ENSO conditions (1996–2005) has been recently published (Vásquez et al. 2006). Although the EN 1997–1998 was catastrophic and produced local kelp extinctions on the coasts of Chile and Peru (Fernández et al. 1999, Godoy 2000, Martínez et al. 2003), site-dependent conditions allowed the persistence of

some kelp assemblages of *Macrocystis integrifolia* and *Lessonia trabeculata* around 24°S (Martínez et al. 2003, Vega et al. 2005). These effects would be related to the frequency and intensity of local coastal upwelling (González et al. 1998, Lagos et al. 2002), which minimised the impact of warming and retained high concentrations of nutrients within the coastal environment (Takesue et al. 2004). A long-term analysis of the structure and organisation of kelp communities in northern Chile (Vásquez & Vega 2004b, Vásquez et al. 2006), which included EN and LN events, showed that the abundance of *Macrocystis integrifolia* (1) increased significantly during EN 1997–1998, (2) decreased during LN 1999–2001, dropping nearly to zero in 2000, and (3) became reestablished and recovered during a period of positive thermal anomalies in 2002–2003 (Figure 18). This pattern

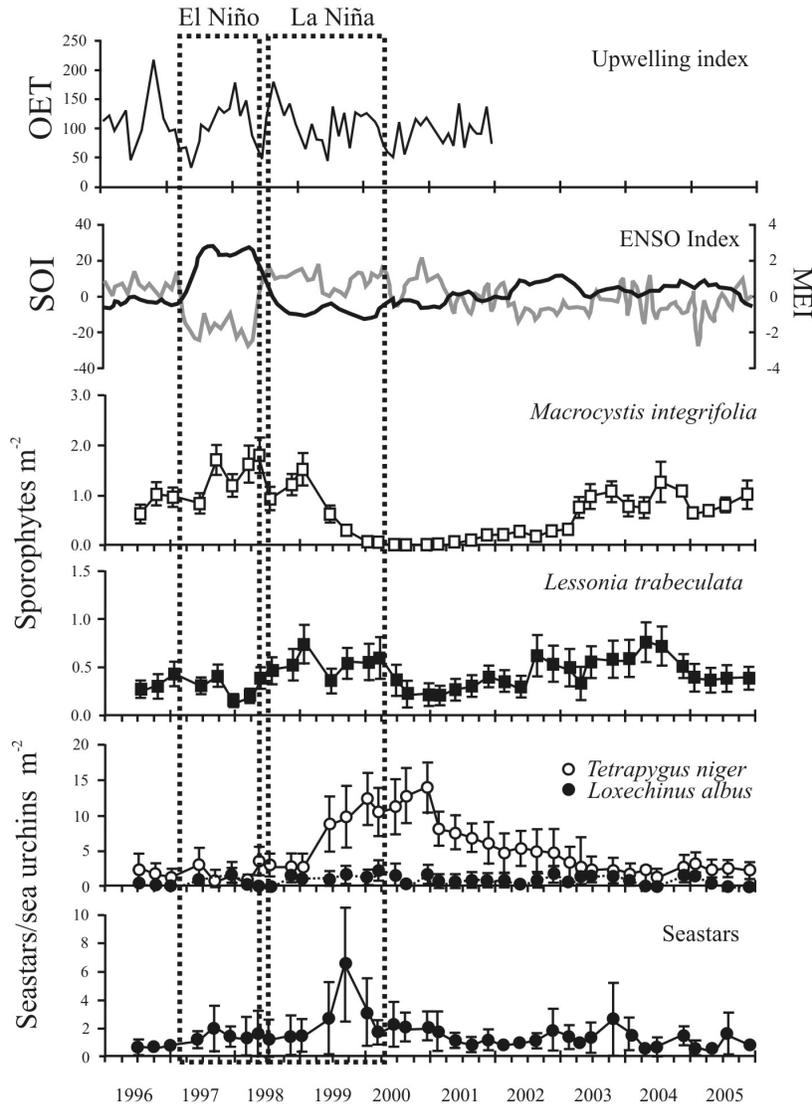


Figure 18 (A) Upwelling index (Offshore Ekman Transport OET), (B) ENSO index (Southern Oscillation Index SOI-grey line and Multivariate ENSO Index MEI-black line), (C) temporal variability of *Macrocystis integrifolia*, (D) *Lessonia trabeculata*, (E) benthic grazers, and (F) benthic predator densities, including El Niño 1997–1998 and La Niña 1999–2000.

was different from that recorded on the California coast, where the rapid recovery of *M. pyrifera* following EN 1997–1998 was favoured by the establishment of a cold period (1998–2000) and the survival of sporophytes in deep environments (Ladah et al. 1999; Edwards 2004). In northern Chile, the recolonisation rate of kelp assemblages occurred comparatively slowly (Martínez et al. 2003; see also Population connectivity, p. 252ff. and Biogeography, p. 255ff.), even though cold conditions prevailing during 1998–2000 enhanced the upwelling effect. In this regard, the slow recovery of *Lessonia nigrescens* after EN 1982–1983 (Castilla & Camus 1992) appeared more related to biotic constraints: recruitment was strongly reduced by a combination of postsettlement grazing and inhibition by encrusting coralline algae, while erect coralline algae played a key role as facilitators, allowing the kelp some escape from grazers and space competitors (Camus 1994a).

On the other hand, the decreased abundance of *Macrocystis integrifolia* was caused by a significant reduction in the adult plant population and the lack of recruitment of juvenile sporophytes (Figure 18). Thus, the disappearance of the *M. integrifolia* population occurred 2 yr after EN 1997–1998 and was inversely correlated with a population increase of the sea urchin *Tetrapygus niger* (Figure 18). In contrast, information from other areas of the southeastern Pacific during EN 1997–1998 showed that superficial warming decreased the abundance of kelp on shallow bottoms, inducing migrations of grazers to deeper zones (Fernández et al. 1999, Godoy 2000, Llellish et al. 2001). In northern Chile, during EN 1997–1998 and LN 1998–2000, different events favoured the increase of sea urchin populations during the cold phase, including (1) induction of mass spawning due to increases in SST and persistence of upwelling events, (2) reduction in density of adult seastars, and (3) changes in the feeding behaviour of the seastar *Heliaster helianthus*, one of the most important benthic predators on Chilean and Peruvian coasts (Tokeshi & Romero 1995b, Vásquez et al. 2006) (Figure 18). Thus, the long-term study of subtidal communities suggests that different bottom-up and top-down factors might control ecosystem changes in northern Chile, including (1) the intensity and frequency of upwelling, which may buffer the positive thermal anomalies of SST and maintain high nutrient levels, favouring kelp persistence during EN events; (2) site-dependent oceanographic conditions, which may generate optimal conditions for spawning, larval development, and recruitment of echinoderms during and/or after EN events; (3) an overall abundance increase of carnivores which is correlated with an abundance decline of the most conspicuous grazers; (4) population dynamics of adult seastars and sea urchins which may become decoupled during EN events; (5) species-specific population dynamics of some predator species (e.g., *Luidia magellanica*), and changes in dietary composition in others (e.g., *H. helianthus*), which may promote population increase of its prey, the urchin *Tetrapygus niger*, during EN events; and (6) changes in abundance of *T. niger*, which might be a key factor controlling the development of two alternate states: environments dominated by kelp beds versus barren ground areas.

In a wider context involving both subtidal and intertidal environments, EN impacts can be summarised as a large-scale bottom-up effect influencing various (and as yet difficult-to-predict) levels of marine food webs. However, this is just the initial path for most impacts, and top-down effects should not be neglected (e.g., see Nielsen & Navarrete 2004). Future research on EN impacts could consider at least five aspects related to the variability of biological effects, which may serve as guidelines or study framework: (1) the southward intensity attenuation of EN signals produces a latitudinal impact gradient, with reduced effects toward higher latitudes (e.g., Castilla & Camus 1992, Martínez et al. 2003); (2) in the spatiotemporal context, many effects are episodic and/or local (e.g., abundance variability), and some others may propagate their effects to larger spatial scales (e.g., distribution changes, local extinctions), being highly persistent over time (e.g., see Camus et al. 1994); (3) on a taxonomic basis, some taxa are recurrently affected (e.g., kelps), others exhibit no significant impacts (e.g., chlorophytes), and some taxa can be more affected in their reproduction while others in their recruitment (e.g., Camus 1994a, Navarrete et al. 2005, Vásquez et al. 2006); (4) the genetic and evolutionary consequences of recurrent phenomena such as mass

mortalities, extinction-recolonisation processes, and variations in population connectivity are presumably of critical significance, but they are just beginning to be explored (e.g., see Martínez et al. 2003; see also Population connectivity on p. 252ff. and Biogeography, p. 255ff.); and (5) interannual variations related to EN and LN may be strongly related to both small-scale processes such as the Madden-Julian Oscillation (Madden & Julian 1971) and large-scale processes such as the Pacific Decadal Oscillation (PDO; e.g., Trenberth & Hurrell 1994, Zhang et al. 1997) or the Antarctic Oscillation (e.g., Gong & Wang 1999), with possible biological implications for benthic community dynamics that are virtually unknown.

Up to now, the ecological knowledge of EN impacts on the marine communities from northern Chile continues to be mainly descriptive, focused on a reduced number of species and places. Nonetheless, prior studies have shed some light on the wide biological scope and geographical extent of such impacts and the need for comparative, multiscale and long-term approaches to obtain meaningful results.

Physiological adaptations of marine invertebrates

Physiological variation is the result of genetic, developmental and/or environmental influences (Spicer & Gaston 1999). Thus, physiological diversity and adaptations are linked to environmental characteristics and variability. The understanding of how living organisms function (i.e., their physiology) is aided by comparing the way different animals deal with environmental constraints (Schmidt-Nielsen 1997).

Major environmental factors affecting the animal's physiology are temperature, oxygen and energy (food) availability. The HCS in northern-central Chile is an interesting scenario for running physiological studies due to changing environmental characteristics, such as (1) the occurrence of a latitudinal temperature gradient, (2) extended zones with permanent and/or seasonal upwelling (cold seawater temperature and low oxygen content), (3) some closed bays with relatively high temperatures (e.g., Antofagasta Bay) compared with the surrounding areas and (4) the occurrence of thermal anomalies like ENSO. The HCS is characterised also by the occurrence of oxygen-minimum waters, where physiological adaptations of organisms should be expected, even of species from shallower (10–50 m) waters, which may occasionally be confronted with low oxygen concentrations (when there is upwelling of oxygen-deficient waters). Surprisingly few studies are available on physiological adaptations to hypoxic conditions of benthic organisms from the HCS. One of these studies was the characterisation of the pyruvate oxidoreductase enzymes involved in the biochemical adaptation to low oxygen conditions in nine benthic polychaetes from the HCS (González & Quiñones 2000). Pyruvate oxidoreductase enzymes permit the metabolism to produce adenosine triphosphate (ATP) at high rates under environmental or physiological hypoxic conditions (Livingstone 1983). Interestingly, these enzymes were found to be more numerous and with different pyruvate consumption rates in the most abundant and worldwide distributed polychaete species (*Paraprionospio pinnata*) (González & Quiñones 2000). Another study of biochemical adaptations to hypoxic conditions in the HCS was done on two key species (in terms of trophodynamics and abundance) of this system, the euphausiid *Euphausia mucronata* and the copepod *Calanus chilensis* (González & Quiñones 2002). The enzyme lactate dehydrogenase (LDH, a key enzyme of the anaerobic pathway) from *Euphausia mucronata* was two orders of magnitude higher than that of *Calanus chilensis*. Higher activities of the LDH indicate higher anaerobic capacities, and this may enable *Euphausia mucronata* to conduct daily vertical migration through the oxygen-minimum layer (see also Zooplankton consumers, p. 214ff). In contrast, low LDH activities restrict *Calanus chilensis* to oxygenated waters (González & Quiñones 2002). The importance of the interaction between oxygen and temperature has been explored in recent studies of the brooding behaviour of decapod crabs (Baeza & Fernández 2002, Fernández et al. 2006b).

Closed bays with relatively high temperatures and productivity in the HCS offer suitable conditions for the permanence and reproduction of the scallop *Argopecten purpuratus*, a species more characteristic of warm waters. An increment of 2.5°C in bottom temperatures (normally 15.5°C) during EN 1982–1983 in Tongoy Bay (30°S) augmented dramatically gonad mass and spawning, and as a consequence spat (juvenile) collection exceeded levels from previous years by 300% (Illanes et al. 1985). However, total gonadal levels of lipids and proteins increased markedly in *A. purpuratus* conditioned for reproduction at 16°C, but these increases were less pronounced at 20°C (Martínez et al. 2000). Moreover, during gonad maturation muscle carbohydrate levels dropped considerably, as well as the activity of a pyruvate oxidoreductase, the enzyme octopine dehydrogenase (Martínez et al. 2000). Muscle carbohydrate (i.e., glycogen) and glycolytic enzymes have been shown to decrease greatly in other scallop species such as *Chlamys islandica* and *Euvola ziczac* (Brokordt et al. 2000a,b). This leads to a decrease in muscle metabolic capacity and thus in escape capacities, which is facilitated by muscle contractions. A reduction of escape capacities during reproduction has been observed in *Argopecten purpuratus* as well as in *Chlamys islandica* and *Euvola ziczac* (Brokordt et al. 2000a,b, 2006).

In the intertidal and shallow subtidal zones of the HCS, temperature is the main variable changing over various spatial and temporal scales, with unpredictable interannual patterns. Under normal conditions, physical environmental conditions are relatively stable in the shallow subtidal between 18°S and 35°S (HCS), where salinity typically ranges between 34 and 35 and temperature may vary from 12°C to 22°C. However, due to terrestrial influence, the temperature conditions in the intertidal are different along this latitudinal gradient. For example, the range of mean temperatures registered in high intertidal pools during the summer is ~13–33°C in Antofagasta (23°S), ~13–30°C in Carrizal Bajo (28°S), and ~11–25°C in Las Cruces (33°S) (Pulgar et al. 2006). During EN, these differences in thermal conditions may be enhanced.

To evaluate phenotypic plasticity or evolutionary responses of organisms to different habitat temperatures, comparative studies have typically focused on species distributed along latitudinal gradients (Vernberg 1962, Graves & Somero 1982, Stillman & Somero 2000, Pulgar et al. 2006). However, local thermal gradients (TGRs) can be formed by fine-scale variation in, for example, the marine intertidal vertical zones. The intertidal zone is characterised by important spatial and temporal gradients of temperatures, which may be equivalent to those found over a large latitudinal gradient. Intertidal organisms have evolved physiological tolerance adaptations that are important in determining the upper vertical distribution of the species. Studies of congeners or conspecifics allow adaptive variation to be clearly demarcated, independent of effects of phylogeny (Stillman & Somero 2000). Crabs of the genus *Petrolisthes* (Anomura: Porcellanidae) are widely distributed not only along the intertidal zone of the HCS, but also worldwide, covering huge latitudinal gradients. One of the few studies of physiological adaptations of marine invertebrates in the HCS (Las Cruces, 33°S) was done in five species of the genus *Petrolisthes* (*P. granulatus*, *P. laevigatus*, *P. violaceus*, *P. tuberculatus* and *P. tuberculosus*) (Stillman & Somero 2000). Each species is found at different vertical levels, from the low (*P. tuberculosus*), mid-low (*P. tuberculatus*), middle (*P. violaceus*), mid-high (*P. laevigatus*) to the high (*P. granulatus*) intertidal. The limits of thermal tolerance (LT_{50}) were strongly correlated with the vertical position of the species in the intertidal zone ($y = 36.02 - 1.88x$, $r^2 = 0.97$) and with the maximal habitat temperature (Table 5) (Stillman & Somero 2000). Thus, species have adapted their upper thermal tolerance limits to coincide with microhabitat conditions. Interestingly, mid-high and high intertidal species (*P. laevigatus* and *P. granulatus*, respectively) live near their limits of thermal tolerance. While these LT_{50} values offer some hints, it may be extremely interesting to explore at which temperatures these organisms enter suboptimal ranges, that is, where they may be able to survive but where growth and reproduction may be compromised. *Petrolisthes laevigatus* from southern-central Chile dramatically reduces oxygen consumption between 18°C and 20°C (maximal average temperature range found in its

Table 5 Thermal tolerance limits (LT_{50}), and spring maximal habitat temperature of *Petrolisthes* along intertidal vertical gradient in a locality at the HCS (33°S)

Species of <i>Petrolisthes</i>	Vertical position in the intertidal	~ Limit of thermal tolerance (LT_{50} , °C)	~ Maximal habitat temperature (°C)
<i>P. tuberculatus</i>	Low	27.5	14
<i>P. tuberculatus</i>	Mid-low	28.5	18
<i>P. violaceus</i>	Middle	30.5	18
<i>P. laevigatus</i>	Mid-high	31.5	28
<i>P. granulatus</i>	High	35.0	33

Note: Data from Stillman & Somero (2000).

habitat), which suggests the beginning of the organism's decompensation, or the commencement of another homeostatic mechanism independent of oxygen consumption (Yaikin et al. 2002). Higher thermal stress or having thermal limits close to actual maximal habitat temperatures might increase the 'cost of living' of the species in the upper intertidal (Somero 2002, Stillman 2002). This higher cost of living would be associated with the cost of repairing thermal damage (heat-shock proteins, Hsp) and adapting systems through acclimatisation (Somero 2002). Although tropical *Petrolisthes* species have higher thermal limits than HCS species, the latter show a wider range of thermal tolerance between low and high intertidal species (Stillman & Somero 2000). Moreover, low intertidal HCS species show greater phenotypic plasticity in their thermal tolerance than high intertidal species (Stillman & Somero 2000). Considering global warming, species inhabiting the upper intertidal zone, living at the 'edge' of their thermal limits, would be more affected than species from the lower intertidal, which live far from their thermal limit and with a greater thermal phenotypic plasticity. These physiological traits may have an important effect on the borders in the latitudinal distribution of a species and consequently also on biogeographic limits.

Thermal effects that occur outside the normal physiological range involve deleterious changes at the cellular level, especially in systems involved with oxygen uptake, delivery and utilisation (Stillman 2002), such as the cardiac system (Frederich & Pörtner 2000). The heart of a crab species living in the upper intertidal has an Arrhenius break temperature (ABT, temperature at which a break occurs in the slope in an Arrhenius plot, i.e., log rate vs. reciprocal of absolute temperature, K) that is 5°C higher than in a crab species from the low intertidal (Stillman & Somero 1996). These differences were associated with the $Na^+ K^+$ ATPase (adenosine triphosphatase) activity, which is necessary for the establishment of the membrane action potential that permits the heartbeat (Stillman 2002). Similar to the rate of heartbeat, oxygen consumption by isolated mitochondria exhibits a 'break' at some high temperatures (Dahlhoff & Somero 1993). Phenotypic plasticity in the ABT of mitochondrial respiration has been observed in abalone *Haliotis* congeners from different thermal habitats (latitude and vertical positions along subtidal-to-intertidal gradient) (Dahlhoff & Somero 1993). Protein synthesis and heat-shock response has been shown to change spatially among gastropod (*Tegula*) congeners from the temperate subtidal to the low intertidal zones (Tomanek 2001) and seasonally in the bivalve *Mytilus trossulus* (Hofmann & Somero 1995). Hsp have the function of refolding and 'rescuing' proteins damaged by thermal denaturation (Becker & Craig 1994, Hofmann & Somero 1995). Intertidal species of *Tegula* showed greater expression of Hsp70 than the subtidal species when temperature increases (Tomanek 2001). The energy cost associated with replacing damaged proteins and maintaining Hsp may be an important proportion of cellular energy demands (Hofmann & Somero 1995, Somero 2002).

Intertidal and shallow subtidal invertebrates present a 'cascade' of physiological responses that enable them to adapt and finally survive changes in environmental conditions. Despite the important

latitudinal and vertical environmental conditions gradient of the HCS, there are few studies of physiological responses of invertebrates living in this ecosystem. The range of temperatures registered in the intertidal (rocky pools) along this latitudinal gradient (Pulgar et al. 2006) is very similar to the TGR from the low-to-high intertidal zone observed in central Chile (Table 5). Therefore, it could be expected to find similar thermal physiological variability and local adaptations of congeners or conspecifics in the latitudinal gradient to those found in the intertidal vertical gradient. Because in this area the pattern of environmental variability shifts from a relatively predictable seasonal pattern to a more unpredictable pattern of high interannual variability (i.e., ENSO), physiological characterisation of congeners or conspecific organisms inhabiting the intertidal and shallow subtidal zones along the latitudinal gradient of the HCS would be particularly interesting. Moreover, since algal availability increases from northern to southern Chile (Santelices & Marquet 1998), and physiological compensation associated with environmental stress increases cost of living (Somero 2002, Stillman 2002), latitudinal changes in food availability should also be considered in future studies. It appears particularly interesting to examine how increased costs of living near the distribution limit of a species influences its reproductive potential.

Reproductive patterns of selected marine invertebrates in the HCS

Some of the factors that vary with upwelling intensity and persistence, such as temperature and PP, are known to critically affect per capita reproductive investment of marine invertebrates (e.g., MacDonald & Thompson 1985, 1988, Clarke 1987, Brey 1995, Phillips 2002). In the northeastern Pacific, reproductive hot spots coincide with regions exhibiting high PP, which suggests not only that bottom-up processes play a central role in explaining reproductive output, but also that spatial heterogeneity in reproduction needs to be considered in conservation and management plans (Leslie et al. 2005). The clear break in eddy kinetic energy and equatorward wind stress reported at 30°S in the southeastern Pacific (Hormazábal et al. 2004) coincides with two contrasting regimes in chl-*a* concentration both in coastal areas and offshore (Yuras et al. 2005). Chl-*a* concentration is negatively correlated with seawater temperature along the HCS (Strub et al. 1991, Thomas et al. 2001b). The effects of small- and large-scale variation in environmental conditions related to upwelling persistence and strength on reproductive patterns along the HCS have recently been analysed.

Primary productivity and gonad production

Gonad and egg production of marine invertebrates do not exhibit a clear latitudinal cline in investment in reproduction along the HCS in central Chile (Fernández et al. 2007). However, gonad production shows variable patterns throughout the study region, which extends from 28°S to 36°S, and this variability appears related to the trophic level of the species being investigated and the proximity of the study sites to upwelling centres. Carnivores such as *Concholepas concholepas* and *Acanthina monodon* do not show variation in gonad investment between 28°S and 36°S (Figure 19). In contrast, some of the dominant intertidal suspension-feeding species, *Perumytilus purpuratus* and *Nothochthamalus scabrosus*, and one of the most abundant herbivores, *Chiton granosus*, exhibit strong variation in gonad production among sites, even between adjacent locations (Fernández et al. 2007). Investment in reproduction of suspension-feeding and herbivore species is constantly higher in some sites (e.g., Los Molles 32°24'S, Consistorial 33°49'S) and lower in others (e.g., Montemar 32°96'S, Matanzas 33°96'S). Furthermore, there is a positive and significant correlation between investment in gonads among *Perumytilus purpuratus*, *Nothochthamalus scabrosus* and *Chiton granosus* (p always < 0.05; *P. purpuratus*-*N. scabrosus*: $R = 0.89$, *P. purpuratus*-*Ch. granosus*:

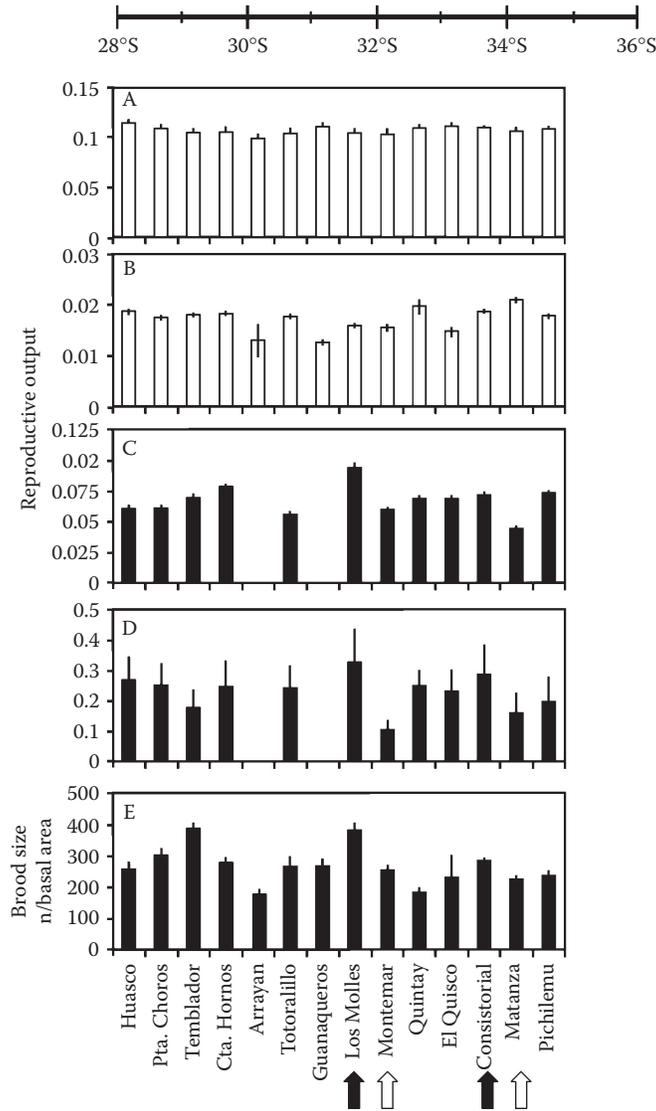


Figure 19 Reproductive output of (A) *Concholepas concholepas*, (B) *Acanthina monodon*, (C) *Chiton granosus*, (D) *Perumytilus purpuratus*, and (E) brood size (number of embryos per unit of basal area) of *Nothochthamalus scabrosus*, along the study site which ranges from 28°S to 36°S in the eastern South Pacific Ocean. The white bars are used for carnivore species, the black bars for herbivore or filter-feeding species. The white arrows indicate upwelling centers, the black arrows point to sites not influenced by upwelling along the HCS.

$R = 0.64$, *N. scabrosus*-*Ch. granosus*: $R = 0.73$; Fernández et al. 2007). Investment in gonads of carnivore species does not show any correlation with the reproductive patterns exhibited by herbivores or suspension-feeding species. The patterns reported were consistent over the 3-yr study (coefficient of variation = 1.3%). These results suggest that the small-scale variation in environmental conditions along the upwelling-favourable region of the HCS seems to affect gonad production and consequently larval production, and therefore that some locations potentially serve as source populations of propagules. Transplant experiments support the hypothesis that local environmental conditions determine reproductive output. Suspension feeders (e.g., *Perumytilus purpuratus*)

and herbivores (e.g., *Chiton granosus*) transplanted between the most and least suitable sites for reproduction in central Chile showed that reproductive output was strongly determined by the site to which the animals were transplanted while the site of origin showed a negligible effect (Fernández et al. 2007). Organisms transplanted to Los Molles showed high reproductive output and organisms transplanted to Matanzas showed low reproductive output, regardless of the site of origin (Fernández et al. 2007). These contrasting results suggest that environmental variables, such as PP, may affect investment in gonads of lower trophic level benthic invertebrates. These environmental conditions seem to be related to the spatial variation of upwelling conditions. The central coast of Chile is dominated by seasonal wind-driven upwelling that forces cold, nutrient-rich water into the upper water column (Wieters et al. 2003). However, it is remarkable that the well-documented relationship between cold upwelled water and high chl-*a* concentration over large spatial scales off the coasts of Chile and California (Strub et al. 1991, Thomas et al. 2001a) is not observed at smaller spatial scales (Wieters et al. 2003). Between 28°S and 36°S, the lowest chl-*a* concentrations are associated with coldest upwelled waters (Wieters et al. 2003). Matanzas and Montemar are sites influenced by upwelling centres, in contrast with the lower influence of upwelling in areas such as Los Molles or Consistorial (Broitman et al. 2001, Wieters et al. 2003). Upwelling centres also show higher growth rate of corticated algae, which are not consumed by herbivores, and low growth of ephemeral algae (Nielsen & Navarrete 2004). Although temperature decreased from 28°S to 36°S and is lower in upwelling centres, gonad production is not correlated with seawater temperature (Fernández et al. 2006a). Most likely, the low chl-*a* concentration associated with upwelling conditions (Wieters et al. 2003) and low abundance of benthic ephemeral algae (Nielsen & Navarrete 2004) are the main factors affecting reproductive output of lower trophic level, intertidal species along the HCS. Evidence from other geographic regions supports the hypothesis that patterns of PP associated with upwelling conditions determine reproductive output (Leslie et al. 2005). However, more information is necessary to clearly identify the set of environmental variables affecting reproductive investment.

Temperature and brooding requirements

Although the effect of temperature on gonad production is not evident along the upwelling region associated with the HCS between 28°S and 36°S, studies conducted over larger spatial scales (and wider temperature ranges) suggest that temperature can affect egg production in species that aggregate embryos. Oxygen is a limiting factor in embryo aggregations of marine invertebrates (Cohen & Strathmann 1996, Lee & Strathmann 1998, Fernández et al. 2003) and temperature affects oxygen availability in different types of embryo packing (Brante et al. 2003, Fernández et al. 2006a). Studies of the brachyuran crab *Cancer setosus* show that brooding females respond to the increased oxygen demand of the embryos at higher temperatures by increasing abdominal flapping frequency, a behaviour that supplies oxygen to the brood (Brante et al. 2003). Similar patterns of female response to embryo oxygen demand have been reported throughout embryo development in other crab species (Baeza & Fernández 2002, M. Fernández et al. 2002). The change in female brooding behaviour (abdominal flapping frequency) produces a higher rate of oxygen supply, dramatically affecting the costs of brooding. Between 10°C and 18°C, a 45% increase in brooding costs was estimated for large-size crabs, such as *C. setosus* (Brante et al. 2003). This substantial increase in brooding behaviour and cost seems to affect egg production and survival (Fernández et al. 2003). Field data showed that gonad investment (or reproductive output) in *C. setosus* is lower in northern Chile (approximately 20°S) than in central (30–33°S) and southern (40°S) Chile. Lardies & Castilla (2001) reported a similar latitudinal trend in reproductive output for *Pinnaxodes chilensis*. Moreover, embryo loss in *Cancer setosus* increases with temperature (Brante et al. 2003), suggesting that temperature also affects embryo survival throughout the brooding period. Reproductive output of most brachyuran crab species does not vary south of 30°S

(Brante et al. 2004). The contrasting pattern in reproduction between populations of brachyuran crabs north and south of 30°S seems also to occur in other species that aggregate embryos. It is interesting that despite the lack of difference in reproductive output of *Concholepas concholepas* between 28°S and 36°S (Figure 19), embryo packing shows a clear break that coincides with the break exhibited by brachyuran crabs (north and south of 29–30°S). The mean number of embryos per unit of capsule area was significantly lower in capsules from sites north of 29°S than south thereof (20.6 vs. 31.8, respectively), over a range of study sites located between 30°S and 42°S. Although there is no dramatic break in temperature at 30°S (Broitman et al. 2001), the pattern of embryo packing is explained by the mean temperature at the study site shortly before egg deposition.

The evidence accumulated to date suggests that the higher brooding costs north of 30°S seem to affect reproductive output and that the effect is consistent across the brooding modes and taxa studied so far. This finding suggests that environmental conditions are less favourable for brooding species in the northern part of the HCS. In fact, large-scale studies of the patterns of species distribution in relation to larval developmental mode support the hypothesis that the spatial distribution of brooding species is explained by the cost of brooding, which is associated with the cost of oxygen provision (Astorga et al. 2003, Marquet et al. 2004). It is less clear if the impact of the cost of brooding on reproductive output may change with adult body size. Recent studies have shown that small crab species perform the same active brooding behaviours as large species (e.g., *Pisoides edwardsi*, *Acanthocyclus gayi*; Fernández et al. 2006b). However, mean oxygen consumption of brooding females, which is a proxy of brooding cost, is not significantly different from oxygen consumption of non-brooding females (Fernández et al. 2006b). These results contrast with previous studies of large species, showing a 2- to 3-fold increase in oxygen consumption by females carrying later-stage embryos over non-brooding females (e.g., *Cancer setosus*: Baeza & Fernández 2002; *Homalaspis plana*: Ruiz-Tagle et al. 2002; *Ovalipes trimaculatus*: Fernández & Brante 2003). Therefore, the patterns described for brooding species may be dependent on adult body size. In fact, the small crab species *Acanthocyclus gayi* and *A. hassleri* do not show any pattern in reproductive output along the region extending from 28°S to 36°S (Espinoza 2006). Although existing evidence on reproductive output along the HCS suggests that the behaviour of populations north and south of 30°S depend on the cost of oxygen provision in larger-size species, more studies are needed in order to generalise the findings on the effects of temperature on brooding costs, the link between adult size and brooding mode, and the consequences on species distribution, especially in regions influenced by upwelling where low oxygen conditions cover extended regions of the ocean (Fuenzalida et al. accepted).

Larval life in the HCS

Oceanographic conditions in the HCS ecosystem expose planktonic larval forms to environmental conditions in which they do not behave simply as a passive particle. Therefore, morphological, physiological and behavioural characteristics present in fish and benthic invertebrate larval forms inhabiting any particular habitat can be interpreted as effective local adaptations evolved to face this unique ecosystem. Herein, the aim is to give a brief overview of some behavioural and feeding traits together with transport processes described in larval forms of benthic invertebrates and fishes inhabiting the HCS.

Behavioural traits

Larvae of many marine benthic invertebrates, differing from lecithotrophic short-lived larvae, spend extended periods in the plankton prior to settlement and metamorphosis (Thorson 1950, Pechenik 1986, 1999). Usually, during their pelagic phase, planktotrophic larvae (PL) of marine benthic

invertebrates must remain suspended, locate and gather food, avoid predators and unfavourable conditions, disperse to new areas and select sites for settlement (Strathmann 1974, Palmer & Strathmann 1981, Scheltema 1986). The importance of larval behaviour has been recognised as an important subject in marine ecology and the recent focus on the role of nearshore oceanographic processes controlling larval dispersal and recruitment of benthic organisms has revived interest in the behaviour of larvae in the plankton (reviewed in Le Fèvre & Bourget 1992). Although larval transport seems to be mainly controlled by hydrographic factors (Thorson 1950), larval behaviour may influence their final destination (e.g., Butman 1987, Pineda 1994a,b). In general, sources of mortality in the dispersal phase for PL are food limitation, extreme conditions of temperature and salinity, low dissolved oxygen, UV radiation and pollution (Pechenik 1986). However, because of the difficulties associated with larval tracking in the field, the relative importance of each potential source of larval mortality in nature is still largely unknown. Field and laboratory experiments have revealed a number of behavioural mechanisms that allow larvae to contend with these selective pressures on mortality. However, specific studies of characteristics displayed by PL throughout the HCS are largely absent. Few published studies regarding larval characteristics linked with ecological importance have been conducted in Chile (e.g., Manríquez & Castilla 2007). Field evidence of a DVM pattern in competent larvae has been described for the muricid gastropod *Concholepas concholepas* (Poulin et al. 2002a,b). It has been suggested that the behaviour of competent larvae of this species may help them to avoid offshore transport during upwelling events. Studies with several crustacean species have shown clear synchronisation between reproduction and the hydrodynamic processes promoting larval transport or retention (Yannicelli et al. 2006a). Similar studies with other PL in the HCS incorporating behavioural or physiological responses to environmental variables such as currents, temperature and salinity are urgently needed. However, along the HCS those studies are precluded by the absence of basic knowledge such as larval identification in many species of Chilean invertebrates. Work to investigate the scale of the source–sink dynamics of PL in the temporally heterogeneous HCS ecosystem is also largely absent. More recent techniques involving chemical tags in calcified structures of PL have been successfully used to identify potential larval source and sink areas, and larval trajectories in the HCS (Zacherl et al. 2003).

Feeding and larval food environment in the HCS

Recruitment is recognised as the leading determinant of population dynamics of benthic invertebrate and fish species and it strongly adjusts the importance and intensity of species interactions in the HCS (see above). Since PL rely on food to grow and develop, availability and quality of food particles during larval development are important factors influencing larval recruitment (Vargas et al. 2006a). Despite the high variability in larval food composition, there are well-documented, persistent, temporal and spatial differences in plankton structure and abundance along the HCS. For instance, large and geographically persistent heterogeneity in chl-*a* has been documented along the Chilean coast (Thomas et al. 2001b, Yuras et al. 2005; and see Dominant primary producers and their role in the pelagic food web, p. 210ff.). The general pattern indicates that a large percentage of chl-*a* is found in the large phytoplankton fraction in permanent coastal upwelling areas off northern Chile (Iriarte & González 2004; see also Dominant primary producers and their role in the pelagic food web, p. 210ff.), as well as during spring/summer at seasonal upwelling sites in central Chile (González et al. 1989, Vargas et al. 2006b). Similarly, a large and geographically persistent heterogeneity in chl-*a* levels has been observed to the north of latitude 32°S (Yuras et al. 2005).

The scarcity of available published data on larval fish and invertebrate feeding makes it difficult to evaluate potential larval survival and recruitment along the HCS. Currently, the largest body of literature is available for larval fish of commercially exploited species. Because of their seasonal

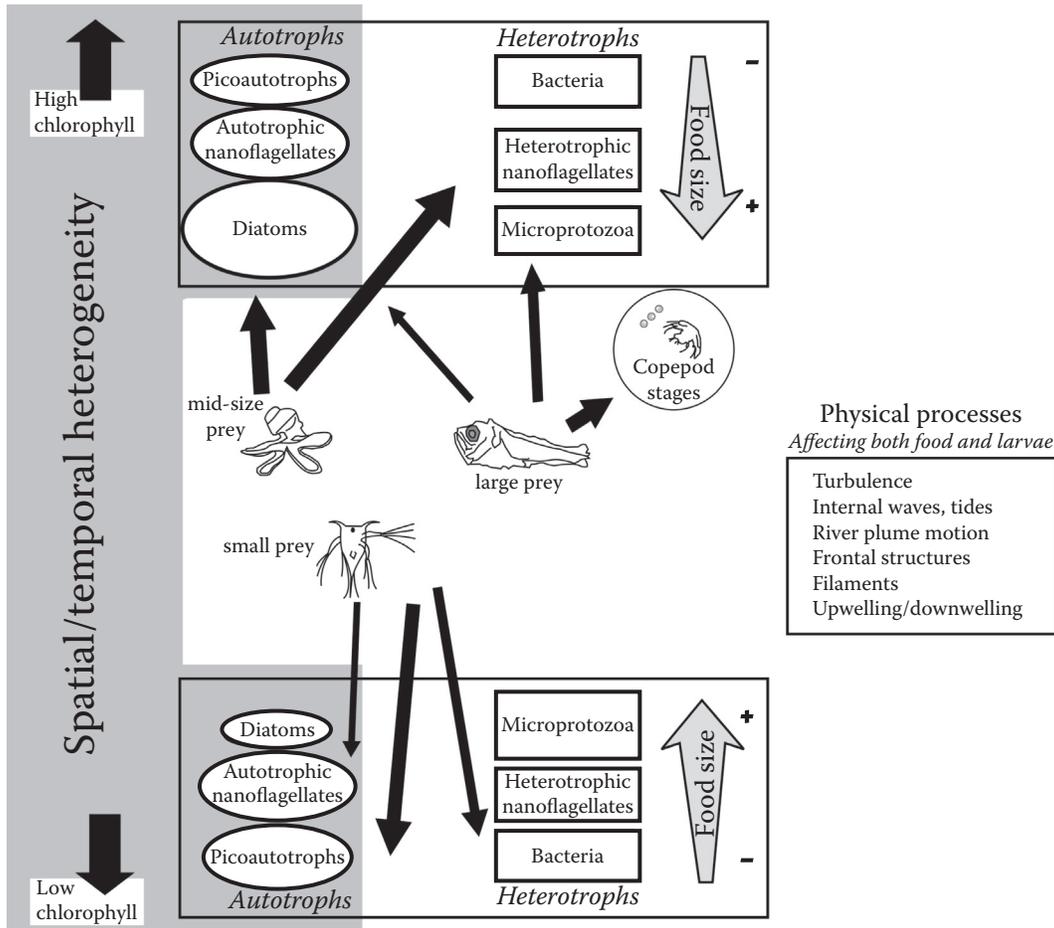


Figure 20 Conceptual scheme of main pathways of interaction in coastal food webs involving invertebrate (i.e., veliger competent larvae and barnacle nauplii) and fish larvae under spatial/temporal variation in chlorophyll levels in the Humboldt Current System. The thickness of the arrows represents main predator-prey interactions. The sizes of the boxes or circles represent the dominance in terms of biomass of a specific food item (both autotrophic and heterotrophic prey) during each condition. Physical processes discussed in this chapter, which affect both larvae and food distribution, are also included. Arrows directed to food items at top or bottom boxes were included for convenience.

nature, in the coastal upwelling area off central Chile (36–37°S), the changes in the phytoplankton protozoan and microplankton community that constitute the food supply for larval fish also occur on a seasonal basis (Vargas et al. 2006b). Accordingly, larvae produced in the middle of winter in the HCS, when PP and seawater temperatures are low and wind-induced turbulence in the upper part of the water column is high, are probably not going to face the same prey as those produced in summer, when upwelling and PP are at maximum (Figure 20). Most of the studies of larval fish feeding have focused on changes in prey field, diet overlap, and their influence on larval feeding over short timescales, between adjacent areas, or have attempted to investigate whether evidence of starvation occurred in wild-collected larvae (Llanos et al. 1996, Balbontín et al. 1997, Pizarro et al. 1998, Llanos-Rivera et al. 2004). For the anchovy, *Engraulis ringens*, in northern Chile (20–21°S), scarce incidence of starvation was even observed during autumn, a season of reduced

plankton production (Pizarro et al. 1998). In northern Chile, the diet of the myctophids *Diogenichthys laternatus* and *Triphoturus oculus*, which feed diurnally and share the upper water column (0–200 m depth), was shown to vary according to prey availability in the field. The diets of both species overlap in periods and areas where food is more abundant (e.g., copepods, copepodids, nauplii, invertebrate eggs and ostracods), but differ under conditions of low prey availability (Rodríguez-Graña et al. 2005). Other studies in central Chile have shown that either microplankton concentrations did not appear limiting in winter (Castro et al. 2000, Hernández & Castro 2000, Castro 2001) or larval diet overlap occurred among several species but during periods of high food abundance (Llanos et al. 1996, Balbontín et al. 1997, Llanos-Rivera et al. 2004). Hence, the few studies carried out on feeding of larval fish along the HCS in Chile suggest that, although the larval food abundance may vary among seasons and localities, starvation due to limiting food availability alone does not seem to be such a common feature, even in seasons of lower production (autumn and winter). For starvation to occur, other factors may be necessary, such as increased turbulence, which may play a concomitant role during the low productivity seasons, at least in southern Chile (Cury & Roy 1989, Castro et al. 2002). Scarce dietary overlap and local morphological and physiological adaptations (i.e., increased reserves in fish eggs and larger yolk size in fish larvae; Llanos-Rivera & Castro 2004, 2006) seem to exist in larval periods when ontogenetically food is highly necessary (i.e., onset of feeding) or when food becomes less abundant in the environment (Balbontín et al. 1997, Llanos-Rivera et al. 2004, Rodríguez-Graña et al. 2005).

For benthic invertebrates, sharp spatial transition in phytoplankton biomass associated with upwelling dynamics has been assumed to have important effects on larval condition (Wieters et al. 2003). This assumption is based on the idea that phytoplankton is the most important food item for PL. A major impediment to understanding how food quantity and quality influence larval life under natural conditions is that virtually all published information comes from laboratory rearing studies in which larvae are offered a monospecific or controlled-mix algal culture. One of the first studies done in the HCS analysing feeding preferences in larval invertebrates, by Vargas et al. (2006a), found evidence that barnacle nauplii (*Jehlius cirratus* and *Notobalanus flosculus*) and veligers (*Concholepas concholepas*) exhibited high consumption of heterotrophs (i.e., ciliates and dinoflagellates), but the size spectrum of food particles removed by barnacle nauplii was in contrast with those for *C. concholepas* veligers. Barnacle nauplii preyed heavily on small picophytoplankton (<2 µm), whereas competent *C. concholepas* veliger larvae were mechanically unable to feed on small cells, and the highest removal rates were of nano- and microphytoplankton (>20 µm). The ability of barnacle nauplii to feed on small prey hinges on the small spaces between their limb setules (Stone 1989). This important finding indicates that omnivorous larval feeding should be the norm in the pelagic ecosystem and might explain why larvae maintain positive growth in environments where phytoplankton is thought to be limiting (Crisp et al. 1985). Therefore, the scarce published information for the HCS suggests that the inference of patterns of larval condition and recruitment over large scales from chl-*a* biomass, now easily measured from satellite images (e.g., Thomas et al. 2001b), has to be regarded with caution. The scenario suggests that a large spectrum of food particles is available for larval feeding, and species may adapt their feeding preferences in relation to temporal/spatial food distribution along the HCS as well as their physiology and energetic reserves to counteract the spatial and temporal variations in food quality and quantity (Vargas et al. 2006b) (Figure 20).

Upwelling and larval transport processes

The wind-driven seasonal upwelling, besides its paramount effect on PP in the coastal zone, induces profound changes in the dynamics of coastal waters that directly affect the distribution and abundance of organisms in the nearshore areas as well as over the continental shelf and slope. To reside

in these hydrodynamically variable but highly productive environments, coastal and offshore organisms have developed a series of reproductive strategies that enable them to counteract the effects of offshore advection in the surface Ekman layer or take advantage of other oceanographic processes to return to the coastal zone (see also Coastal oceanography, p. 205ff.). For instance, on a seasonal timescale, small pelagic clupeiform fish tend to synchronise their reproductive timing with processes that induce shoreward transport and coastal retention. Probably the best-documented species in the HCS of central Chile are the anchovy (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) that reproduce during winter, when the wind-driven Ekman layer is directed shoreward and thus eggs and larvae are retained in the coastal area (Castro et al. 2000, Castro 2001, Cubillos et al. 2001, Hernández-Miranda et al. 2003). Shelf-break, slope-demersal and mid-water fish species, such as Chilean hake (*Merluccius gayi*), big eye flounder (*Hippoglossina macrops*), and the mesopelagic *Maurollicus parvipinnis*, instead seem to prefer early spring reproduction when subsurface waters drive their eggs and larvae to the coast during the upwelling season, where they develop in the season of higher production (Vargas et al. 1997, Vargas & Castro 2001, Landaeta & Castro 2002, Landaeta et al. 2006). This strategy, originally described for some large offshore copepods such as *Rhincalanus nasutus*, and more recently observed also in the galatheid *Pleuroncodes monodon* and the majid *Libidoclaea granaria*, is currently accepted as a common feature among several types of organisms that have in common larvae inhabiting subsurface waters in central Chile (Castro et al. 1993, Yannicelli et al. 2006a,b). Other species of decapod crustaceans also synchronise their reproduction with the seasonal changes in hydrodynamics for their transport or retention (Yannicelli et al. 2006b). In this group, however, several species reproduce during the upwelling season in spring and summer and their horizontal distribution seems to be associated with their behavioural ability for vertical migration (i.e., *Neotrypaea uncinata*, *Pagurus* sp.). Other species with protracted larval periods such as *Emerita analoga* and *Blepharipoda spinimana*, which reproduce late in summer and early spring and then reside in the upper water column without signs of vertical migration, probably use more than a single retention process, as yet unknown, because their reproduction occurs over periods of contrasting hydrographic processes (Yannicelli et al. 2006b). Among molluscs, there is scarce information; for instance, the larval retention and shoreward transport mechanism of the gastropod *Concholepas concholepas* are the only information reported for the HCS. In this case, avoidance of the surface Ekman layer by competent larvae appears to be accomplished by an inverse vertical migration that reduces their time exposed to seaward flow and keeps the larvae between the coast and an upwelling front (Poulin et al. 2002a,b). Coastal oceanographic processes such as upwelling shadows have also been reported (Escribano et al. 2002) as larvae retention mechanisms and such might constitute an understudied coastal larval retention system along the HCS.

Tidal transport of larvae, associated with frontal structures near the coast, the entrance of estuaries or large bays, has also been reported recently for central and southern Chile. Internal tidal bores associated with semi-diurnal temperature changes coincided with bivalve, gastropod and crustacean settlement, suggesting that coastward larval transport occurred during these events in summer (Vargas et al. 2004). In Corral Bay (~40°S), changes in larval fish distributions coincident with changes in the estuarine front position in different tidal phases have been reported by Vargas et al. (2003) as an indication of potential larval tidal transport. More recently, with the aid of fine-resolution current profiles and stratified larval collections over 24-h cycles, semi-diurnal changes in water flow patterns and of decapod and larval fish fluxes in and out of the Gulf of Arauco have been estimated (Yannicelli et al. 2006a, R. Veas unpublished data). The overall larval fluxes were modified by their vertical position in the water column, the diurnal vertical migration patterns and the tidal cycle. Interestingly, although clearly associated with tidal phases, the larval fluxes experienced by these decapod and fish larvae in the Gulf of Arauco did not correspond exactly to selective tidal stream transport (STST) as it has been reported at the entrance of other bays and estuaries in other coasts of the world (Forward et al. 1998).

Seaward and alongshore exportation of larvae in river plumes, filaments and eddies seems to be a common feature along the HCS. In northern Chile, a mixture of coastal and offshore larval fishes, both in the coastal and adjacent offshore areas, has been repeatedly reported in different seasons and years (Loeb & Rojas 1988, Rojas et al. 2002, Rodríguez-Graña et al. 2005). Besides the existence of a narrow continental shelf, at least three oceanographic processes involving larval transport have been advocated to explain such patterns: (1) seaward surface Ekman transport and upwelling plumes, (2) the presence of filaments, and (3) warm-water intrusion during EN years, all well-documented processes in northern Chile (González et al. 2000b, Sobarzo & Figueroa 2001). In central Chile, surface Ekman transport and cold-water filaments have also been reported to export chl-*a*, meroplankton and ichthyoplankton from the coastal zone (Cáceres 1992, Morales et al. in review) and they have been used to explain part of the larval mortality rate estimations in the coastal zone (Castro & Hernández 2000, Landaeta & Castro 2006). Larval transport associated with river plumes, mesoscale processes not occurring in northern Chile, has also been proposed as a determinant of barnacle larval transport (Vargas et al. 2006c). Such plumes are also potential areas of increased larval food availability at the frontal area. Other still-unknown oceanographic processes capable of transporting larval forms alongshore probably occur in the HCS. In fact, it is worth noting that almost no reports exist on the role of the Humboldt Current itself or the Chile-Peru poleward undercurrent as a means of alongshore latitudinal larval transport (except for potential transport of larval *Pleuroncodes monodon* in subsurface waters off central Chile; Yannicelli 2005).

In summary, a number of larval transport processes have been described along the central and southern part of HCS. Three of them seem particularly important when considered from an ecological perspective: (1) larval transport (seaward and shoreward) in the surface Ekman layer, (2) exportation from the coast in filaments (especially off the Mejillones Peninsula in northern Chile and off the Talcahuano area of central Chile) and (3) the coastward subsurface larval transport in upwelling waters in spring and summer with the concomitant mixing of offshore and coastal species near shore. Examples of important differences between northern and central Chile are the influence of oceanographic processes such as EN events (much stronger in northern Chile) and of river plumes (absent in northern Chile). Overall, populations of invertebrates and fishes along the HCS develop multiple strategies to cope with the intense periods of transport during early life stages. Timing the reproductive seasons with specific oceanographic events is most common. However, specific reproductive timing depends on the local sites of reproduction, capability of larvae to move vertically in the water column, length of larval life history/cycle and other not so well studied processes (i.e., retention in upwelling shadows) or those occurring during the adult life stage (seasonal growth, energy accumulation, oogenesis) that may finally affect the larval characteristics mentioned above.

Life-history adaptations of macroalgae

The macroalgal flora along the HCS is characterised by the presence of endemic species (32%) mixed with species of different biogeographical affinities, including subantarctic (34%), widely distributed (23%), tropical (3.5%) and amphi-equatorial (7%) species (Santelices 1980). In general, this species composition, which is comparatively poorer than that reported for other regions and increases in number toward higher latitudes (Lüning 1990, Santelices & Marquet 1998), responds to the relative biogeographic isolation as a consequence of the predominant direction of the water circulation regime in the HCS (Santelices et al. 1980, Meneses & Santelices 2000). However, an increasing number of invasive species as a result of human activities (ship transport, aquaculture, etc.) has recently been reported with concern about their impact on indigenous species (Castilla et al. 2005a). For example, recent surveys indicate an increase of subtropical elements, a decrease in endemic species and two break points in species composition at 12°S and 42°S (Meneses & Santelices 2000).

Environmental gradients and strategies of resistance, recovery and recolonisation

Although benthic algae are not in direct contact with the main stream of the HCS, subsystems such as the Arica-Mejillones Current or Gunther Undercurrent are located close to the coast (<100 km) (Strub et al. 1998) and hence strongly influence macroalgal assemblages. On the other hand, the biogeographic patterns and ecology of macroalgae of northern-central Chile may be affected by upwelling events and by changes in the oceanographic conditions due to EN episodes. Both processes can interact on local and temporal scales: the permanent coastal upwelling can buffer and moderate superficial warming of the sea and depletion of nutrients during EN (Vega et al. 2005). The first factor has not been well studied for the case of the macroalgae; however, the effects of EN have received much attention in the last decades (Camus 1990, Vásquez & Vega 2004b).

Over the last 30 yr, studies of seaweed ecology have traditionally focused on conspicuous genera such as *Lessonia*, *Durvillaea* and *Macrocystis*. Their distribution, reproductive phenology and recruitment patterns as well as ecological functions on the rocky shores have been well documented for communities between 40°S and 20°S (Santelices et al. 1980, Moreno & Sutherland 1982, Santelices & Ojeda 1984, Vásquez 1992, Westermeier et al. 1994, Tala et al. 2004 and references therein). These brown algae represent the major biotic factors structuring the intertidal and subtidal communities, directly affecting coastal processes through changes in species diversity, biomass and PP (Ojeda & Santelices 1984, Santelices & Ojeda 1984, Vásquez & Santelices 1990, Santelices 1991, Vásquez 1992, Camus 1994a, Ortiz 2003, Tala & Edding 2005, Vega et al. 2005).

Because the coastal scenarios along this region are relatively similar in terms of prevailing oceanographic conditions, it may be argued that most macroalgae are exposed to the same environmental factors and thus show similar adaptations. However, considering the phenology, algae respond to environmental variability basically in two ways (*sensu* Kain 1989): (1) 'season anticipators' can grow and reproduce in a strategic annual rhythm suitable for the species, which does not necessarily require suitable environmental conditions but rather an environmental trigger (e.g., day length, nutrient level; Lüning & tom Dieck 1989); and (2) 'season responders', by contrast, grow and reproduce when environmental conditions are favourable (e.g., suitable light conditions). Whether these two life-strategy mechanisms operate in algae along the HCS has not been well addressed; however, some patterns of abundance and reproduction as summarised in Figure 21, based on large geographic distributional scales (described, e.g., for *Lessonia*, *Durvillaea*, *Macrocystis* and some genera of Rhodophyta) may be associated with 'season anticipation' or 'season responses'. However, taking into account that upwelling processes, ENSO or human activities (e.g., pollution due to mining discharges) modify local environmental conditions, the existence of other adaptive mechanisms to withstand these perturbations cannot be ruled out. With the exception of the well-documented consequences of EN on population dynamics of the dominant kelp *Lessonia* (Camus 1994b, Martínez et al. 2003, Vega et al. 2005), questions related to functional strategies of other macroalgal assemblages during and after mass extinction events within the HCS have been less addressed. A latitudinal asynchrony in biological processes would be related to different climatic regimes affecting life-history traits (Mediterranean vs. desert climate in southern-central and northern Chile, respectively). However, local environmental conditions exert a strong pressure on the observed patterns and the later recruitment, mainly related to seasonal grazing intensity, habitat distribution (intertidal versus subtidal) and water movement (Santelices & Ojeda 1984, Camus 1994a, González et al. 1997, Buschmann et al. 2004b, Tala et al. 2004, Vega et al. 2005). In this sense, species that reproduce continuously may show advantages in unpredictable environments compared with strictly seasonal species. Thus, the knowledge about environmental thresholds for life-history adaptations (expression of functional responses to optimise resource use, e.g., light, temperature and nutrients, or to withstand environmental stress) is crucial in understanding the biogeographical patterns of macroalgae.

THE HUMBOLDT CURRENT SYSTEM OF NORTHERN AND CENTRAL CHILE

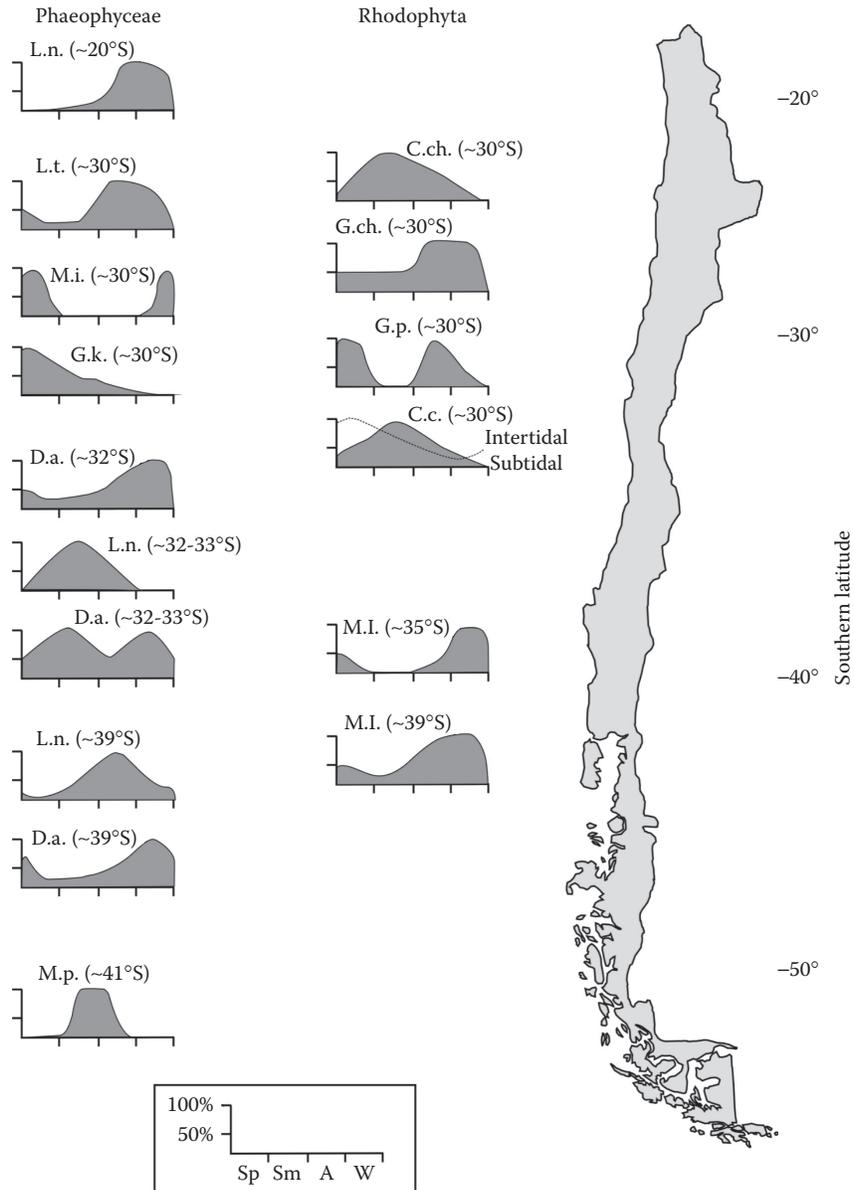


Figure 21 Seasonal patterns of reproductive phenology in macroalgae along latitudinal gradients in Chile. Small inserts show seasonal phenology: Sp, Spring; Sm, Summer; A, Autumn; and W, Winter. Information was adapted from: *Lessonia nigrescens* (L.n.) (Camus 1994a, Westermeier et al. 1994); *L. trabeculata* (L.t.) (Tala et al. 2004); *Macrocystis integrifolia* (M.i.) (Buschmann et al. 2004b); *Glossophora kunthii* (G.k.) (García 1996); *Durvillaea antarctica* (D.a.) (Santelices et al. 1980, Westermeier et al. 1994, Collantes et al. 2002); *Macrocystis pyrifera* (M.p.) (Buschmann et al. 2004b); *Chondrus canaliculatus* (C.c.) (Vega & Meneses 2001); *Chondracanthus chamissoi* (C.ch.) (González et al. 1997); *Gelidium chilense* (G.ch.) (Dantagnan 1993); *Gastroclonium parvum* (G.p.) (Rivera 1992); *Mazzaella laminarioides* (M.I.) (Santelices & Norambuena 1987, Westermeier et al. 1987).

Temperature tolerance

Thermal adaptations of the life-history stages, mainly for growth, reproduction and survival requirements, are key factors explaining the geographic distribution of benthic algae. In general, two major aspects characterise temperature demands of macroalgae distributed along the HCS: (1) there is a close correlation between the upper survival temperature of gametophytes and the northern distribution limits of the species and (2) algae occurring between 18°S and 40°S show higher temperature tolerance (18–28°C) than algae south of 40°S (17–23°C), coinciding with the latitudinal influence of the HCS and the boundaries of the two traditionally recognised biogeographic regions (Chilean-Peruvian and Magellan provinces) (Santelices 1980, Wiencke & tom Dieck 1990, Peters & Breeman 1993, Santelices & Marquet 1998, Martínez 1999). For example, brown algae with Antarctic/subantarctic distribution commonly found between 18°S and 40°S (e.g., *Adenocystis utricularis* and *Scytothamnus fasciculatus*) have maximal survival temperatures close to 18°C and 24°C (Wiencke & tom Dieck 1990). These lethal values are above the mean monthly temperatures measured around 18°S (14–19.5°C) and 37°S (11.7–15.5°C) (Gorshkov 1985). However, when the upper limit for gametogenesis is regarded, these species do not reproduce at temperatures >13–15°C (Peters & Breeman 1993). Such thermal requirements suggest that they may survive moderate EN episodes, but probably a recovery through sexual reproduction may become limited. In the case of species restricted to the HCS (e.g., the red alga *Chondracanthus chamissoi*), the growth of both gametophytes and sporophytes increases at temperatures of 25°C, which is 5–6°C higher than water temperature in northern Chile (Bulboa & Macchiavello 2001). This is a known phenomenon in macroalgae and may reflect a reasonable safety limit to survive unpredictable increases of temperature for a long time (e.g., months during EN) or may represent a potential for shifting the distribution boundaries northward. It must be emphasised that most of the macroalgae from northern-central Chile studied so far show a capability of growth at very low temperatures (>10°C), indicating clearly an adaptation to the cooling effect of the HCS and reflecting their subantarctic affinities (Wiencke & tom Dieck 1990, Peters & Breeman 1993, Santelices & Marquet 1998).

Physiological and morphofunctional adaptations

In general, there are only a few ecophysiological studies addressing adaptations of the life history of macroalgae to varying light and nutrient conditions and they have normally been restricted to the genera of commercial importance (e.g., *Lessonia*, *Gracilaria*, *Gelidium*, *Mazzaella* and *Porphyra*) (Oliger & Santelices 1981, Hoffmann & Santelices 1982, Hoffmann et al. 1984, Correa et al. 1985, Hannach & Santelices 1985, Avila et al. 1986, Bulboa & Macchiavello 2001, Véliz et al. 2006). Although physiological performances (measured as growth or photosynthesis) are comparable to those of species from other biogeographical regions, much of the existing information is site-specific and has been gathered from individual species, indicating adaptations to narrow ranges of environmental variability. However, in genera such as *Gracilaria* and *Porphyra*, which are exposed to highly changing environmental conditions in enclosed bays, estuaries or upper littoral zones, broader ranges of environmental tolerance may be expected (Gómez et al. 2004, 2005a).

Due to its physical configuration, the coast along the HCS is characterised by high energy, and hence physical perturbations such as wave action or sand erosion/accretion fluctuations are important and often govern the population dynamics of various infralittoral algae such as *Lessonia*, *Mazzaella* and *Gymnogongrus*. Thus, algae have developed a suite of morphofunctional adaptations such as alternation of crustose and erect morphs, large size and seasonal regulation of abundance (Santelices et al. 1980, Jara & Moreno 1984, Santelices & Ojeda 1984, Santelices & Norambuena 1987, Gómez & Westermeier 1991, Westermeier et al. 1994, Vega & Meneses 2001). In many cases, these adaptive strategies operate in the early development of the life cycle and in both isomorphic

and heteromorphic phase expressions. Processes such as coalescence of spores (Santelices et al. 1999, 2003), regrowth from crusts or vegetative propagation (Hannach & Santelices 1985, Gómez & Westermeier 1991, Macchiavello et al. 2003), selective mortality of early developmental stages (Martínez & Santelices 1998), differential phase ratios (Vega & Meneses 2001) and synchronisation of spore release (Edding et al. 1993, Tala et al. 2004) have been described in algae from northern-central Chile, which are related to potential selection under changing environmental conditions. While the seasonal and latitudinal gradients in environmental conditions along the HCS are recognisable, the magnitude of their impact on the physiological and reproductive biogeography of benthic algae remains diffuse. Therefore, comparative studies focused on assemblages from different sites along the HCS are needed in order to define, for example, the environmental thresholds involved in reproductive fitness, physiological adaptation and recovery capacity.

A special case: enhanced solar radiation

Ozone depletion (with the concomitant increase of UV-B radiation) over the Antarctic region, which in spring can reach areas as far north as 36°S, has opened the debate about its consequences on the marine biota of cold and temperate regions (Madronich et al. 1995, Sobolev 2000). Short wavelengths (UV-B) affect photosynthesis in different ways and have detrimental effects on DNA and other key cell components (Bischof et al. 2006). Recent studies indicate a potential impact of current solar UV radiation on photosynthesis of intertidal macroalgae from the southern limit of HCS (39°S; Gómez et al. 2004, Huovinen et al. 2006). In northern Chile (30°S), zoospores, gametophytes and embryonic sporophytes of subtidal *Lessonia trabeculata* and the intertidal *L. nigrescens* show elevated sensitivity to UV exposure, leading to high spore mortalities and decreases in germination under current UV doses (Véliz et al. 2006). In general, UV sensibility of early stages correlates with the depth-distribution patterns of the parental sporophytes, suggesting that this factor may play a relevant role in depth zonation of benthic algae in this region (Gómez et al. 2005b). Recent surveys indicate that intertidal species display various photoprotective mechanisms, in particular the ‘dynamic photoinhibition’, regarded as a down-regulation of the photosynthetic apparatus to quench the impact of excess energy (Gómez et al. 2004). Some intertidal algae also have noticeably high contents of UV-absorbing substances (e.g., mycosporine-like amino acids) (Huovinen et al. 2004). Whether algae from different latitudes exhibit a differential susceptibility to UV radiation in the context of the HCS remains unclear and future work should give new insights into the ecophysiological strategies of macroalgal assemblages in scenarios of climate change.

A brief history of exploitation of natural resources in the HCS

First coastal settlers

Evidence of coastline occupation off Peru and Chile may date from as early as 11,000 yr ago (Llagostera 1979, Muñoz 1982, Báez et al. 1994, Keefer et al. 1998, Sandweiss et al. 1998, Méndez 2002, Méndez & Jackson 2004, Santoro et al. 2005). One of the first studies of the earliest human habitation along the coast of northern-central Chile (Arica to Coquimbo) was carried out by Junius Bird in 1941 during excavations of shell middens. This author (Bird 1943, 1946) showed that the earliest evidence of human settlements on this coast went back to ~6000 yr before present (BP) and people used highly specialised artifacts with an efficient maritime adaptation. According to Santoro et al. (2005) evidence of the earliest inhabitants (~11,000 yr BP) is difficult to find since most prehistoric sites are now on drowned landscapes. However, there is clear evidence that coastal populations in northern-central Chile used marine natural resources during the Holocene (Llagostera 1979). It is thought that early fishermen dived in subtidal waters to collect molluscs and they also

spear large fish and marine mammals such as sea lions (*Otaria juvata* and *O. flavescens*) (Santoro et al. 2005). A report on the navigation off the west coast of South America carried out by Lothrop (1932) showed artifacts used by aboriginal people of northern Chile. Most remarkable was a raft composed of two cylinders of seal hides tied together to support a small platform on top, and while voyages out of sight of land were rarely attempted, it was not uncommon to remain at sea for 2 or 3 days (Lothrop 1932).

Llagostera (1979), working between 21°S and 25°S, found evidence of groups of people with the ability to exploit natural resources from coastal waters ~10,000 yr BP, and he found remains of molluscan species such as *Concholepas concholepas*, *Fissurella* spp., *Tegula atra*, *Choromytilus chorus*, several species of fishes (e.g., *Isacia conceptionis* and *Trachurus murphyi*), and semi-fossilised bones of sea lions and dolphins. Reports from southern Peru suggest specific sites where mainly fish and seabird resources were exploited (Keefer et al. 1998), while at other (more ephemeral) sites they processed mainly molluscs (Sandweiss 2003). Studies from southern Peru and northern Chile demonstrated that the resources exploited by early coastal settlers of the HCS changed with time (Llagostera 1979, Sandweiss et al. 2001), which is taken as an indication of climate change and EN events, causing gradual or abrupt changes in available resources. Similar observations were made in central Chile near 32°S (Báez et al. 2004). For the late Holocene (4000–2000 BP) Méndez & Jackson (2004) reported a high degree of mobility of coastal people in central Chile, who apparently moved between different sites in a region, exploiting the accessible resources at a given site in an opportunistic manner.

A systematic study of remains of marine invertebrate fauna from central Chile (Curaumilla, 33°S) defined the ecological role of early inhabitants as shellfish gatherers (Jerardino et al. 1992). According to these authors, they probably modified areas of the rocky intertidal, causing decreases in mean sizes of *Concholepas* and *Fissurella*. Interestingly, Llagostera (1979) suggested that the appearance of larger shells of *Concholepas* in shell heaps is indication of an increasing radius of action and the exploitation of new fishing grounds. This author also remarked that the appearance of some fish species (e.g., cusk eels, locally called 'congrío', from the genus *Genypterus*, which can only be fished at greater depths) around 3000 BP is indication that coastal fishermen started to venture farther out to sea during that time period.

In general, prehistoric people used littoral resources in an opportunistic manner, and during the past millennia they increasingly widened their radius of action, improved their navigating skills (rafts) and developed their fishing techniques (fishing nets, hooks). Extraction of marine resources was not only for subsistence of local groups, but also for an intensive transfer of fish toward inland sites (Briones et al. 2005). Local people persisted and exploited marine resources until well after the appearance of the Spanish (Llagostera 1979). The resources collected and captured by prehistoric people are the same that still today play an important role in the fisheries of northern and central Chile.

Artisanal benthic fisheries

The present artisanal fisheries in the HCS between 18°S and 35°S are very diverse, comprising ~13 species of algae, ~45 species of invertebrates (molluscs, crustaceans, echinoderms, tunicates) and ~68 fish species (SERNAPESCA 2005). Before the 1980s, fisheries in general were of low level and stable since products only went to local markets and the intensity of exploitation was comparatively moderate (Stotz 1997, González et al. 2006). During the mid-1980s the export of most of the resources was initiated, producing increases in captures, and once the accumulated biomass was used up, the resources remained at low and fluctuating levels (Figure 22). In general, these fluctuations have been interpreted as the classical signs of a badly regulated fishery, as

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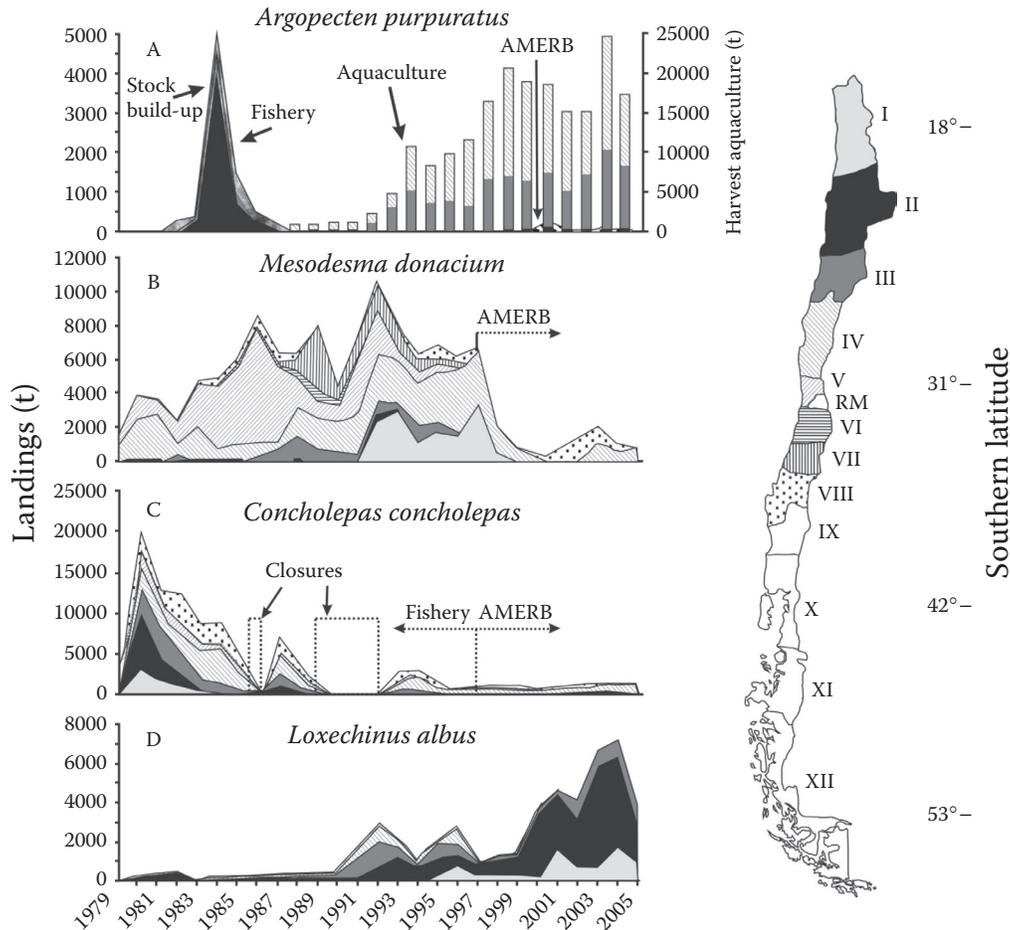


Figure 22 Landings of the four most valuable invertebrate resources in Regions I–VIII, according to fishery statistics of SERNAPESCA: www.sernapesca.cl and AMERB, ‘Area de Manejo y Explotación de Recursos Bentónicos’ (MEABR, Management and Exploitation Area for Benthic Resources).

described by Hilborn & Walters (1992): discovery of a stock, development of its fishery and subsequent overexploitation and eventually collapse.

In order to improve the management status of benthic fisheries (mainly dive fisheries for invertebrates and algae), Chile has established a system of Territorial User Rights for Fisheries (TURF), called Areas de Manejo y Explotación de Recursos Bentónicos (AMERB or Management and Exploitation Areas for Benthic Resources MEABR, which are the diverse names and shortcuts under which they have been described in the literature) (Castilla 1997, Stotz 1997, Castilla & Fernández 1998, Aviléz & Jerez 1999, Bernal et al. 1999, Meltzoff et al. 2002, González et al. 2006). This management tool grants exclusive fishing rights over a defined coastal area to legally established organisations of local fishermen. These areas are exploited according to a management plan, developed by professionals, approved by authority, and then worked by fishermen under the permanent supervision of the administrative authority. This system was initiated in practice by fishermen at the beginning of the 1990s, but legally established in 1997 (Stotz 1997). In general, it has proven to be a good tool to increase stocks and recover depleted fisheries (Stotz 1997, Castilla

& Fernández 1998, González et al. 2006), albeit it appears to be deficient in particular situations (e.g., Gelcich et al. 2006).

Since resource stocks are continuously monitored in management areas, with captures well controlled and registered, it has been possible to begin to understand the underlying nature of fluctuating landings. Contrary to the above-described classical pattern of a badly managed fishery, it has often turned out to reflect the natural variability of the environment of the HCS. Global-scale phenomena, such as EN events, which produce an outburst of some resources and disappearance of others, together with more localised processes of upwelling and current systems, generate a complex, spatially and temporally changing, mosaic of conditions. Fluctuating fisheries are mainly the consequence of this, the fishermen following (and suffering) natural variations, but not always causing them, as generally assumed. The following description of the four most valuable resources fished by artisanal fishermen illustrate this.

Case studies

Scallop fishery

The scallop fishery can be considered as a ‘boom-and-bust’ fishery, where the ‘boom’ is caused mainly by EN events (Wolff 1987, Stotz 2000, Wolff & Mendo 2000, Stotz & Mendo 2001, von Brand et al. 2006). During EN, recruitment of *Argopecten purpuratus* is intense, and during following years, given the normal fast growth of the species (Stotz & González 1997), huge stocks of scallops build up, with fluctuations of several orders of magnitude between years (Figure 22A, stock increased with EN 1982–1983; Figure 23A stock increased with EN 1997–1998) (Stotz & Mendo 2001). However, following the increased scallop stocks, the development of similar predator populations and/or the shift of prey preference of predators in response to increased scallop abundance (Ortiz et al. 2003), together with the fishery, leads to an increasing mortality, which finally generates the ‘bust’ (Figure 23A) (Wolff 1987, Jesse & Stotz 2002, León & Stotz 2004). Fishermen are just able to take advantage of part of the EN production before the natural mortality, caused mainly by predation (e.g., by *Octopus mimus*), but also by mass strandings (González et al. 2001), takes most of the scallops away (Figure 23B). Normal (LN) years are characterised by small and, due to spatially (Aguilar & Stotz 2000) and temporally variable recruitment, fluctuating scallop stocks, which supply a low-level fishery (Figure 22A). Taking advantage mainly of natural recruitment while preventing predation, in northern Chile aquaculture has been able to build up stocks and harvest at levels several times above fishery production (Figure 22A) (Stotz 2000).

Surf clam fishery

The ‘macha’ *Mesodesma donacium* fishery also shows boom and bust fisheries along the coast (Figure 22B). In the past, on most sites a relatively stable low-level fishery existed, produced by fishermen working in the intertidal zone. During the mid-1970s fishermen learned also to dive for this resource, which means putting the boat behind the breakers (‘rompiente’), diving, loaded with at least 40–50 kg of lead, through the surge and then working underneath the breakers. This began in Region V (32–35°S). After having depleted the local stocks in Region V, some fishermen came over to Region IV (29–32°S), where the local fishermen quickly learned the same technique. This has generated a tradition of divers, mainly from Regions IV and V, working on the macha along the entire Chilean coast, making use of and depleting macha stocks throughout the country (Figure 22A). However, after the establishment of AMERBs for this resource, other reasons for the depletion became apparent. With the EN 1997–1998 all the macha beds between Arica and Coquimbo, managed conservatively within AMERBs, died off within a few days. The beds in Coquimbo were smothered by mud, washed into the bay by a river flood due to heavy rainfall (Miranda 2001). For

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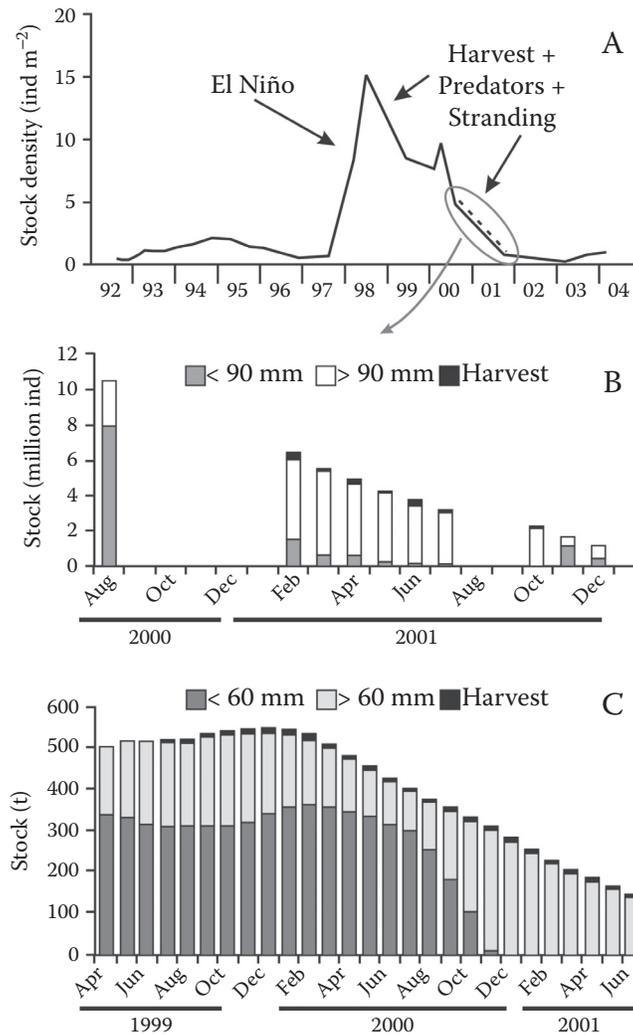


Figure 23 (A) Stock size of the scallop *Argopecten purpuratus* in an AMERB, (B) the impact of the harvest on the decrease of the same scallop stock, and (C) of a *Mesodesma donacium* stock in another AMERB, ‘Area de Manejo y Explotación de Recursos Bentónicos’ (MEABR, Management and Exploitation Area for Benthic Resources).

Arica no specific reason was identified, but increased temperatures have been mentioned as a cause of mortality for the same species in Peru (Arntz et al. 1987, 1988). In the Coquimbo area, the only beds left were in Tongoy Bay, which were exploited according to what was considered then a very conservative strategy. However, despite dynamic (and apparently conservative) management, these beds also disappeared (Figure 23C) (Aburto & Stotz 2003). Captures were almost irrelevant compared with the natural decrease (Figure 23C), which was not renewed by recruitment, because larval supply is spatially (Ortiz & Stotz 1996) and temporally very irregular or absent during many years. A similar situation was shown for macha beds managed within management areas in Region VIII, where, due to the almost complete lack of recruitment, the stocks within the AMERBs collapsed by 2004 (Figure 22B) (Stotz et al. 2004). Following their disappearance during or after

EN events, the recovery of local macha beds can be extremely slow, as observed in Peru (Arntz et al. 2006).

The 'loco' fishery (sold as 'Chilean abalone' in international markets)

The loco fishery makes use of the muricid gastropod, *Concholepas concholepas*, described as a top predator in the intertidal systems (Castilla & Paine 1987), but with its fished populations mainly occurring in the subtidal zone (Stotz 1997). In such areas and given that its main prey items are suspension feeders (barnacles, tunicates), the species appears more as a browser, through its prey taking advantage of high PP in the water column near upwelling areas (Stotz 1997, Stotz et al. 2003). Thus, production and consequently fishery landings vary greatly along the coast, with main landing sites coinciding with the most important upwelling areas (Figure 24) (Stotz 1997). Given

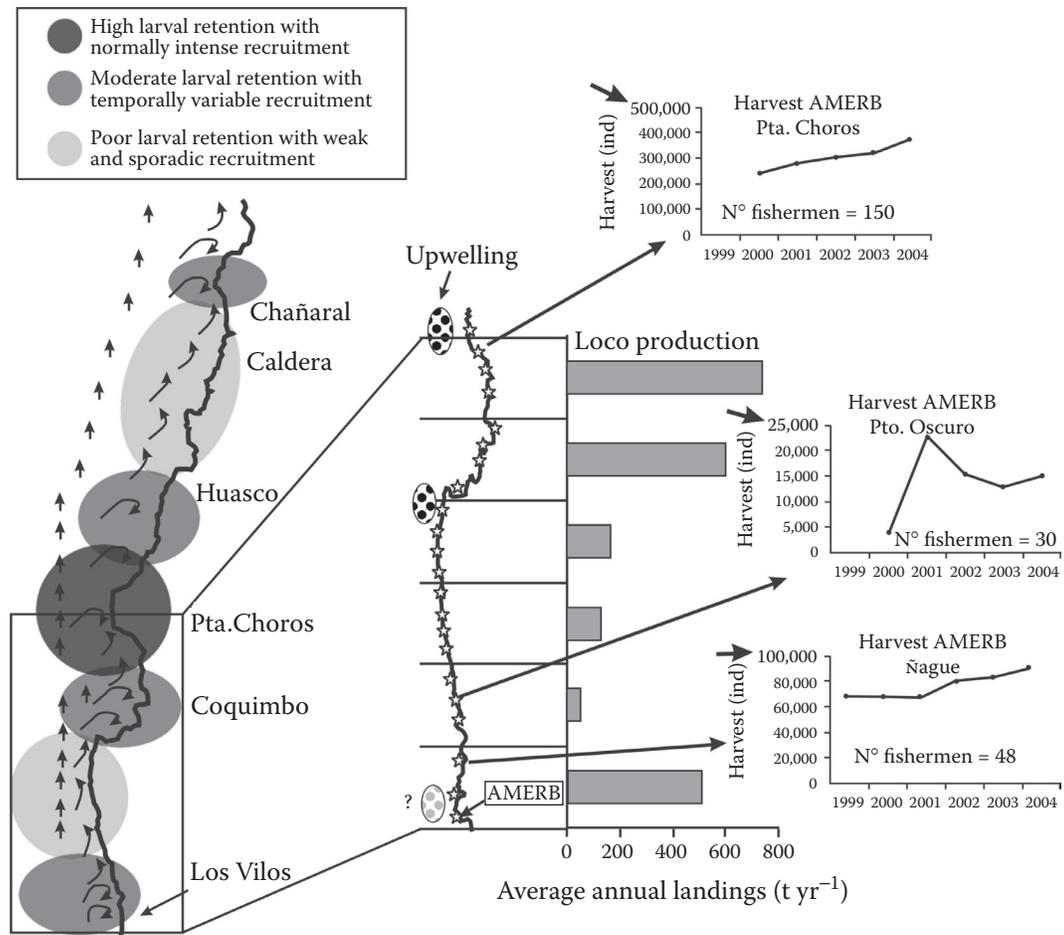


Figure 24 *Concholepas concholepas*: Variability of larval retention and recruitment along the coast of Regions III and IV, production (average of the period 1985–1995) along the coast of Region IV and harvests of three AMERBs located at coastal areas differing in production (note the scale of y-axis). (Figure adapted from J. González et al. (2004) and Stotz (1997)) Harvest data of AMERB obtained from SERNAPESCA (www.sernapesca.cl); stars show for Region IV the approximate locations of the AMERBs, 'Area de Manejo y Explotación de Recursos Bentónicos' (MEABR, Management and Exploitation Area for Benthic Resources).

its complex reproductive biology, which starts with reproductive aggregations for copula, the laying of egg capsules in which the larvae develop for about 30 days, then followed by a 3-month period of pelagic life, the result is high recruitment variability at temporal and spatial scales, depending on coastal oceanography and topography, and the potential for retention areas (Stotz 1997, J. González et al. 2004) (Figure 24). Larvae settle and metamorphose mainly on adult barnacles covering adult shells (Manríquez et al. 2004) or in association with recently settled barnacles (Stotz et al. 1991b), which may vary greatly between years and sites (Stotz et al. 1991a). This produces a very complex metapopulation structure (J. González et al. 2004, 2006). However, given its long life, with individual growth varying greatly (depending on food availability), fluctuations become partly attenuated when the individuals finally recruit to fisheries at an age between 3 and 4 yr with a size of 10 cm of peristomal opening length (Pérez & Stotz 1992, Stotz & Pérez 1992, Stotz 1997). Thus, while spatial variability of the fisheries is great, the temporal variability at each site becomes partially attenuated (Figure 22C after 1996), with fluctuations at the level of two to three times, which nevertheless means significant changes in the income for fishermen (Figure 24, harvest in AMERBs). The establishment of AMERBs, which was mainly motivated by the closure of the loco fishery at the same time (1989–1992), coincided with a period of increased loco stocks along most parts of the central Chilean coast, probably favoured by the closure and a short period in which fishermen agreed to strictly obey that measure (Stotz 1997). The relationship of the number of fishermen to the size of the management area was at that time generating an acceptable income, but this situation has mostly changed drastically in the following years. At present, many fishermen located at coastal areas with low production are dissatisfied and willing to abandon their AMERBs (compare magnitudes of harvest of AMERBs and number of fishermen in the organisation, shown in Figure 24).

Sea urchin fishery

The urchin *Loxechinus albus* fishery in the HCS between 18°S and 35°S is perhaps one of the most variable ones, in this case natural variability probably being increased as a consequence of captures. In central Chile (Regions IV–VIII), urchins are restricted to shallow areas with great surge on the exposed coast, in which the species is partly safe from the predation of the rock shrimp *Rhynchocinetes typus* (Stotz 2004), a species with abundance and distribution pattern that responds to the variable existence of refuges from its own predators (Caillaux & Stotz 2003). This produces a very patchy distribution of sea urchins. Recruitment occurs mainly inside the adult aggregations, where recruits are protected by the spine canopy (Stotz et al. 1992). Thus, when fishermen, taking advantage of calm weather conditions, reduce the stocks, subsequent recruitment is probably heavily affected. The observation is that once a site is fished for this species, it only recovers about 10 yr later (Stotz 2004). Further north (Regions I–III, mainly between 20°S and 23°S), the fluctuations attenuate slightly and landings increase, as large *Macrocystis* beds appear (Stotz 2004). There, a more conservative exploitation is carried out inside the AMERBs, conserving patches, and this strategy has allowed an increase in numbers, the sustainable exploitation of which nevertheless still needs to be demonstrated (Figure 22D).

Resource dynamics and management of artisanal benthic fisheries

The great natural spatial and temporal variability of resources, and hence fishery production, which characterises the HCS between 18°S and 35°S, poses a great challenge to management. Fishermen, through AMERBs and legal restrictions, are not allowed to move away when a resource goes through a low cycle, as they used to do in the past. Illegal movement, though still occurring, is also increasingly prevented in practice by conflicts with the respective local fishers. This produces

the risk that fishermen continue fishing on a weakened population, perhaps producing its collapse to a degree where recovery is severely compromised. Additionally, the distribution of fishermen along the coast within each region in general is not well adjusted to its spatial productive variability, thus creating great differences of income along the coast, with fishermen's organisations located at productive sites getting increasingly richer, and others at unproductive sites (as shown with harvest in AMERBs in Figure 24) getting increasingly poorer, which could be a source of conflicts (Gelcich et al. 2005, Stotz & Aburto 2006). The challenge is to advance to an integral management strategy in which fishermen, instead of rotating between fishing zones along the coast, rotate between fisheries of different resources or among other related activities (processing, tourism, etc.) in order to produce income during years or months of poor production. This means a change from a specialist to a generalist strategy, but with very strict control of their numbers, such that they are well adjusted to local production levels. Complementary stock enhancement, using biological and ecological knowledge and aquaculture experience, might help to mitigate natural fluctuations (Stotz et al. 1992, Zamora & Stotz 1994, Pacheco & Stotz 2006). In order to avoid the risk of increased fishing pressure (caused by restricting movements of fishermen) on already weakened populations, the establishment of a network of small reserves along the coast should be considered, which should also aid in reducing natural recruitment variability (see also Stotz & Aburto 2006).

Bioeconomic aspects of industrial crustacean fisheries

An important crustacean bottom-trawl fishery exists in northern and central Chile, particularly between Regions II and IV. This fishery, which includes the nylon shrimp (*Heterocarpus reedi*), yellow squat lobster (*Cervimunida johni*) and the red squat lobster (*Pleuroncodes monodon*), is conducted on the continental shelf at depths ranging from ~100 to 600 m. The exploitation of these resources began in the 1950s as fauna accompanying catches of hake *Merluccius gayi* and was subsequently developed into a fishery specific for these crustaceans (Arana & Nakanishi 1971, SUBPESCA 1999a,b). A growth phase for these fisheries occurred between 1958 and 1968, during which annual landings of nylon shrimp reached 11,000 t. Subsequently, landings declined to less than 3000 t in 1979. Between 1980 and 1986 landings remained below 4000 t, except for 1983, when landings exceeded 6000 t. The last period is interesting in its analysis since it coincided with three fundamental factors: (1) from 1979 to 1982 the exchange rate (Chilean peso/U.S. dollar) was 39 Chilean pesos/U.S. dollar, which produced a depressive economic effect, resulting in the collapse of fisheries companies; (2) in 1983 the occupation of new fishing grounds south of Region IV increased the catch levels above those previously obtained; and (3) from 1984 to 1986 a reorganisation of the fishing fleet occurred due to the opening of the fishery for the red squat lobster (*Pleuroncodes monodon*) along with an increase in world prices for this resource. Between 1989 and 1991 the fishery was closed in Regions V and VIII, but it remained open in northern Chile. In this northern area after 1986 there was an increase in landings of squat lobster reaching 10,620 t in 1995. After this year there was a clear decrease in these landings, reaching 4000 t in 2000.

Since 1995, the three species are subject to catch quotas per boat owner, based on a total allowable catch (TAC), which is determined annually, following direct resource evaluations. A period of difficulty in the crustacean fisheries due to decreasing stocks began in 1999 in northern-central Chile (SUBPESCA 2005a,b). The TAC per Fisheries Unit of nylon shrimp (Regions II–VIII) dropped over four subsequent years from 10,000 t in 1997 to only 4000 t in 2000 (i.e., a 60% decline). The TAC of the fishery for the yellow squat lobster in Regions III and IV dropped from 6000 t in 1998 to 4000 t in 2000, representing a reduction of 33% during that time period. This substantial reduction in landings caused a major decline in the activities of the fishing fleet and the packing plants. During 2002, some companies closed, with important losses in employment producing socioeconomic impacts in the regions affected (Pérez 2003, 2005). This brief overview

underscores that the fishery of these benthic crustaceans is highly dynamic, driven not only by biological factors, but also by administrative decisions and economic considerations. In the following section some relevant information on the biology of these three species is provided before presenting a case study highlighting the relationship between catch-based stock estimates and species biology.

Basic biology of nylon shrimp and squat lobsters

The main bathymetric distribution of these species shows a strong overlap with the OMZ between ~50 and ~600 m, where they occur on gravel and mud bottoms (SUBPESCA 1999a,b). Their latitudinal distribution ranges from 25°S to 39°S (*Heterocarpus reedi*), from 6°S to 40°S (*Pleuroncodes monodon*), and from 29°S to 38°S (*Cervimunida johni*) (Acuña et al. 1997, 1998, Quiroz et al. 2005). Little is known about their food resources. All three species themselves are important prey organisms for demersal fish predators (e.g., flounders and hake), and it has been discussed that the OMZ may represent a refuge from predation (Villarroel et al. 2001). Most information about the biology of these crustacean species is based on analysis of specimens obtained from commercial or research catches.

Heterocarpus reedi

Available data suggest seasonal migrations with the main concentrations of shrimp found at great depths (>400 m) in austral summer, at shallow depths during austral winter (<200 m), and at intermediate depths in autumn and spring (SUBPESCA 1999a). During austral summer/early autumn, a comparatively large proportion of individuals has a soft carapace, which indicates that moulting is frequent during this time period (SUBPESCA 1999a), possibly accompanied by mating. Following this period, ovigerous females are found throughout winter and early spring (May–November) with a peak abundance in July–August (SUBPESCA 1999a). Larval release is initiated in September. Fecundity has been estimated at 1000–10,000 eggs, and it is generally assumed that each female produces one clutch per year (SUBPESCA 1999a). Catches have consistently shown higher proportions of females than males, with males smaller in size than females.

Cervimunida johni

Moulting and copulation are thought to occur mainly during the summer months (SUBPESCA 1999b). Embryo incubation extends from May to November, with the highest proportion of ovigerous females observed in July–August (in September–October in the northern zone) (SUBPESCA 1999a,b). Larvae are released during the spring months. Fecundity has been estimated at 500–14,000 eggs in Regions III and IV, although some females in these and other regions have been found with >20,000 embryos. Males reach substantially greater sizes and weights than females, and average size at first maturity (of females) varies substantially among years (Acuña et al. 2005). It is generally assumed that each female produces only one clutch per year, and Arancibia et al. (2005) suggested that *C. johni* is a slow-growing species, with individuals living up to 11 yr.

Pleuroncodes monodon

Based on the main occurrence of ovigerous females it has been suggested that mating occurs mainly in late summer/early autumn (Palma & Arana 1997). Embryo incubation extends from April to November, with the highest proportion of ovigerous females observed in July–August (Palma & Arana 1997). All embryonic developmental stages were found between June and October (Palma & Arana 1997), suggesting that not all females mate at the same time. The first planktonic larvae

appeared in June, and early developmental stages were found in the plankton until December (Palma 1994), supporting the suggestion that reproduction is not synchronised among females. Gallardo et al. (1994) reported the first benthic stages in March with very high densities of recently settled squat lobsters in April. Roa et al. (1995) identified nursery areas in places with very low oxygen concentrations from where juveniles migrate to nearby adult habitats. It is generally assumed that females produce only one clutch per year, but the extended reproductive period and the apparently short incubation period of 2–3 months (Palma & Arana 1997) could allow some females to produce more than one clutch per year. Fecundity has been estimated at 1800–34,000 eggs in Region VIII (Palma & Arana 1997), and most females reach sexual maturity at carapace lengths of ~25 mm. Red squat lobsters are estimated to live from 5 to 10 yr (Roa & Tapia 1998).

Biology and stock estimates

As can be seen from the preceding section, information on the biology of the nylon shrimp and the squat lobsters is mainly based on demographic data (size at first reproduction, fecundity, sex ratio, per cent ovigerous females, embryo developmental stages), but little information is available on their behaviour. A close analysis of monthly landings suggests possible seasonal changes in behaviour during the year and indicates that it is important to incorporate this information in stock estimates (Pérez 2005).

Pérez (2005) proposed that the biomass of the nylon shrimp showed well-defined cycles of availability (*sensu* Menge 1972), which were not related to its true abundance in biomass (*sensu* Menge 1972). The first cycle (termed the ‘short cycle’) occurs from September to December and is characterised by a decrease in availability (minimum in October), followed by a recovery (maximum availability in December). This leads to a cycle of greater length (termed the ‘long cycle’), characterised by a decline in available biomass, reaching a minimum in April and followed by an increase again reaching a maximum in August. Reasons for these cycles are not clear, but it has been suggested that they are related to the moult and reproduction. In this sense, a sudden decrease in availability could be due to recently moulted individuals hiding from predators (Pérez 2005).

The total biomass of *Heterocarpus reedi* in Region IV in September 1997 was estimated to be about 5000 t, but not all of these shrimp were susceptible to fishing gear, resulting in an available biomass (to the fishery) of 4200 t (for details see Pérez 2005). The estimated total biomass decreased to 2000 t in August 2000 (Week 143), representing a decline of 60% from that estimated at the initiation of the simulation (Figure 25A). However, the percentage variation in the catch per unit effort (CPUE) was not proportional to the decrease in abundance within periods of maximum availability (Figure 25A). At the beginning of the study period, the CPUE was 0.59 t haul⁻¹, and in August 2000 this decreased to 0.45 t haul⁻¹, representing a decrease of only 24%. In recruitment, at each fishing station in 1997–1998 and 1998–1999 the difference between the control curves and availability allowed the identification of two time windows for recruitment, one of lesser intensity in December and one of greater intensity extending through June and July. This seasonal variation in the availability of the resource to the fishing gear has a direct influence on the population estimates and consequently the determination of TACs. Therefore it was recommended to include this biological information in stock evaluation and to conduct the corresponding research cruises during periods of maximum availability of the resource (Pérez 2005).

Crustacean fisheries and economic considerations

Fisheries respond not only to fluctuations in stock abundance but also to economic considerations. From the economic perspective, the annual TAC system has produced an increase in the fishing

THE HUMBOLDT CURRENT SYSTEM OF NORTHERN AND CENTRAL CHILE

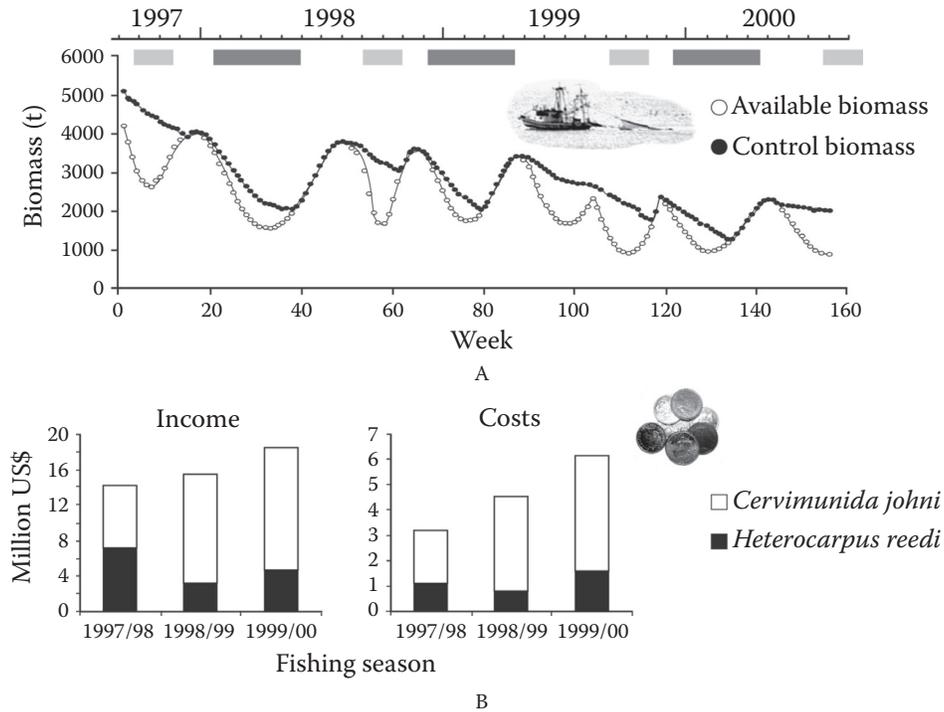


Figure 25 (A) Biomass dynamics of the nylon shrimp in Region IV. Available biomass is the biomass that is available to the fishery and control biomass is the estimated total biomass of the resource according to the model by Pérez (2005); bars above figure represent short cycles (light shading) and long cycles (dark shading) when resource becomes unavailable to fishery for biological reasons; for further details see text and reference. Weeks are numbered beginning with the week of 1 September 1997. (B) Comparison of total income with total costs by resource of crustacean trawl fishery in Region IV.

effort, measured in terms of hauls, resulting in a decrease in the expected economic benefit based on administrative measures. Pérez (2003) explored the bioeconomic effect produced by the decrease in CPUE in the nylon shrimp and yellow squat lobster fisheries in northern Chile during 1997–2000. A biological-technological simulation model was used by Pérez (2005), which took both physical and biological variables into account. An economic submodel was incorporated into this model in order to carry out an integrated analysis of the crustacean fisheries, which included the subsector involving catches and their processing. The economic results obtained, when integrated with the catch results and size of the stocks, allowed the dynamics of this fishery to be explained in Regions III and IV during 1997–2000, when the catch increased by 21%, and final production increased by 24% (measured as frozen tails), although the variable costs increased by only 11% (Figure 25B). In this same period the fisheries costs increased by 117% and the total production cost increased by 93%. The results showed that part of the economic benefit was lost due to the effect of a decrease in the biomasses of both resources and an excessive increase in the average production costs (due to increased costs of fishing and extraction).

This example underscores the importance of incorporating economic reference points in addition to biological (biomass) and fishery variables (CPUE and catch). Furthermore, basic biological data (larval ecology, settlement biology, habitat requirements, seasonal migrations, and mating behaviour) still need to be revealed for these three crustacean species. At present, very little is

known about the influence of oceanographic factors on recruitment success and stock dynamics of crustaceans from the continental shelf off northern-central Chile. Most current information suggests that their life history is driven by seasonal factors, and presently available data do not permit an examination of the effects of interannual variability in oceanographic conditions (e.g., ENSO) on their population dynamics. Future studies should address these questions in order to achieve a sustainable fishery.

Pelagic fisheries and fisheries management, 1980–2005

The Chilean purse seine fleet mainly exploits five pelagic fish species: anchovy (*Engraulis ringens*), jack mackerel (*Trachurus murphyi*), chub mackerel (*Scomber japonicus*), and Pacific sardine or pilchard (*Sardinops sagax*) and common sardine (*Strangomera bentincki*). There were doubts about the taxonomic status of jack mackerel (Stepien & Rosenblatt 1996, Oyarzún 1998), but a recent molecular study revealed that the name *Trachurus murphyi* should be conserved (Poulin et al. 2004). In the official landing statistics it is also recorded as *T. murphyi*, but the Technical Reports of the Undersecretary of Fisheries refer to it as *T. symmetricus*.

History of the catches

Aguilar et al. (2000) described the development of the Chilean pelagic fisheries based on the landings of anchovy, jack mackerel and pilchard from 1970 to 1995. Herein the period from 1995 to 2005 (also known as the ‘regulated’ period) is included, which adds two additional species: chub mackerel and common sardine, and their landings since 1980.

The total annual landings captured by the Chilean purse seine fleet during the study period showed a steadily increasing tendency from 1980 until 1995, from 3.4 million t to almost 6.9 million t, driven mainly by the increase in jack mackerel landings and secondarily by anchovy landings, which replaced the Pacific sardine, the most important species during the early 1980s (Figure 26). After that, the total annual catch decreased to around the same level found at the beginning of the study period, with the exception of 1998, when both species simultaneously showed a sharp decline in their landings. However, as stated, these are ‘regulated’ landings since catches are the result of fixed total annual quotas and therefore not necessarily representative of resource availability.

Administratively, four of the five species included in this analysis are latitudinally assigned to fisheries units, each of which comprises two to five administrative zones: Regions I–II (18°25’S–26°06’S), Regions III–IV (26°06’S–32°18’S), Regions V–IX (32°18’S–39°37’S) and Regions X–XII (39°37’S–56°30’S), and there is a strong difference in landings between the respective fishery units (Figure 26). Therefore, annual landings are analysed by species and these latitudinal fisheries units to visualise their importance in each of them. In the following text each Fisheries Unit is defined by the Regions it contains, e.g., Fisheries Unit I-II.

Landing statistics of anchovy show the typical characteristics of engraulids, with successive increases and decreases, attaining highest landings of 2.7 million t in 1994, but landings usually do not surpass 1.5 million t. Anchovy landings are most important in northern Chile (Fisheries Unit I–II) (Figure 27). In contrast to all other species, jack mackerel showed a continuous increase until 1995, when annual landings reached 4.4 million t, after which catches continuously decreased again. Throughout this period, catches in central-southern Chile (Fisheries Unit V–IX) had overriding importance (Figure 27). The highest landings of chub mackerel were attained in 2003 with 0.5 million t. This species has shown a steady increase in landings during the study period. At the beginning of the period, landings of chub mackerel were mainly in northern Chile (Fisheries Unit I–II) but since the year 2000 also increased in central-southern Chile (Fisheries Unit V–IX).

THE HUMBOLDT CURRENT SYSTEM OF NORTHERN AND CENTRAL CHILE

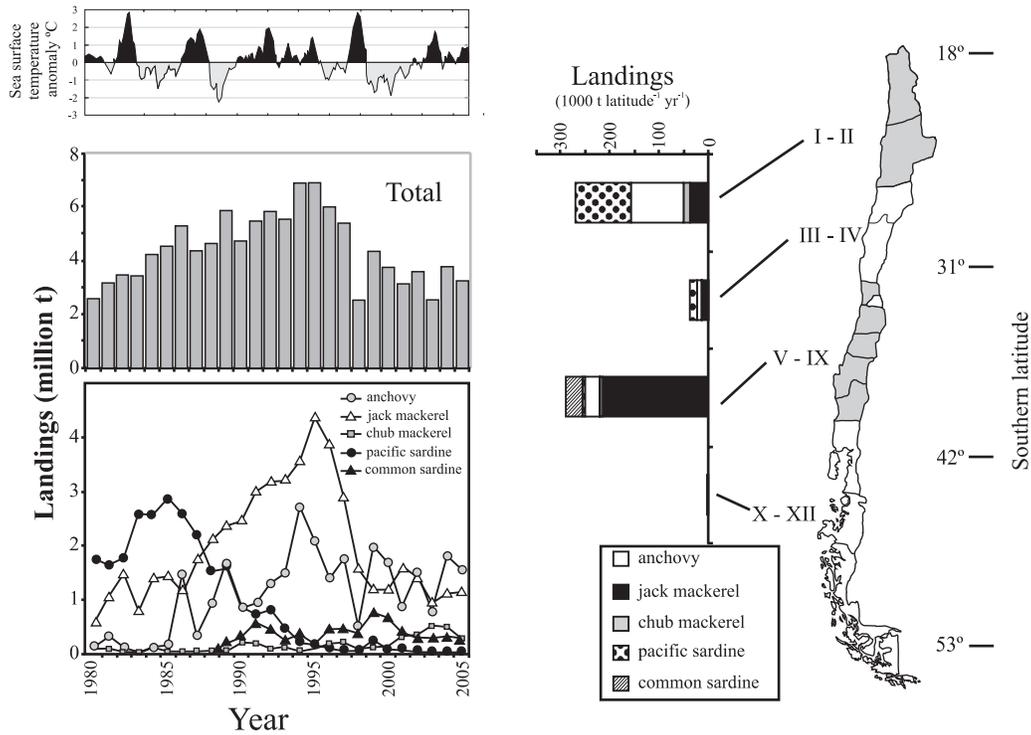


Figure 26 Total annual landings for the five most important pelagic species caught by the Chilean purse seine fleet during the period 1980–2005; left panel shows SST anomaly, total landings and landings of the five species; right panel shows average landings per latitude and year in each of the four fisheries units, calculated for the time period 1980–2005.

(Figure 27). The highest landings of Pacific sardine were attained in 1985 with almost 2.9 million t. During the 1980s this species was the most important small pelagic fish captured in Chilean waters but catches continuously decreased during the late 1980s, reaching very low levels in the mid-1990s. The Pacific sardine was most important in northern Chile (Fisheries Unit I–II) but gained proportionally in importance in central-southern Chile (Fisheries Unit V–IX) during the early 1990s (Figure 27). The highest landings of common sardine were attained in 1999 with 0.75 million t. During the 1980s this species was very scarcely captured in Chilean waters but from then on showed a steady increase (Figure 27). Landings of the common sardine were most important in the central-southern Chile (Fisheries Unit V–IX).

Relationships with oceanographic variations

The coastal areas off the Chilean coast are known for being typical of an EBC system, where upwelling is a characteristic oceanographic feature. Fonseca & Farías (1987) and other authors described the presence of active upwelling centres in several areas of the Chilean coast, like Iquique (Fuenzalida 1990) and Antofagasta in Fisheries Unit I–II (Blanco et al. 2001), Caldera and Coquimbo (Acuña et al. 1989) in Fisheries Unit III–IV, Valparaíso (Johnson et al. 1980) and Concepción (Cáceres & Arcos 1991) in Fisheries Unit V–IX.

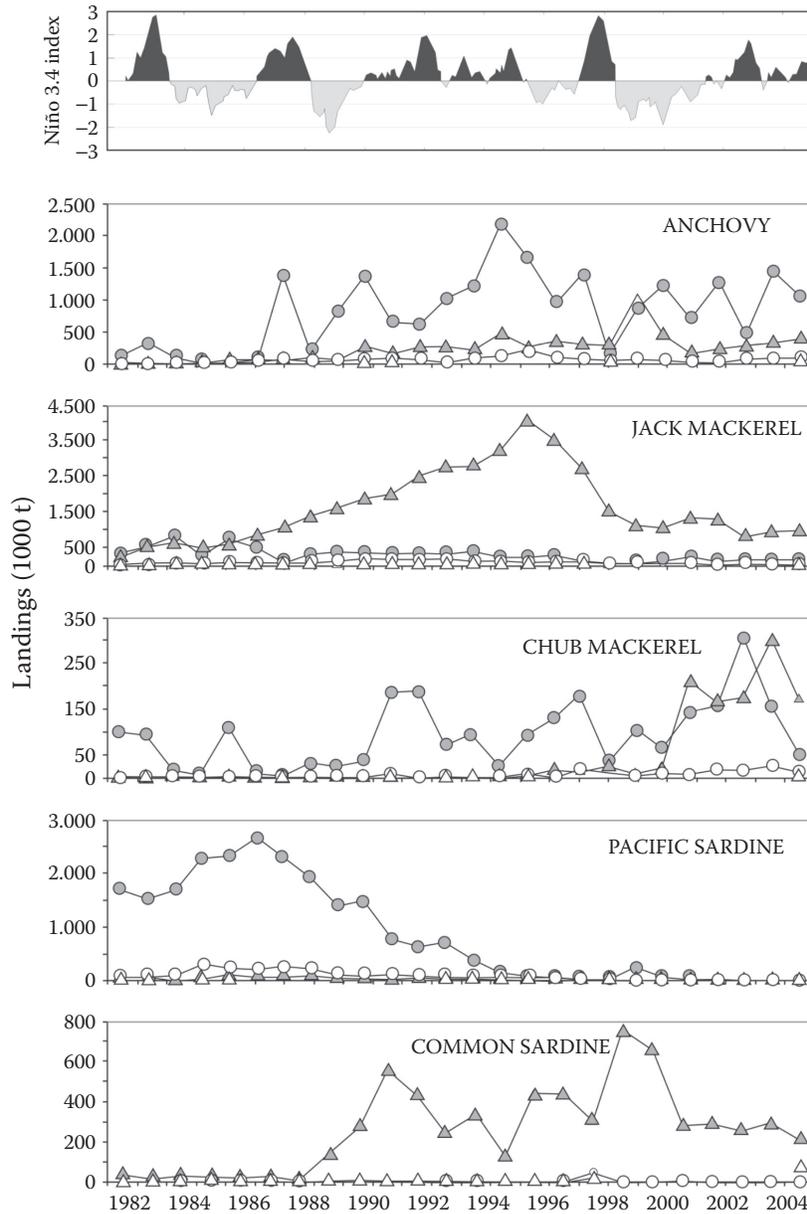


Figure 27 Total annual landings for the five most important pelagic species caught by the Chilean purse seine fleet during the time period 1980–2005 in the respective fisheries units; grey dots represent Fisheries Unit I–II, open dots Fisheries Unit III–IV, grey triangles Fisheries Unit V–IX, and open triangles Fisheries Unit X–XII.

Yáñez et al. (1996) conducted a survey to assess the possibility of introducing the use of SST, obtained from NOAA (National Oceanic & Atmospheric Administration) satellite data, for the small pelagic fisheries resources and found significant relationships between species yields and TGRs. Jack mackerel yields were largely related to strong TGRs next to oceanic waters, while anchovy and common sardine yields were mainly associated with the development of coastal upwelling events. Comparison with the SST anomalies shows that landings of anchovy negatively correlate

with SST anomalies (Yáñez et al. 2001); also chub mackerel landings seem to correlate with SST (Figure 27). In contrast, interannual variations in the landings of the other three species seem to be largely independent of variations in SST (Figure 27). The stabilisation of maximum anchovy landings between 1.5 and 2.7 million t during the 1990s and the parallel decline of the landings of the Pacific sardine in the HCS (and the entire southeastern Pacific) reflects another regime shift from the warm 'sardine regime' to a cool 'anchovy regime' (Chavez et al. 2003, Alheit & Niquen 2004, Halpin et al. 2004). These regime shifts occur on multidecadal scales and are probably related to the PDO, but the mechanisms driving these changes are not yet well understood.

Silva et al. (2003) studied the relationship between chl-*a* concentration, SST, and fishing yields of anchovy, Pacific sardine and jack mackerel in northern Chile during summer and autumn 1999. CPUE superimposed over SST images confirmed that the anchovy has a more coastal distribution than Pacific sardine and jack mackerel, being found in the frontal zone of coastal areas. In the southeastern Pacific, the jack mackerel is a heavily exploited pelagic species, and its presence in the HCS in autumn and winter is assumed to be mainly due to an inshore feeding migration (Bertrand et al. 2004). During warmer years, jack mackerel may immigrate into coastal waters where they are thought to exert high predation pressure on anchovy (Alheit & Niquen 2004). Changes in SST associated with EN events may also affect the migration pattern of jack mackerel, which needs to be taken into account in stock assessment and management plans (Arcos et al. 2001).

Management of pelagic fisheries

According to Aguilar et al. (2000) the traditional method used to conserve fish stocks and prevent overfishing is to set a TAC for the fishery. Typically, TACs aim to restrict fishing effort to its MSY (maximum sustainable yield) level. Once these 'safe biological limits' are reached, fishing is prohibited. But TACs do not, by themselves, address the overcapitalisation issue. Consequently, many fisheries economists recommend that the designated TAC is distributed to industry participants in the form of individual transferable quotas (ITQs), quasi property rights that restrict additional access to the fishery. Under these rules, failure to acquire an ITQ effectively forces vessels out of the fishery, thereby reducing fishing effort and increasing harvesting efficiency.

The Chilean General Law of Fisheries and Aquaculture considers three types of access to the fishery: (1) *Full Exploitation Regime*, which includes setting an annual quota or TAC by fishing unit, which can be temporally divided during the year and also modified once during that same period (once the full exploitation regime is assigned to a given species no more fishing vessels are allowed to enter the fishery); (2) *Recovering Fishery Regime* is the fishery under a state of overexploitation, subject to a capture ban of at least 3 yr, to obtain its recovery and where an annual quota (or TAC) can be established; and (3) *Early Developing Fishery Regime*, which is a demersal or benthonic fishery with open access where an annual quota can be established and where no fishing effort is applied or if it is done it is less than 10% of this quota.

In 1993 the first pelagic fisheries in Fisheries Unit I–II were assigned the status of Full Exploitation Regime, and by 2000 this had extended to four of the five fisheries (anchovy, jack mackerel, Pacific sardine and common sardine) and to all fisheries units. The chub mackerel is one of the few commercial species that is still under 'open access', with no regulation to date.

Alternative management tools have been developed and used in the last years: in 1998, the use of a geographical positioning system for the industrial and artisanal fleets was established; later in 2001 the Límite Máximo de Captura por Armador (LMCA, maximum capture limit per owner) was introduced for the industrial fleet in the fisheries for the small pelagics anchovy, sardines and jack mackerel in all fishery units, which is essentially an ITQ, and at least had the effect of reducing the fishing fleet. The LMCAs are determined using captures (1997–2001) and corrected hold capacity (authorised hold capacity in cubic metres times authorised area length divided by total

length of fishery unit, Law 19.173). This action was set to last until 2002, but was later extended until 2012 (Law 19.849). Finally, in 2004 a similar management tool was established for the artisanal fleet, the Regimen Artesanal de Extracción (RAE, Artisanal Capture Regime), which in this case assigns the artisanal fraction of the Annual Global Quota to one or more artisanal fishermen's organisations in each fishery unit, which in turn divide it between members.

As becomes evident from the preceding paragraphs the currently valid management rules (full exploitation, Global Annual Quota, LMCA, etc.) have been implemented when landings started to decrease or stocks had already dramatically declined. Therefore, fisheries of small pelagic fisheries in the HCS off Chile are presently managed at much lower population levels than they used to be in previous decades. In fact, stocks of anchovy and common sardine in central Chile are considered to be overfished (Cubillos et al. 2002). The interaction between administrative effects on landings and fishery-induced impacts on stocks complicate the detection of direct relationships between environmental factors and fish stocks. In addition to fishery-independent stock surveys, studies of the basic biology of individual species, of biological interactions (predators, competitors, food), and of the role of climatic and coastal oceanography are required in order to improve our understanding of the factors driving the population dynamics and distribution in northern-central Chile.

Aquaculture

According to the latest reports published by the Food and Agriculture Organization of the United Nations (FAO 2006), the contribution of aquaculture to the world supply of fish and shellfish "continues to grow faster than any other productive sector of animal food origin". The world production of aquaculture registered in 2002 rose to 51.4 million t (including aquatic plants), with Asian countries producing 91.2% of this. In 2002, Chile contributed only 1.4% of the world's total production, but it is among the 10 countries showing the fastest growth in aquaculture production. Fisheries and aquaculture are for Chile one of the most important economic activities with a total income of U.S. \$2,246 million in 2003, of which aquaculture contributed U.S. \$1600 million. The largest share of the Chilean aquaculture production (80%) is from southern Chile (41–46°S), with salmon and mussels and to a lesser extent oysters, seaweeds and more recently red abalones (*Haliotis rufescens*) being the most important resources (FAO 2006).

Aquaculture activities along the coast of northern-central Chile (18–35°S), although not reaching the same levels as in southern Chile, have been continuously growing during the past two decades (FAO 2006). Given that the shorelines of northern-central Chile are relatively exposed to wave action and fully subjected to the effects of ENSO, it is particularly important to take these factors and interannual variability in oceanographic conditions into account. In fact, all aquaculture centres in northern and central Chile are located in relatively sheltered bays. The main natural resources cultured in northern-central Chile are scallops (*Argopecten purpuratus*) and seaweeds (*Gracilaria chilensis*), and their natural populations are also exposed to strong seasonal and inter-annual variations. Small-scale culture of some other species (bivalves *Mesodesma donacium* and *Tagelus dombeii*, gastropods *Concholepas concholepas* and *Fissurella* spp., sea urchins *Loxechinus albus*) has also been attempted but has not reached a commercial stage, mainly due to biological (long larval periods) and logistic (food supply) reasons. Several introduced species are also cultured in northern Chile, namely the Pacific oyster (*Crassostrea gigas*), which has been cultured on a small scale since 1970, and during recent years increasingly abalones (*Haliotis rufescens* and *H. discus hannai*).

The main resource cultured during the past two decades in northern Chile is the scallop *Argopecten purpuratus*. Culture centres are located in bays, namely Isla Santa Maria and Bahía Mejillones (22°S), Bahías Caldera, Calderilla and Inglesa (27°S), and Bahías Guanaqueros and Tongoy (30°S). Standing stocks and productivity in these bays are below those of similar bays in

Peru (Uribe & Blanco 2001). It has long been recognised that natural scallop stocks vary together with ENSO variations, mainly because settlement of small settlers (spat) is strongly favoured during EN events (Narvarte et al. 2001). Due to this relationship, the local scallop industry is affected in a positive way by EN, which can lead to an increase in spat collection by >300% (Illanes et al. 1985). In a research project on the effect of environmental factors on scallop culture, data of water temperature, gonad indices, larval abundance and recruitment (spat collection) were gathered between 1981 and 1984 in Tongoy Bay (Illanes et al. 1985). The EN event led to a temperature increase of 2°C above the pre- or post-EN levels at the sea surface and of 2.5°C at the bottom (20 m). During the EN period, the Gonad Index of adults registered a maximum (25) and a minimum (6.8) with a massive evacuation of gametes, a situation never observed during normal years (Illanes et al. 1985). Similar observations were made in southern Peru by Wolff (1988), who concluded that *A. purpuratus* is a continuous spawner with spawning peaks during late austral summer and autumn (February–March). Under the unusually high water temperatures during EN 1982–1983 (2–2.5°C above the normal temperatures), the recuperation time between two spawnings was shortened, indicating that maturation was accelerated and spawning probably intensified under these conditions. This interpretation was confirmed by the highest larval concentration found within the period. Wolff (1988) stated that it is not clear along the Peruvian coast that past EN favoured the scallops stocks. The EN 1972 apparently did favour stocks, as catches were significantly higher than during the 3 yr before and after this event, but the weaker EN 1976 did not have the same effect. In 1979, which was a ‘normal’ year, the catches still exceeded the catches of 1972. Limo (in a personal communication to M. Wolff) reported enormous numbers of *A. purpuratus* during the strong EN 1925 in Ancon Bay, north of Lima. In order to reduce the dependency on natural variations in supply of small recruits, intense efforts have been undertaken to produce settlers in the laboratory (Uriarte et al. 2001), but this only satisfies part of the requirements for scallop spat. The fact that natural spat is still obtained at much lower costs than spat produced in the laboratory may have led to the strong increase in spat collectors observed during recent years in Tongoy Bay (Figure 28). Possibly, the decreasing spat collection efficiency between 1998 and 2001 (when the total number of spat collectors in the bay exceeded 2.5 million bags) is indication that the carrying capacity is reached and that spat collectors are starting to compete for the available settlers.

Culture of *Gracilaria chilensis* in northern Chile is mainly developed on shallow soft bottoms in sheltered parts of the bays (e.g., Pizarro & Santelices 1993). Since sheltered bays are relatively scarce along the coast of northern and central Chile, aquaculture of this seaweed in this area does not reach the amounts harvested in southern Chile. Edding & Blanco (2001) observed a decrease in productivity and yield of ‘agar’ from *G. chilensis* cultured in Region IV (29°59’S) during EN 1997–1998. This may be more related to the decrease in nutrient concentrations and increase of visibility instead of the higher water temperatures. Furthermore, these authors cited González (1998), who reported that increased wave action during EN resulted in an important reduction of biomass. Growers of *G. chilensis* in Region IV also reported heavy damage to culture fields on shallow subtidal soft bottoms caused by storms during EN (R. Rojas personal communication). However, Santelices et al. (1984) stated that recovery of *Gracilaria* sp. after storms is unexpectedly fast due to regrowth of thalli from the portions buried in the sand. Overall, the production of *G. chilensis* in northern Chile does not seem to be severely affected by ENSO, but is rather determined by stock density and harvesting frequency (Pizarro & Santelices 1993). The relatively limited interannual variability in extracted and cultured biomass (Figure 28) further supports the suggestion that management rather than environmental conditions drive the production of *G. chilensis* in northern Chile.

During recent years first attempts have been made to culture large kelps from northern and central Chile (e.g., Edding et al. 1990, Edding & Tala 2003) in order to satisfy the growing needs of the abalone culture. This is considered particularly important since EN can have dramatic impacts

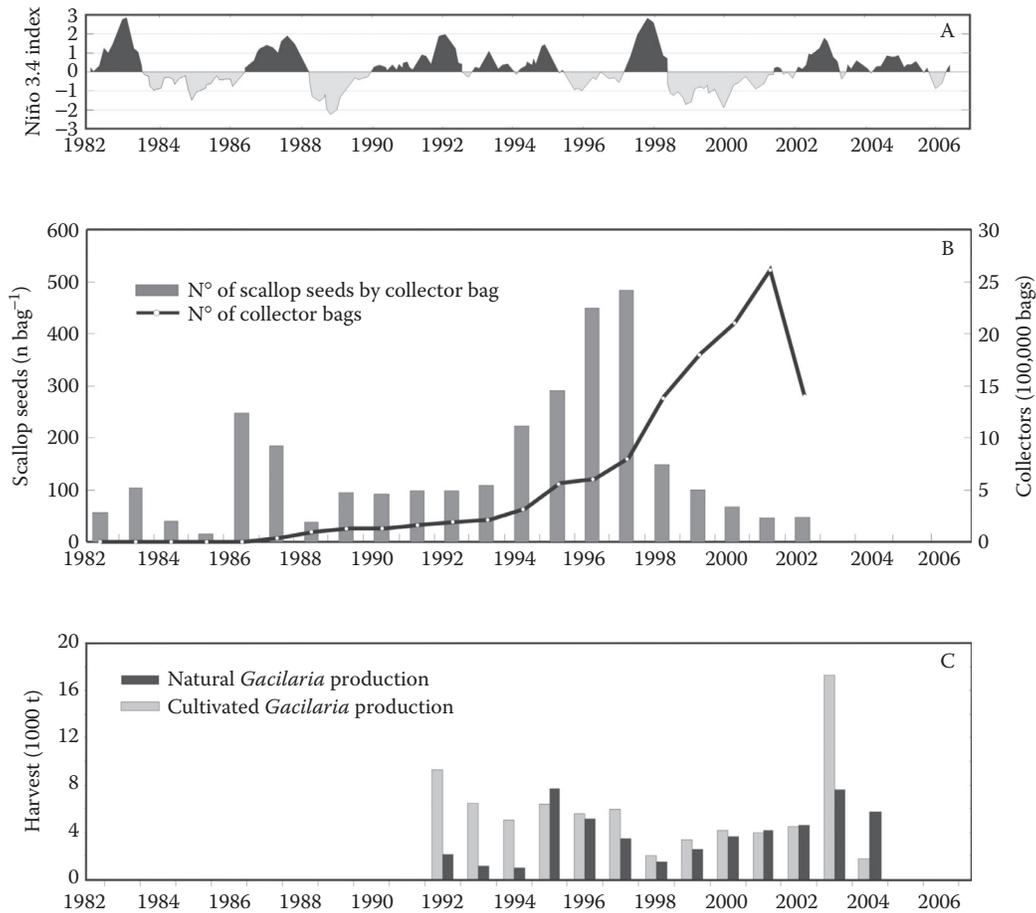


Figure 28 (A) SST anomalies for the time period 1982–2006 (from <http://iri.columbia.edu/climate/ENSO/>); (B) average number of scallop *Argopecten purpuratus* settlers per collector bag (individuals bag⁻¹) and the number of collector bags placed in Bahía Tongoy (30°S); (C) harvest of *Gracilaria chilensis* between 18°S and 35°S from natural banks and from culture beds. (Source for A and B: SERNAPESCA, Region IV, Chile.)

on the populations of large kelps and other macroalgae in northern Chile (Vásquez 1999). Kelp aquaculture is presently in a developmental phase and has not yet achieved economic importance.

Other resources currently being investigated for aquaculture in northern Chile are bivalves from sandy beaches (*Mesodesma donacium*, *Tagelus dombeii*). Culture of these bivalves is aiming at stock repopulations after extinction of local stocks (see also Artisanal benthic fisheries, p. 278ff.).

Additionally, there are several introduced species that are presently cultured in northern Chile. The Pacific oyster (*Crassostrea gigas*) was originally introduced in northern Chile in the 1970s, and despite fast growth rates, aquaculture activities then moved to southern Chile because there culture costs are cheaper (bottom culture vs. suspended culture in northern Chile). The production in northern Chile is marginal, and there are only two oyster companies remaining. During the first half of 2004 these produced only 935 t, which represents a 46.8% decrease compared with the production during the first half of 2003. The influence of ENSO on the production of oysters is not well known, but since Pacific oysters have a wide range of temperature tolerance EN effects may be minor (or positive).

Other species introduced to the coast of Chile are abalone, originating from California and Japan. These have been mainly cultured in land-based facilities, but due to an increasing production and limited holding capacities on land, sea-based culture (as already established in southern Chile) is also considered for northern-central Chile. The production of abalones increased from 1 t in 1998 to 342 t in 2005, and for the year 2006 it is expected that the Chilean abalone industry will produce >500 t. Only in Region IV, currently five abalone production centres are established and an additional five centres have solicited permits to initiate new aquaculture activities during 2006. The present abalone production in Chile is mainly based on the red abalone (*Haliotis rufescens*). However, the Japanese abalone (*H. discus hannai*), which has a better market value, is also raised, but to a lesser degree since culture technology has higher requirements (and costs) than those for red abalone.

Although the land-based abalone culture is not directly affected by variations in environmental conditions, ENs may have severe effects on abalone culture because they can produce strong impacts on the population of large kelp, the main food resource presently used in abalone culture. The lack in supply of fresh food algae may produce serious bottlenecks in the culture of abalone. Some of these problems are occurring presently and the National Fisheries Service (SERNAPESCA) is concerned with the overexploitation of kelp, restricting the extraction from natural kelp beds and promoting research for cultivation and management of seaweeds. This scenario presents important challenges for applied research in the near future.

In general, aquaculture in northern and central Chile does not reach the levels it has in southern Chile. Some of the main reasons for this are related to the fact that the coast of northern Chile is (1) mostly exposed to wave action and (2) is strongly affected by important interannual variations in oceanographic conditions. Future efforts should probably focus on the development of land-based culture facilities and integrated systems where animals and algae are produced in combination (Chopin et al. 2001).

Conservation of marine biodiversity and Marine Protected Areas

The HCS extending from Ecuador to southern Chile is considered as one of the large marine ecosystems for high-priority attention (Boersma et al. 2004). The growing use of coastal areas by human activities is also increasingly threatening marine biodiversity in the HCS. The most important threats are overfishing, aquaculture, pollution by sewage and mining activities, runoffs of chemicals used for agriculture, oil spills and tourism activities (Vásquez et al. 1999, Fernández et al. 2000).

All countries, including Chile, that have ratified the Convention on Biological Diversity (CBD) treaty agreed to develop a network of Marine Protected Areas (MPAs, as defined by IUCN 1994) to ultimately protect 10% of the marine environments by 2012, based on an ecosystem approach (Wood 2006). However, the actual establishment rate of MPAs (4.5% annual increase) reveals that the work plan is unrealistic and will not be achieved before the second half of this century (Wood 2006). The Chilean case is a paradox as its economic exclusive zone (EEZ) corresponds to 17.8% of the Latin-American EEZ and is three times larger than its terrestrial territory (~18% of which is already protected; Pauchard & Villarroel 2002). However, only 0.03% of the Chilean EEZ (0.67% of the territorial sea) is protected as MPAs (CONAMA personal communication). Further, only 14% of the surface area of these MPAs are located within the HCS of northern and central Chile (18°S to 41°S). Considering that ~95% of the Chilean population is located between 18°S and 41°S and the growing human impact in coastal areas, this zone represents one of the greatest challenges for marine conservation.

The Chilean fisheries management policy, through creation of Management and Exploitation Areas (AMERBs) for benthic resources from coastal habitats, is focusing on economically important

target species, largely ignoring habitats, ecological interactions and other important ecosystem components (e.g., species dispersal). Although management areas can provide nursery grounds for target species (e.g., the Chilean abalone, *Concholepas concholepas*, keyhole limpets *Fissurella* spp. and the red sea urchin *Loxechinus albus*), this approach is often criticised for its weakness in providing a long-term ecological and economic viability and uncertainty in its efficiency (NRC 2001). The establishment of MPAs has proven to be a useful tool to achieve conservation and preservation goals (e.g., resources, communities, habitats), either as no-take MPAs or multiple-use MPAs (MUMPAs) (NRC 2001). Among the different tools existing in the Chilean legislation for protecting coastal areas, two types of no-take MPAs (marine reserves and parks) were foreseen in the law since 1989 but have only recently been established (Morales & Ponce 1997, Fernández & Castilla 2005). According to the Chilean laws, marine reserves are not focused on ecosystem protection but rather on exploited resources and their habitats and eventually may allow partial extractions if stocks reach very high levels of abundance. Three marine reserves are located between 18°S and 41°S (Table 6): La Rinconada to preserve a genetic stock of the scallop *Argopecten purpuratus* and Isla Choros-Damas and Isla Chañaral for allowing the recovery of several over-exploited benthic invertebrates (and their habitats). Furthermore, two MUMPAs, Isla Grande de Atacama and Lafken Mapu Lahual, have been created by the National Environmental Agency (CONAMA) with international private funding (GEF) as two of the three Chilean MUMPAs. In contrast to the marine reserves, these MUMPAs aim at the conservation of biodiversity integrating socioeconomic interests by creating not only no-take areas, but also areas where fishery and outdoor activities (e.g., diving, ecotourism) are permitted. While no-take zones have not yet been established in the MUMPA Isla Grande de Atacama, they have recently been identified (C. Gaymer et al. unpublished data) and will be declared in the near future. Finally, a small no-take MPA is located at Las Cruces, mainly for scientific purposes. Although very few MPAs exist in Chile, initiatives for conservation are facilitated by the Chilean law, which established an exclusive zone for artisanal fisheries within 5 nautical miles from the shore (e.g., prohibits trawling).

The MPAs Isla Choros-Damas, Isla Chañaral and Isla Grande de Atacama in northern Chile have been subjectively chosen through the use of expert criteria, based on the presence of some important ecological communities representing the HCS. The subtidal zone of these three MPAs is characterised by kelp beds of *Lessonia trabeculata*, *L. nigrescens* and *Macrocystis integrifolia* and several invertebrate populations overexploited during decades, and now vulnerable, such as the Chilean abalone *Concholepas concholepas* and the red sea urchin *Loxechinus albus* (i.e., extraction prohibited). Moreover, these MPAs are the habitat of some emblematic and/or endangered species, such as the bottlenose dolphin *Tursiops truncatus*, the sea otter *Lontra felina*, the Humboldt penguin *Spheniscus humboldti* and the Peruvian diving petrel *Pelecanoides garnotii*, and Isla Grande de Atacama is the southernmost site where the wedge-rumped storm-petrel *Oceanodroma tethys kelsalli* occurs. Biological corridors (Kaufman et al. 2004) permitting those species along with other seabirds to travel between these three MPAs are not included in the present MPA design. Additional MPAs between the marine reserves and the MUMPA would help to ensure undisturbed migration of marine birds and mammals. Ultimately, given the use of both terrestrial and marine environments by some species (e.g., Humboldt penguins) (Fariña et al. 2003b, Ellis et al. 2006), the selection of priority sites for conservation/preservation should integrate both environments, looking for common hot spots that would increase efficiency and reduce conservation costs.

MPAs offer a management tool to preserve hot spots of native species diversity; however, these hot spots can be strongly affected by invasion of exotic species which could compromise the effectiveness of MPAs (Byers 2005, Klinger et al. 2006). Introduction of invasive species in Chile becomes a serious concern with the increase of aquaculture (Castilla et al. 2005a). The Isla Grande de Atacama MPA is south of a bay (Bahía Inglesa) where intense scallop culture takes place and where the highest density of the exotic seaweed *Codium fragile* for the Chilean coast has been

Table 6 Main characteristics of marine protected areas (MPAs) in the Humboldt Current System (HCS) between 18° and 41°S

Name	Status	Establishment year	Mean latitude	Size (km ²)	Distance to next MPA (km) to south	Main conservation goals	Major threats	Main communities and target groups	Biological survey
La Rinconada	Marine Reserve	1997	23°28' S	3.4	404	Genetic reserve	Illegal extractions	Scallop bed	Every year since 1997
Isla Grande de Atacama	MUMPA	2004	27°10' S	35.5	213	Biodiversity protection	Invasive species	Kelp beds, barrrens, marine mammals and birds	1 in 2002
Isla Chañaral	Marine Reserve	2005	29°02' S	4.3	20	Overexploited species recovery	Illegal extractions	Kelp beds, barrrens, marine mammals and birds	1 in 1999
Isla Choros-Damas	Marine Reserve	2005	29°15' S	25	470	Overexploited species recovery	Illegal extractions	Kelp beds, barrrens, sea grass, marine mammals and birds	1 in 1999
Las Cruces	No-take MPA	2005	33°30' S	0.15	791	Scientific research	Illegal extractions	Kelp beds, barrrens	Every year since 1982
Lafken Mapu Lahual	MUMPA	2005	40°43' S	44.6		Biodiversity protection	Conflicts with indigenous people	Kelp beds, marine mammals and birds	1 in 2006

reported (Neill et al. 2006). Recently, patches of *C. fragile* have been observed within the MPA (R. Villablanca personal observations), highlighting the importance of considering connectivity with surrounding areas and the constraints of aquaculture sites for selecting location of MPAs (Micheli et al. 2004).

The establishment of MPAs in Chile has so far been based on anecdotal recommendations (e.g., resource management, tourist attractions) rather than scientific criteria. This approach is considered inadequate to effectively protect biodiversity (Meir et al. 2004, Sutherland et al. 2004). Current strategies for implementing MPA networks require a systematic planning conservation method to identify optimal sites for protection of biodiversity (Sayre et al. 2000, Beck & Odaya 2001). The first step in planning an MPA is the assessment and mapping (Geographic Information System — GIS) of the coastal marine biodiversity, the physical environment and major threats (e.g., human uses) and then the identification of priority sites using Decision Support Systems (DSS) based on algorithms (Sala et al. 2002, Leslie et al. 2003). A DSS based on species richness has been used to identify priority areas for marine vertebrate conservation along the Chilean coast (Tognelli et al. 2005). Habitat classification is generally considered as the conservation goal in the DSS (Roberts et al. 2003). However, benthic surveys along the Chilean coast (C. Gaymer & C. Dumont unpublished data) revealed that communities are probably more appropriate to characterise the benthic environment and consider the ecosystem processes (e.g., trophic cascades; Shears & Babcock 2003), ecological interactions (e.g., predator-prey; Micheli et al. 2004) and population connectivity (e.g., larval dispersal; Palumbi 2003). Moreover, there is an urgent need for more scientific information in Chilean marine biodiversity (e.g., there is a lack of taxonomic expertise), population connectivity (e.g., identifying source and sink populations) and ecological processes (in particular species interactions in subtidal habitats are poorly studied).

Although ecological knowledge is a key component in developing MPAs, the management effectiveness is the most important challenge for the success of an MPA (Mascia 2004, Pomeroy et al. 2004). A major difficulty arises from the way in which marine reserves and MUMPAs have been established in Chile. The former were created by an imposition from the central authority (fisheries ministry) without consulting the stakeholders, who are mostly in disagreement with this new status. This establishment strategy has turned enforcement into a complicated task for the fisheries authority, and this may turn into a major threat for the success of present and future MPAs. For example, since its creation in 1997, the marine reserve La Rinconada has been affected by frequent illegal extractions of scallops (M. Avendaño personal observations). Social conflicts due to lack of communication between the authority and the stakeholders are also present within the recently created marine reserves Isla Choros-Damas and Isla Chañaral. In contrast, a participative process took place in the establishment of the MUMPA Isla Grande de Atacama, incorporating most of the relevant actors (i.e., administrative authorities, stakeholders, managers, scientists and fishermen), offering the opportunity to evaluate contrasting interests in order to reduce potential conflicts. Social costs should be evaluated before the establishment of MPAs and a formal educational process should be implemented by the authorities to teach the importance of MPAs in developing sustainable exploitation of resources (Mascia 2004). The government should also negotiate compensations and propose alternative activities (e.g., tourism) to fishermen, who are the ancestral users of the MPA areas, and avoid creating high expectations (Mascia 2004, Sobel & Dahlgren 2004).

Ideally, an international MPA network (from Ecuador to Chile) including the connectivity among MPAs should be implemented to effectively preserve biodiversity in the HCS. This should be achieved using the support of international tools and agreements, and international non-governmental organisations (NGOs) in order to co-ordinate and improve the quality of scientific information and reduce the costs (Balmford et al. 2004). Moreover, the Chilean government must contribute to funding for implementation and functioning of MPAs as successful conservation experiences from all over the

world have demonstrated that self-funding (e.g., through tourism business) is not feasible (Balmford et al. 2004).

Outlook, long-term research vision and future research frontiers

An outlook of the pressing scientific questions and tasks to be addressed in the short/mid-term future (during the next decade) within the HCS of northern and central Chile should, as a minimum, include (1) studies of ocean–atmosphere interactions and offshore oceanography, (2) research in inshore and offshore oxygen–minimum ecosystems, (3) research on inner inshore coastal oceanography and benthic–pelagic linkages, (4) development of an ecosystem-based adaptive resource management approach to fisheries that integrates socioeconomic aspects, (5) implementation of a coastal overarching network system for marine conservation–management, (6) novel approaches in coastal mariculture, (7) studies of marine non-indigenous species (NIS), (8) marine molecular biology, particularly on genomics, and (9) training of Chilean marine taxonomists.

A long-term HCS vision (during the coming two decades) should also, as a minimum, include (1) intensification of precautionary and integrative ecosystem management; (2) implementation of a high-sea conservation policy; (3) intensification of research on the continental slope, deep-sea and abyssal ecosystems; (4) scientific and technological research on deep-sea gas (methane) hydrates; and (5) evaluations of the effects of future climate change.

Short/mid-term scientific outlook

Research on ocean–atmosphere interactions and offshore oceanography

The HCS offers unique opportunities for offshore oceanographic studies (e.g., Strub et al. 1998) and considered as a whole, Chile and Peru represent between 15% and 20% of the world's fishery landings. Large-scale fluctuations in ocean climate (ENSO and the PDO) dominate interannual and interdecadal variability in the ocean, which in turn are linked to upwelling and climate changes (Chavez et al. 2003) and are considered key elements in the HCS functioning. Upwelling systems presently are experiencing 'anomalous changes' such as profound changes in the physical and biogeochemical properties in the California Current Systems (Freeland et al. 2003, Grantham et al. 2004), massive nitrogen loss in the Benguela upwelling system (Kuypers et al. 2005), and hydrogen sulphide eruptions in the Atlantic Ocean off southern Africa and linked abrupt degradation of upwelling systems (Bakun & Weeks 2004, Weeks et al. 2004, Arntz et al. 2006). Such interannual and decadal variability and anomalous changes may intensify due to global climate changes, which will also affect the HCS, causing important changes in productivity, biogeochemical cycling and fisheries. Research on these and related oceanographic topics is urgently needed for the HCS.

Research on inshore and offshore oxygen–minimum ecosystems

Oxygen–minimum zones (OMZs) in the ocean generally form along the EBCs. The decomposition of upwelling–derived biomass in combination with sluggish circulation of mid-water masses strongly enhance the hypoxia conditions, as is the case in the HCS (Levin & Gage 1998, Morales et al. 1999, Levin 2002, Helly & Levin 2004, Ulloa & De Pol 2004). The HCS is characterised by the relative shallowness of the oxygen–minimum layer. The OMZ produces peculiar environments with organisms highly resistant to low oxygen concentrations (Levin et al. 2001, Gallardo et al. 2004). These environments are unique in the HCS and quite different from those off California (Arntz et al. 2006). They offer diverse opportunities to develop frontier research, ranging from

evolutionary adaptability, primary and secondary production, biodiversity, and species invasions (Castilla & Neill 2007) to impacts on fisheries.

Research on nearshore coastal oceanography and benthic-pelagic coupling

The nearshore oceanography (coastal border to about 2–3 km offshore) is one of the least-known areas of the world's oceans. In this regard, during the past 5 yr several lines of research have been developed in central Chile (e.g., Poulin et al. 2002a,b, Kaplan et al. 2003, Wieters et al. 2003, Narváez et al. 2004, Vargas et al. 2004, Piñones et al. 2005) and further research efforts are needed. Unless improvements in the knowledge of nearshore oceanography are achieved, coastal ecology cannot be properly understood. This includes topics such as dispersal of nearshore propagules, benthic resource fisheries and sustainability issues, coastal conservation and pollution impacts. Linking nearshore oceanography and the coastal benthic-pelagic systems remains as a challenge, not only along the HCS (Castilla et al. 2002a, Escribano et al. 2002, Lagos et al. 2002, Marín & Moreno 2002), but also around the world (Shanks 1983, 1995, 2002, Largier 2002).

Development of an integrative and adaptive resource management approach to fisheries

Pelagic, benthic and demersal marine resource management in Chile is regulated by the Ley de Pesca y Acuicultura 1991 (Fishery and Aquaculture Law, FAL 1991), under the responsibility of the Subsecretary of Fisheries, Ministry of Economy. For the management and administration of fisheries, among other regulations, the law (1) defines the 'artisanal fishery' referring to vessels/boats <50 t and <18 m long, separating fishers into four major categories and distinguishing them from the 'industrial fisheries'; (2) establishes the allocation of a 5-mile wide coastal stretch from 18°20'S to 41°28'S exclusively for the operation of the artisanal fishery fleet; (3) includes an artisanal and industrial National Register Fisher System restricting the spatial movements of fleets; (4) promotes co-management and allocates exclusive AMERBs and TURFs (for artisanal fishery associations); and (5) regulates overexploited stocks via area closure systems and allocation of transferable and non-transferable quotas (Defeo & Castilla 2005, Castilla & Gelcich 2006, Castilla et al. 2007). Hence, it is herein suggested that the 1991 Chilean FAL contains modern and advanced fishery regulation concepts and management tools to potentially promote the rationalisation of Chilean fisheries. An important step forward in this direction must be the introduction of an integrated socio-biophysical ecosystem fishery approach (FAO 2003, Castilla & Defeo 2005). To promote this approach at least three elements need to be considered: (1) the proactive participation of stakeholders (artisanal and industrial) in the co-evaluation of stocks, (2) a proactive government approach to adaptive co-management (e.g., artisanal fisheries, AMERBs and TURFs) via the use of experimental fisheries and further socioeconomic studies, and (3) an increase in the number of Chilean scientists engaged in fishery biology and modelling of resource dynamics. In particular, this last point is considered critical in achieving the stakeholder participation in stock evaluation and management because well-trained scientists and communicators are needed to make information available transparently, while simultaneously consulting and incorporating the perceptions of fishermen. Fostering fisheries sciences would probably also enhance international collaboration, thereby also promoting refereed frontier publications (which presently are extremely scant; Castilla et al. 2005b).

Implementation of a coastal overarching network system for marine conservation management

A novel and overarching integrative approach to jointly address coastal conservation and management issues along the Chilean coast needs to be implemented in the next decade. The aim will be

to build a coastal conservation management network, including no-take and multiple-use MPAs, sanctuaries, marine concessions and AMERBs (Castilla 2000, Secretariat of the Convention on Biological Diversity SCBD 2004, Fernández & Castilla 2005, Castilla & Gelcich 2006). The present authors believe that, based on present progress, this overarching framework can be achieved in Chile (following guidelines given by the SCBD 2004). In fact, along ~18–41°S at present there are already established >300 AMERBs, two main MPAs for multiple uses (Isla Grande de Atacama and Lafken Mapu Lahual; see CONAMA-PNUD 2006), four declared and active marine reserves and several other categories of protected areas (Fernández & Castilla 2005). Connecting these areas and providing them with one unified administrative umbrella will furthermore meet the goals of the Chilean National Biodiversity Strategy Plan, which attempts to protect 10% of relevant marine Chilean ecosystems by 2012 (Rovira 2006). This overarching network system must also consider external threats such as pollution, which is an important issue in Chile due to pollution resulting from mining activities, agriculture and ship paints (Correa et al. 1999).

Novel approaches in coastal mariculture

The Chilean coastline along the HCS is very exposed to the open ocean, generally lacking wave-protected embayment, and is thus not particularly suitable for the development of mariculture activities. Exceptions are the bays or bay systems of Mejillones, Antofagasta, Caldera, Coquimbo and Dichato, where scallops, oysters, mussels and *Gracilaria* are cultured on a limited scale. Inland mariculture has also been developed, particularly for introduced species of the genus *Haliotis*. If further progress for mariculture in the HCS will occur, the challenge remains in the development of novel technologies for sea bottom or raft culture systems in exposed and offshore systems.

Research on marine non-indigenous species

The number of NIS along the HCS is surprisingly low when compared with similar upwelling or non-upwelling systems around the world (Castilla et al. 2005a). It has been suggested that this results from a combination of factors such as less-stressed coastal environments or the scarcity of estuaries, gulfs and enclosed bays. Furthermore, it has been hypothesised that it might be linked to the existence of the coastal shallow oxygen-minimum zones (Castilla & Neill 2007). These aspects need further research. Moreover, the rate at which NIS are presently being introduced for aquaculture purposes (e.g., salmon, abalone, algae) needs to be carefully monitored since, for instance, escapees (e.g., salmon) from culture pens may impact native species and communities (Buschmann et al. 2006b). The potential for the introduction of diseases and pests into HCS coastal environments, linked to the development of aquaculture (e.g., Radashevsky & Olivares 2005, R.A. Moreno et al. 2006b, Neill et al. 2006), must also be monitored.

Research in marine molecular biology, particularly on genomics

The use of molecular biology techniques in marine organisms is seen for Chile as a new research frontier (Castilla et al. 2005b), allowing a range of questions to be addressed, covering evolutionary biology, taxonomy and phylogeny (e.g., Letelier et al. 2003, Véliz et al. 2003, Thiel et al. 2004), ecology and invasive species (Castilla et al. 2002b) and above all population aspects linked to fisheries (Cárdenas et al. 2005). We anticipate that during the next decade this research, particularly on marine genomics, should substantially increase.

Training of Chilean marine taxonomists

In Chile the training of marine taxonomists must increase. For this the establishment of specific programmes is needed that support the formation and hiring of taxonomic experts, publication of

monographs and field guides, visiting taxonomist programmes with the objective to tackle certain groups and provide publications that allow easy identification of the HCS species, visiting scholarships for national scientists to foreign institutions and museums, increased support for functioning species collections, and an innovative programme to link specimen collections and molecular information. The enhancement of marine taxonomic research in Chile embodies the vision that biodiversity and ecological functioning are key components of the HCS. If this ecosystem is going to be fully understood, and fishery, environmental sustainability and conservation programmes are to be implemented, then the improvement of taxonomic expertise is seen as crucial.

HCS long-term scientific vision

Intensification of precautionary and integrative ecosystem management

A consideration of the research needs for the HCS indicates that fishery sustainability (subsistence, small-scale and industrial fisheries) will continue for a long time to play a critical role in the economy and human well-being of Chile. Presently, the FAO Code of Conduct Fishery Precautionary Principles and the socio-biophysical ecosystems fishery management approach (FAO 1995, 2003) are the two most novel management tools regarding sustainability of world fisheries. Following the failure of traditional single-species approaches (Defeo et al. 2007), the present authors consider these tools as key elements for an efficient fisheries management in the HCS, and scientists in Chile need to be trained and prepared to properly use them. Therefore, an intensification of scientific research in these areas with respect to the HCS is foreseen. There is a particular need for communication between scientists, users, administrators and politicians. Due to the overriding importance of the HCS for the Chilean society (fisheries, aquaculture, shipping, tourism), integrative management requires one unifying administrative body that oversees, monitors and evaluates all activities within the HCS of Chile. This entity should incorporate representatives of all interest groups and co-ordinate communication among them on both the national and international levels.

Implementation of a high-sea conservation policy

So far, Chile has not developed a high-sea conservation policy, and there is no policy for unique offshore oceanic realms, such as sea mountains and deep-sea environments, or populations of migratory mammals, birds and fishes. Extensive and international protection measures for highly mobile, migratory marine vertebrates in the dynamic high sea of the HCS are needed. The implementation of such policies remains an important challenge for Chile.

Intensification of the research on continental slope, deep-sea and abyssal ecosystems

The Chilean portion of the continental slope, deep-sea and abyssal realm of the HCS continue to be some of the least-known oceanographic ecosystems. Aside from isolated studies (e.g., Glud et al. 1999, Thurston et al. 2002), little is known about the OM accumulation, benthic ecology or species diversity in the unique deep trenches off the Chilean coast. During the next two decades or so Chile has to make an effort to improve the understanding of the HCS trenches and also to increase research in offshore oceanography. In order to achieve this goal, the country urgently needs to improve access to oceanic work platforms, including modern research vessels (Castilla et al. 2005b).

Scientific and technological research on deep-sea gas (methane) hydrates

Gas hydrates are solid crystals formed by a cell of water molecules containing methane, ethane, CO₂ or H₂S and are found inside pores of sedimentary rocks. Methane hydrates are considered to

be one of the strategic energy compounds for the future (they commonly occur below the permafrost shield and in sediments of ocean margins). Gas methane hydrates are abundant on the continental margins between Papudo (central Chile) to Valdivia (southern Chile). First evaluations in this area indicate gas methane hydrate reserves for 10^{13} m³ (Morales 2003). The technology to access these hydrates is developing fast, and Chile must be part of the advance and innovation processes. Geological oceanography in Chile is poorly developed (although the number of geologists in the country is high). Therefore the training of marine geologists and the substantial increase of marine geological research in Chile remains an important task (and opportunity) for the future (Castilla et al. 2005b).

Evaluation of the effects of future climate change

It is known that greenhouse warming and other human alterations may increase the possibility of large and abrupt regional or global changes in climatic events, oceanic circulation (especially related to deep-water formation), sea-ice dynamics (Smith et al. 2006), and wind velocity (Bakun & Weeks 2004). Future wind increases, due to greenhouse effects, may eventually affect one of the HCS key characteristics, such as the rate of upwelling events (Bakun 1990, Bakun & Weeks 2004). For instance, an increase of 15% in wind would represent an increase of ~40% in the typical rate (late twentieth century) of sea upper layer volume replaced per day (water renewal). In the Benguela Current System off Namibia, the present atmospheric greenhouse-related intensification of coastal upwelling appears to be causing the abrupt degradation of the ecosystem (Weeks et al. 2004). Therefore, in a scenario with concentrations of greenhouse gases increasing, climate change (e.g., pattern of wind increase and intensification of upwelling) along the HCS needs to be surveyed under a long-term monitoring scheme.

HCS frontier research opportunities

As pointed out there are several research opportunities along the HCS, such as studies of the OMZ and related ecosystems, upwelling and climate change, fishery productivity, co-management, conservation and socio-biophysical approaches to fisheries. In addition there are other very exciting and novel frontier lines of research such as studies of the biogeochemical role of Archaea (Woese & Fox 1977) in the HCS. These organisms are also linked to the OMZ and appear to be particularly abundant in this system. This line of research has recently started in Chile and needs to be strengthened.

Further topics that extend far beyond the scope of the present review but that appear to be relevant in the present context are linked to socioecology, anthropology and paleo-oceanography. For example, how do the processes occurring in coastal waters of the HCS affect the terrestrial environments and human populations along the Pacific coast of South America (past, present and future)? Palaeo-oceanography and anthropology can offer exciting insights from the past that will also help to master future challenges.

Conclusions

Upwelling is the major driving force of ecological processes in the HCS by promoting high PP both in the plankton and in the nearshore benthos. Additional processes influenced by upwelling are transport of propagules and biogeochemical processes. Besides their high nutrient concentrations, one main feature of the upwelled waters from the HCS along the Chilean coast is that they have low concentrations of dissolved oxygen. This restricts vertical migration of most zooplankters, including of larvae, thereby affecting dispersal. Furthermore, the low oxygen concentrations drive

the dynamics of the benthos communities along the continental shelf and also the remineralisation of OM. There is indication that the upper depth limits of the low-oxygen fauna oscillates with upwelling strength (and EN). In parallel with these oscillations, the lower depth limit of benthos communities from the upper sublittoral zone shifts up and down. This community experiences at its upper depth limit the impact of EN events, where individual species or the whole community may temporarily disappear (due to water temperature, wave action or burial under terrigenous sediments). These extinction events affect the shallow sublittoral and intertidal biota along the HCS in northern and central Chile, but their intensity varies between events, often resulting in differential elimination of particular species, while leaving others unaffected or favouring them. Similar variation in effect size is seen along the latitudinal gradient, where EN impacts (which may occur at all trophic levels) attenuate toward higher latitudes. This leads to different constellations in the interaction webs found in pelagic and benthic communities. Spatial variability in upwelling, which mitigates EN effects, further enhances the variability in the ecological responses. The diffuse pattern of biogeographic limits observed in northern-central Chile is expression of this high variability. Studies of individual growth, reproductive potential, dispersal, recruitment, physiology and population connectivity of organisms from the HCS demonstrate the importance of life-history traits for improving predictability of ecological processes in this area. The high temporal and spatial variability in oceanographic conditions and ecological processes in the HCS of northern-central Chile complicates management and conservation decisions (such as calculation of catch quotas or identification of important areas for recruitment or growth). Recent studies have revealed small-scale variability in reproductive potential, larval supply, recruitment and growth. This indicates that spatially explicit conservation measures (e.g., MPAs) require information of high temporal and spatial resolution. For most parts of the coast of northern and central Chile such data are not available. Given this present gap in information and the urgent need for efficient conservation of this large marine ecosystem, a large-scale approach is proposed. Future conservation measures should also include terrestrial environments such as seabird breeding sites, dune fields and estuarine habitats. Research and administration activities along the HCS face important challenges that require substantial efforts, in particular a continuous and fluent communication among all involved parties. In order to achieve this, a common umbrella organisation that co-ordinates all these activities (and permits rapid exchange of opinion and information) appears to be highly desirable.

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