Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation

Diversidad, dinámica y biogeografía del ecosistema costero bentónico de Chile: revisión y bases para conservación marina

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ABSTRACT

Despite Chile has been one of the pioneering countries in studies of human impact on marine communities, and despite the enormous economic and social significance that the marine environment has for the country, the development of marine conservation programs and the scientific basis for sustainability has not kept pace, with the exploitation rate of marine fisheries and the increasing use of the coast for other purposes. Although we think that the establishment of any conservation policies along the vast coastline of Chile must be based on a multitude of approaches and considerations, scientific, biological, and ecological principles should guide much of these efforts. In this paper, we attempt to present a general overview of the current knowledge about the ecology and biogeography of nearshore systems in Chile. Based on the most relevant existing information, our goals are to: 1) Identify major biogeographic and ecological features of nearshore ecosystems, and the obvious gaps in information, 2) identify the most harmful human activities impacting the structure and dynamics of these systems, and 3) suggest the possible use of indicators to assess the conservational status of different environments along the coast. This overview shows, on one side, the geographic areas of deficitary knowledge on nearshore environments that are critical for future marine conservation and management plans, and on the other, the availability of high quality information for other geographic areas along the coast. Regarding the taxonomy and large-scale patterns of species distribution, important gaps in information were detected, however no big changes in the total number of species are expected in the future. There are few large-scale patterns of species distribution are reported in the literature, and in this contribution, but more work needs to be done, particularly for some taxa, to identify areas of high species diversity as well as areas which possess unique characteristics in terms of ecosystem processes (e.g., particular disturbance and upwelling regimes in coastal marine ecosystems) and species (e.g., endemic and keystone species). For most marine invertebrates and macroalgae, hotspots in species diversity are present in southern Chile. New studies addressing the causal factors generating these large-scale patterns of species distribution are also needed; information about coastal oceanography and larval supply is still poor. This information crucial for the design of a marine reserve network. The information available on community structure and ecosystem functioning, especially highlighting the effect of human impact, comes from very few geographic regions. More information about community structure for other areas of the coast is required, particularly considering the strong differences in temperature, circulation patterns, habitat heterogeneity, species composition, as well as of upwelling and El Niño effects along the 4,000 km of coastline. Finally, we list what we think are the most harmful human activities by area and environment along the coast, and integrate this information to suggest possible environmental indicators, and basic needs and guidelines for marine conservation in Chile.

Key words: Chile, marine conservation, biogeographical patterns, community structure, human impact.

RESUMEN

A pesar de que Chile ha sido un país pionero en estudios del efecto del impacto humano sobre la estructura comunitaria en ambientes marinos, y a pesar de la enorme importancia económica y social que el ambiente marino tiene para el país, el desarrollo de programas de conservación marina y de bases científicas para la sustentabilidad no se han generado a la misma tasa a la que han explotado los recursos y se ha utilizado el ambiente costero para diversos fines. Aunque nosotros pensamos que el establecimiento de planes de conservación a lo largo de la costa de Chile debe basarse en varios factores, los principios científicos, biológicos y ecológicos deben guiar muchos de estos esfuerzos, y en este trabajo nosotros intentamos presentar una visión general del estado actual del conocimiento sobre la ecología y la biogegrafía del sistema costero en Chile. En base a la información más relevante existente, nuestros objetivos son: 1)

identificar las características biogeográficas y ecológicas del ecosistema costero y también vacíos en información, 2) identificar las actividades humanas más dañinas que tengan impacto en la estructura y dinámica de estos sistemas, y 3) sugerir el uso de posibles indicadores para determinar la situación de diferentes áreas de la costa de Chile, y las necesidades de conservación. Esta revisión muestra, por un lado, áreas geográficas con información crítica deficitaria para planes futuros de manejo y conservación marina, y por el otro lado, la disponibilidad de información de alta calidad para otras zonas geográficas del país. Respecto de la información existente sobre taxonomía y patrones de distribución de especies a gran escala, existen importantes vacíos de información; no se esperan en el futuro grandes cambios en el número total de especies. Existen pocos estudios sobre patrones de distribución de especies a gran escala, y más información es necesaria para identificar áreas de alta diversidad de especies, especialmente para algunos taxa, como también para identificar áreas que posean características únicas en relación a especies (endémicas, especies claves) y a procesos ecosistémicos (disturbios, surgencias). Para la mayoría de los invertebrados y macroalgas, las áreas de alta diversidad de especies se encuentran en el sur de Chile. Nuevos estudios dirigidos a entender los factores que podrían generar patrones a macroescala son necesarios, como también información sobre oceanografía costera y disponibilidad de larvas. Esta información es clave para el diseño de una futura red de parques marinos. Por otro lado, la información disponible sobre estructuras comunitarias y funcionamiento ecosistémico, especialmente sobre el efecto del impacto humano, provienen de pocas regiones geográficas. Mas información sobre otras zonas geográficas es requerida, particularmente si se consideran las diferencias notables en temperatura, patrones de circulación, heterogeneidad del habitat, y composición de especies, como también el efecto de surgencia y de El Niño a lo largo de los más de 4.000 km de costa de Chile. Finalmente, listamos las que consideramos son las actividades humanas más dañinas para el ambiente marino, e integramos esta información para sugerir posibles indicadores ambientales y necesidades básicas y sugerencias para conservación marina in Chile.

Palabras clave: Chile, conservación marina, patrones biogeográficos, estructura comunitaria, impacto humano.

INTRODUCTION

The profound influence of humans in marine systems has been recognized in the last few decades, and has been the major driving force behind the creation of marine protected areas as a vehicle for marine conservation (Dayton et al. 1995, Lubchenco et al. 1995, Allison et al. 1996). Marine protected areas have increased dramatically over the last years in response to different objectives, ranging from preservation of biodiversity, protection of particular species, groups of species or critical areas (Norse 1993), to the prevention of overfishing (Davis 1989, Dugan & Davis 1993) and even enhancement of fisheries (Moreno et al. 1984, Castilla & Durán 1985, Moreno et al. 1986, Castilla & Bustamante 1989, Castilla & Fernández 1998). However, the implementation of marine reserves is relatively new, and the theoretical basis for marine conservation is still poor in comparison with terrestrial ecosystems (Allison et al. 1998).

Although it may be tempting to take advantage of the experiences with reserve designs from terrestrial systems and apply them to the marine environment, both systems differ dramatically from minor to very fundamental factors. For instance, while the greatest species diversity is found on land, marine systems have a much greater diversity at higher levels of organization (e.g., orders, phyla; Ray 1991), which implies a greater diversity of development and body plans as well as evolutionary lineages. Marine organisms also exhibit a number of important differences in life history, and this single factor could have several effects (e.g., Valentine & Jablonski 1983). On the one hand, dispersal of early life history stages can occur over long distances, which could imply that some marine species may be less vulnerable to extinction than terrestrial ones. On the other hand, the use of different habitats during the life cycle of marine species suggests that conservation efforts directed at just one site may be ineffective for population recovery. The differences in the type, the scale, and the variability of the processes affecting both systems suggest that the approaches developed for conservation of terrestrial ecosystems may very well fail in the marine environments (Allison et al. 1998).

As in other developed and under developed countries, the establishment of parks and reserves in Chile, as well as the biological basis for the design of protected areas, is more advanced in terrestrial than in marine environments (Ormazábal 1993). The majority of the population of Chile lives along its approximately 4200 km of coastline, with most major cities located on the coast. Moreover, Chile is one of the world leading countries in exportation of fish products. Although the bulk of these landings consist of pelagic resources, nearshore invertebrates and algae have an important share and a disproportionately large economic and social impact since more than 30,000 fishermen are involved in the fishing activity (e.g., Bustamante & Castilla 1987). Despite the enormous economic and social significance of marine environments for the country, the development of marine conservation pro-

grams and the scientific basis for sustainability has not kept pace with the exploitation rate of marine fisheries and the increasing use of the coast for other purposes. Besides fishing, human impacts on the marine environment include coastal aquaculture, species introductions, habitat alteration and pollution related to human settlement and multiple activities, including those occurring far inland. The nature of human activity in the marine and terrestrial environments differs, including the scale of its potential impact. Exploitation of marine resources takes place in open access areas, in contrast to privately owned lands in terrestrial systems, triggering distinct behavioral and economic reactions. Most marine fisheries remove top predators, and secondarily herbivores (Pauly et al. 1998), while herbivores are the main target in the exploitation of terrestrial systems (although not necessarily wild species). There is evidence that pollutants have more dramatic impacts on marine species than in terrestrial ecosystems. These varied activities can have important, diverse and yet unquantified effects on the marine ecosystem, affecting the bottom-up and top-down regulation of the marine communities, as well as altering natural habitats.

While worldwide the effects of many human activities have not been properly investigated, Chile has been one of the pioneer countries in studies of human impact on marine communities (Moreno et al. 1984, Castilla & Durán 1985, Oliva & Castilla 1986, Moreno et al. 1986, Castilla & Bustamante 1989, Castilla 1999). The establishment of two coastal marine reserves in Las Cruces and Mehuín evidenced the dramatic direct and indirect effects of humans on invertebrate and macroalgal species (Moreno et al. 1984, Castilla & Durán 1985, Oliva & Castilla 1986, Moreno et al. 1986, Castilla & Bustamante 1989; there are no reports of long term monitoring programs in Montemar, Castilla 1996). These small marine reserves (approximately 5 ha, Castilla 1996) were not only key in demonstrating and quantifying the nature and intensity of fishing on nearshore communities, but partly as a result of these "human-exclusion experiments", there is now a strong effort from some government agencies directed at regulating management and exploitation areas, and at the establishment of a network of marine protected areas in Chile (González et al. 1997).

Although the establishment of any marine conservation policies along the vast coastline of Chile must be based on a multitude of approaches and considerations, we think that scientific, biological, and ecological principles should guide much of the efforts. In this paper, we present an over-

view of the current knowledge about the ecology and biogeography of the nearshore ecosystem in Chile, emphasizing new results not considered in previous reviews, and derive basic guidelines for marine conservation. We emphasize patterns and processes at meso- to large-spatial scales along the Chilean coast, although the majority of the information comes from local, within-site studies. Our goal is not to examine in detail different coastal systems but, based on the most relevant existing information, 1) to identify major biogeographic and ecological features of nearshore ecosystems and gaps in information, 2) to identify the most harmful human activities impacting the structure and dynamics of these coastal systems, and based on the above, and 3) to suggest the use of indicators for the conservational status of different systems along the Chilean coast. Within the continental shelf, we arbitrarily distinguished three major ecosystems: a) nearshore intertidal (rocky or sandy bottoms), ranging from the extreme high water spring to the extreme low water spring; b) nearshore subtidal, ranging roughly from the extreme spring low water to depths of about 30 m; and c) farshore subtidal, ranging from about 30 to 200 m in depth. We focused on the first two ecosystems. Nearshore system (or ecosystem), coastal system (or ecosystem) and coastal environment were used indistinctly throughout the manuscript to refer to intertidal rocky shores, intertidal sandy bottoms, and shallow subtidal areas. We first summarize the major physical and geographic features of the coast, localizing the distribution of major ecosystems and known human impacted areas. Secondly, we briefly describe large-scale, biogeographical patterns and potential causal factors, to then concentrate on the structure and dynamics of local communities for different habitats. Finally, we list what we think are the most harmful human activities by area and habitat along the coast, to then integrate this information and suggest possible indicators of human impact and basic needs for conservation.

Main features of the Chilean coast

The approximately 4,200 km of the Chilean continental coast have a clear north-south orientation along the southeastern Pacific coast of South America, crossing different environmental conditions strongly associated with latitude (from ca. 18 to 56° S). Most of this coast occurs along the subduction of the oceanic Nazca plate under the continental South American plate. In this area, earthquakes of large magnitude are frequent, pro-

ducing coastal uplifts or subsidences (Castilla 1988). Deep oceanic trenches and a narrow continental shelf are also characteristic features of the area (Castilla & Oliva 1990).

The Chilean continental shelf (up to a depth of 200 m) covers a total surface of about 27,472 km², with a mean width of about 6.54 km (Gallardo 1984). This area has the following special characteristics that influence nearshore ecosystem: (a) upwelled waters and abundant marine resources (ranked among the richest in the world; Arntz et al. 1991), (b) particularly strong influence of large-scale perturbations, such as El Niño-Southern Oscillation (ENSO), (c) coseismic coastal uplifts or subsidences due to earthquakes (Castilla et al. 1993), and (d) large areas of sea bottom exhibiting low oxygen availability (Fossing et al. 1995). The relative importance of each event varies along the extended latitudinal gradient.

From an oceanographic point of view, several circulation patterns have been proposed by different authors. A summary of the main oceanographic features has been presented by Castilla et al. (1993) and Strub et al. (1998). The main cell of circulation is connected to the South Pacific anticyclone gyre and driven by the West Wind Drift, which reaches the South American continent near the 40-45° S and branches into two main current systems. The southern, poleward flowing branch is known as the Cape Horn system, and the northern, equatorward flowing branch comprises what is called the Humboldt or Chile-Perú Current system (Fig. 1). As yet, most of the emphasis has been placed on the far shore oceanography. The geomorphological characteristics of the coastline and the little attention that nearshore oceanography has received make difficult the assessment of the influence of these two oceanic branches on coastal (few miles from shore) circulation.

One of the main oceanographic features of central and northern Chile is the upwelling of subsurface waters into surface layers, which creates anomalous low temperatures and high productivity (Arntz et al. 1991, Strub et al. 1998). Along the Chilean coast, there are numerous well-identified areas of upwelling that together sustain one of the richest pelagic fisheries of the world (e.g., Iquique, Coquimbo, Valparaíso and Punta Lavapié). The coastal upwelling systems that occur over 3,000 km along the continental shelf off Southern Perú and North and Central Chile have a very high primary and secondary production (Arntz et al. 1991). In this area, the mineralization of organic matter results in extensive oxygen depletion of the water column up to 60 m above the sea floor, with temporal O_2 variations between 0 and 5 mM (Fossing et al. 1995).

Among the large-scale perturbations that affect the Chilean coast, the main oceanographic anomaly is the El Niño event and its atmospheric counterpart, the Southern Oscillation (ENSO; Castilla et al. 1993). One of the prevailing interpretations is that ENSO events occur as an internal cycle of positive and negative feedback within the coupled ocean-atmosphere climate system of the tropical Pacific. Baroclinic equatorial Kelvin waves are generated and propagated eastward toward South America, depressing the thermocline and raising the sea level. The net result of this event is an increase in surface seawater temperature of about 3-5° C and an increase in sea level of up to 20 cm from Perú to Chile (Enfield 1989). Another large-scale perturbation is caused by periodic earthquakes. The coast of central Chile has been affected by large earthquakes at a regular period of 83 ± 9 years (mean ± SD; Comte et al. 1986), and many of them have produced important uplifts and subsidences of coastal rocks. These vertical uplifts translate into sea level changes for coastal benthic organisms, and the magnitude of these changes can be remarkable (Castilla 1988).

According to Viviani (1979), the Andes Mountains, that run close and parallel all along the coast, create special climatic conditions. Four distinct areas (Fig 1) can be identified along the Chilean coast (see Castilla et al. 1993):

1) Arid coast: This area extends from 18 to 27° S and is characterized by a northward-trending cliff that is several hundred meters high in some areas (Araya-Vergara 1976). The land climate is defined as arid (Di Castri & Hajek 1976) or hyperarid, but littoral zones and coastal waters are not correspondingly warm because of coastal upwelling. These upwelling processes weaken during warm seasons of the year or warm periods such as the ENSO. Isotherms in surface water are found nearly parallel to the coastline, ranging from about 16-20° C depending on the season of the year and prevailing winds (Fig. 1; Viviani 1979, Santelices 1991). From a geomorphological point of view, this area shows an almost straight coastal rim with very few sheltered bays and no high-waterflow rivers reaching the ocean.

2) Semiarid coast: This area extends from about 27 to 32° S, and is characterized by Plio-Quaternary marine terraces extending from the shoreline to about 150-200 m offshore. According to Viviani (1979), in this area the climate is Mediterranean, with rainfalls concentrated during the winter season and increasing with latitude. There are clear seasonal trends in seawater temperature, but in general they are between 2 to 4° C lower than in the arid area (Fig. 1; Robles et al. 1974). Numer-

ous upwelling zones exist along the coast (e.g., Punta Lengua de Vaca, Curaumilla). This area also has an almost straight coastline with very few sheltered bays or offshore islands and few rivers reaching the sea (e.g., Limarí, Choapa, Aconcagua).

3) Central coast: This area extends between approximately 32° S and 42° S. The climate is also Mediterranean, with rainfalls occurring mostly during winter and with periods of drought during summer. Average seawater temperature shows a dramatic decrease in this area (Fig. 1). There are many high-waterflow rivers (e.g., Bio-Bio, Cautín, Toltén, Calle-Calle) reaching the sea, and the oceanic temperate climate (Di Castri & Hajek 1976) favors runoff erosion (and hence sedimentation), particularly in winter. South of 39° S there are many estuaries, which resulted
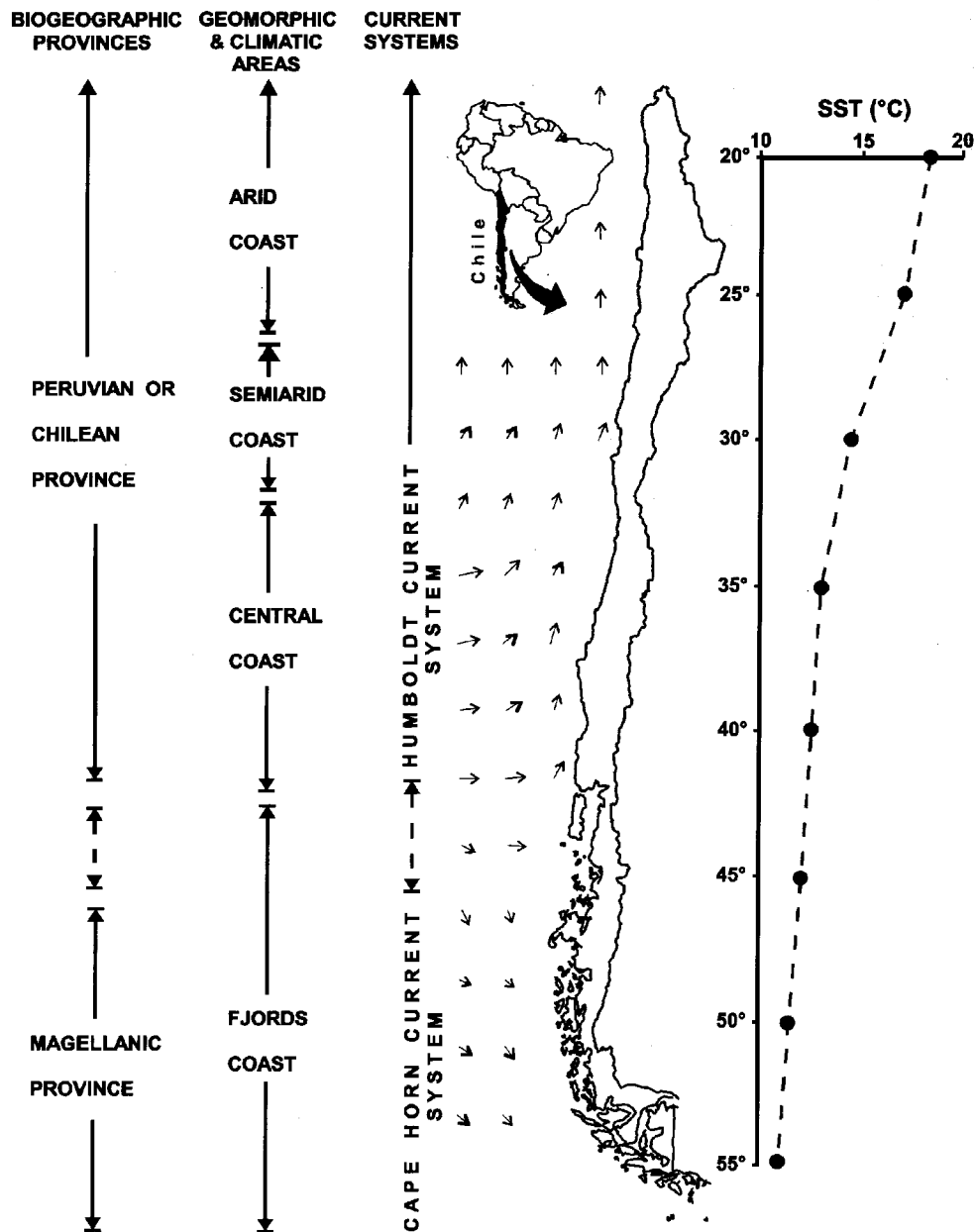

Fig. 1. Schematic representation of the main structural features (biogeographic, geomorphic and climate, and current systems) of the Chilean continental coast (adapted from Castilla et al. 1993).

Representación esquemática de las principales características de la costa de Chile continental (regiones biogeográficas, clima y sistema de corrientes, adaptado de Castilla et al. 1993).

from submergence by Holocene transgressions. From a geomorphological point of view, this area is rougher than the previous one in terms of wave impact and shows extensive beaches and dune fields. Sheltered bays are common, and Chiloé Island is the main coastal geomorphologic feature of the coastal area.

4) Fjords coast: This area extends from about 43°30′ to 56° S and according to Pickard (1971), is one of the best examples of deep and rugged fjord coasts in the world. The climate is oceanic with rainfall ranging between 2,000 and 3,000 mm/year and homogeneously distributed throughout the year. The shoreline is highly indented. In this area the fjords penetrate inland through the glacially dissected Andes Range, and numerous short and low-waterflow rivers are found between 52° and 56° S. A strong and shallow picnocline produced by a freshwater layer seems to characterize the water column within the fjords. Average seawater temperature is the lowest of the coast of Chile (Fig. 1).

Tide ranges also vary along the coast of Chile, from semi-diurnal tides of 1.5-2 m amplitude from Arica to Valdivia, to 8-14 m of amplitude between Puerto Montt and Punta Dungeness (Viviani 1979). In the fjords area tidal amplitude varies between nearby locations. Other important factors that vary along the coast are related to human settlement and activity, and are reported below (Tables 3 and 4).

Large-scale patterns of the biota and their potential causal factors

Large-scale patterns of biotic and abiotic factors provide key information for identifying areas of high species diversity as well as areas which possess unique characteristics in terms of ecosystem processes (e.g., particular disturbance, upwelling regimes) and species (e.g., endemic species, keystone species). This knowledge is essential for the identification and design of nature reserve networks. Since hot-spots of diversity, rarity, endemic, and endangered species vary across taxonomic groups, as it has been shown by studies in terrestrial taxa (Prendergast et al. 1993, Dobson et al. 1997), no single area would support all the processes and species important for conservation. Thus, the problem of identifying and selecting areas for conservation usually requires the application of area selection methods that allow identification of a combination of characteristics that would jointly maximize the preservation of species and ecosystem processes in the long term (Pressey et al. 1993, see Csuti et al.

1997 and Prendergast et al. 1999 for a review). Our goal in this section is to summarize the existing information on large-scale patterns of species distribution for different taxa, identifying areas of high species diversity across taxonomic groups and the possible causes generating these patterns. Since most of these studies did not focus exclusively on the nearshore, it was not always possible to separate the near from the farshore. We used mostly published studies, but also present unpublished data from the authors of this contribution, who will reveal details of those studies elsewhere. Finally, we call attention to the major gaps in the existing information.

The study of large-scale patterns of species distribution and ecosystem processes in Chile has been limited to traditional biogeographical analyses. In these studies, discontinuities in compositional affinities of the biota along geographic gradients were used to determine biogeographic provinces and infer probable causes for their borders as well as the probable geographic origin of the species. Documentation of patterns at mesoscales (between the local-scale of experimental studies and the continental scales of traditional biogeographic analyses), are virtually non-existent (but see Camus 1998, Brazeiro 1999, and below). The main reason for the lack of studies at the meso-scale is the scarcity of appropriate databases. For instance, while some information exists about geographic ranges for a great number of species, sampling intensity and distribution along the coast is so scattered that it is not possible to examine latitudinal trends in diversity or site occupancy with more than ten degrees latitude of precision.

From a biogeographic point of view, the southeastern Pacific shelf area is within the so-called Temperate Pacific Realm, which to the north borders the Panamic Province around Paita, in Perú (4-5 °S). The existent information about biogeographic provinces and compositional affinities show different patterns for macroalgae and benthic invertebrates within this realm (Viviani 1979, Castilla 1979, Santelices 1980, Brattström & Johanssen 1983, Santelices & Marquet 1998, Lancellotti & Vasquez 1999). For benthic invertebrates, several studies have attempted a zoogeographic zonification of the coast based on the distribution of the species (e.g., provinces, transition zones, borders; see below, Table 1; Dall 1909, Carcelles & Williamson 1951, Boltovskoy 1964, Stuardo 1964, Marincovich 1973, Knox 1960, Hartmann-Schroeder & Hartmann 1965, Dell 1971, Smenov 1977, Viviani 1979, Sebens & Paine 1979, Brattström & Johanssen 1983, Lancellotti & Vásquez 1999). Different taxa and

TABLE 1

Summary of the results of the three most recent studies about zoogeographic units and borders in Chilean waters. The total number of species included in each case, as well as the taxonomic groups considered are listed. The major biogeographic breaks in species distribution and the transition zones are included for both litoral (< 50 m) and sublitoral environments (> 50 m). ND indicates no data

Resumen de los resultados de los tres estudios más recientes sobre unidades zoogeográficas y sus límites en Chile. El número total de especies incluídas y los grupos taxonómicos considerados en cada caso son también listados. Los mayores quiebres biogeográficos en la distribución de especies y en las zonas de transición son listados separadamente para ambientes litorales (< 50 m) y sublitorales (> 50 m). ND indica que no hay datos disponibles

Publication	Taxonomic Groups Analyzed	Number of species	Biogeographical and Transitional Regions	
			Litoral	Sublitoral
Viviani (1979)	Cirripedia, Macrura, Brachyura, Anomura (Porcellanidae), Polyplacophora, Bivalvia (Pelecypoda), Asteriodea, Echinoidea, Holothuroidea, Bryozoa	282	North: 12° S South: 40-46° S	South: 41° S (no clear break point, many small break points between 35-45)
Brattström and Johanssen (1983)	Actiniaria, Cirripedia, Macrura, Brachyura, Anomura, Polyplacophora, Gastropoda, Bivalvia, Asteriodea, Ophiuroidea, Echinoidea, Holothuroidea, Ascidiacea	240	North: 33° S South: 42° S Transition 33-42° S (42 strong breaks 42-48 weak breaks)	North: 33° S South: 42° S Transition 33-42° S
Lancelloti and Vasquez (1999)	Porifera, Anthozoa, Polychaeta, Mollusca (Polyplacophora, Gastropoda, Bivalvia), Crustacea (Cirripedia, Amphipoda, Isopoda, Brachyura, Anomura), Echinodermata (Asteriodea, Ophiuroidea, Echinoidea, Holothuroidea), Ascidiacea	1,597	(< 100 m) North: 18-35° S Center: 35-48° S South: 48° S	ND

depth were considered in each of these studies (Table 1), and although they proposed different biogeographic schemes, there are general coincidences. First, there are two major biogeographic provinces (but see Lancellotti & Vásquez 1999): (a) the Perú-Chile Province (from Paita in Perú to Valparaíso in Chile) and (b) the Magellanic Province (Chiloé, Island to cape Horn). The exact latitude of each province varies up to 2-3 degrees among the different authors. Secondly, most authors recognized a more diffuse 'transition zone' in central Chile, from around Valparaíso down to Chiloé Island.

Differences among studies can be partly due to the species included and the ranges of depth distribution used in each analysis. In general, shallow water species have been analyzed separately from deep-water species (but see Table 1), and the effect of this factor can be easily observed. The biogeographic break at 42° S is stronger for shallow than for deep-water species (Brattström & Johanssen 1983). Also, the number of species with northern origin is higher in shallow waters while the number of species with southern origin

is higher in deeper waters (Brattström & Johanssen 1983). Subantartic species are found in the north only in deep waters. The taxonomic groups included in the analysis conducted by each author may have also contributed to the small discrepancies (see Table 1). Viviani (1979) suggested a clear asymmetry in the latitudinal distribution of different taxonomic groups (see also Brattström & Johanssen 1983). Thus, the use of different taxonomic groups in a pool of species classified only by depth could produce different outcomes. Independent analyses by taxonomic group could determine if the discontinuities in compositional affinities of the biota along geographic gradients are consistent among taxa, and also if the same causes could affect in similar ways the different taxa. For instance, the distribution of isopod and amphipod species (not used by Viviani 1979 and Brattström & Johanssen 1983) could have affected the determination of the discontinuity at 48° S recently suggested by Lancellotti & Vásquez (1999). Both groups show high number of species and a discontinuity between 45 and 50° S. The pattern of species distribution may continue

changing slightly as distribution ranges are modified (when less studied regions, or deeper waters are better known).

Circulation patterns, heterogeneity of the coast, salinity, temperature, and tidal amplitude are some of the factors consistently mentioned to explain the distribution of species along the coast of Chile. Large changes in patterns of water circulation in the southeastern Pacific correspond remarkably with the most critical biogeographic boundaries around Paita and Tumbes in Perú and the Chiloé Island in Chile (Fig. 1), giving support to this factor. Ongoing studies show that the total number of mollusk species increases towards high latitudes and the mean latitudinal range of the species decreases in accordance with Rapoport's Rule (Valdovinos, Navarrete & Marquet, unpublished data). No effect of temperature was found to explain the increase in mollusk species richness at high latitudes (Roy et al. 1998), and instead a strong correlation between number of species and heterogeneity of the coast was detected (Valdovinos, Navarrete & Marquet, unpublished data). Another factor that may also be important in explaining the distribution of marine invertebrates is the distribution of reproductive and developmental modes of the different taxonomic groups along the latitudinal gradient. However, information about modes of development and length of planktonic time is poor for most taxa in comparison with other geographic areas of the world (Table 2). The identification of causal factors to explain the patterns of distribution of

marine invertebrates is critical, and although similar causes could explain the distribution of several taxa, some may be taxa specific. The general pattern suggests that there is a "diversity hotspot" in southern Chile (South of 42° S), although we think that it does not occur for all invertebrate taxa (e.g., Brachyuran, Anomuran).

The biogeographic analysis of the marine flora of the Chilean Pacific coast shows a different pattern than for marine invertebrates. One area of species affinity is found from the Magallan Strait to Cape Horn (54-55° S), composed of mostly subantartic and endemic species, many with restricted distribution. A second, broader area extends between 5 and 53° S and shows many endemic species, several bipolar species, and a gradual northward decrease in the number of antarctic species. Within this region, a small discontinuity is observed at 30° S (probably related to upwelling events, Santelices 1980). Santelices (1980) hypothesized different distribution centers may have generated the current pattern. The outstanding phytogeographic features of this region seem to be the high degree of endemism (32.3%), the strong influence of subantartic species (34.4%), and probably as a consequence, the decrease in species richness towards the equator (Santelices 1980). Other species of macroalgae are widely distributed (22.8%), bipolar (7.1%) or tropical (3.4%). In a recent paper, Santelices & Marquet (1998) described the latitudinal variation in species richness and geographic range size for 380 marine benthic algae along the coastline

TABLE 2

Percentage of the total number of described species within a given taxonomic group for which exist information in our databases on body size, developmental mode (eg. brooders, broadcasters), larval type (lecitotrophic or planktotrophic), duration of plantonic life, and geographic ranges of species distribution. For comparison, we included within brackets the information available (also in %) for developmental modes for invertebrates along the coast of California (except for Crustaceans)

Porcentaje del total de especies descritas por cada grupo taxonómico para las cuales existe información en nuestra base de datos sobre tamaño corporal, modo de desarrollo (incubadores o dispersores), tipo de larva (lecitotrófica o planctotrófica), duración del tiempo de vida planctónico, y rango de distribución geográfica de las especies. A modo comparativo, se incluye entre paréntesis la información disponible (también en porcentajes) para los modos de desarrollo de los invertebrados a lo largo de la costa de California (excepto para Crustaceos)

Taxa	Size	Developmental Mode	Larval Type	Planktonic life	Distribution
Gastropoda	80.5	35.5 (85)	11.6	8.3	94.5
Bivalvia	87.6	28.0 (34)	14.0	8.5	98.8
Polyplacophora	83.2	58.9 (50)	39.3	1.8	100.0
Echinodermata	86.8	56.6 (79)	25.0	21.1	94.7
Brachyura	100.0	100.0	100.0	16.2	100.0
Isopoda	49.0	100.0	100.0	1.0	100.0
Anomura	94.9	100.0	100.0	8.5	100.0

of Perú and Chile (latitude 10° to 55° S), and showed that the number of species increases with latitude from about 20 at latitude 5° S to more than 130 at latitude 55° S. This "anomalous" latitudinal species diversity pattern has also been reported for the Pacific coast of North America (Gaines & Lubchenco 1982). The pattern is associated with a progressive decline in species mean latitudinal range size as diversity increases, following the Rapoport's Rule (Stevens 1989, 1996). As reported above, the same pattern seems to occur for marine invertebrates (Valdovinos, Navarrete & Marquet, unpublished data). Hotspots of diversity of marine invertebrates (pooling Gastropoda, Bivalvia, Placophora, Echinodermata, Isopoda, Anomuran and Brachyuran) and macroalgae are found south of 50° S (>897 species), between 35 and 40° S (819-896 species), and between 25 and 30° S and 40 and 50° S (748-818 species).

Large scale biogeographic analysis of coastal fish species are lacking, but ongoing studies show that coastal fishes assemblages of littoral marine fishes also exhibit important compositional breaks around 40-42°S, but in this case, diversity decreases toward higher latitudes (Ojeda et. al. in press). The intertidal fish fauna of northern Chile is relatively poor, with no more than 6 to 7 species in Antofagasta (23° S; Ojeda, unpublished data). This fish assemblage is conformed by a subset of the species also found along the central Chilean coast (ca. 33° S), including the kyphosids *Graus nigra* and *Girella laevifrons* and the blenioid *Scartichthys viridis*. Rocky intertidal fish fauna of central Chile (30 – 33° S) is fairly diverse with 18 to 20 species (Varas & Ojeda 1990, Muñoz & Ojeda 1997). This assemblage is composed of resident species (Blenniidae, Tripterygiidae, and Clinidae) and transient or temporary species that inhabit the intertidal pools as juveniles (e.g., Kyphosidae; Varas & Ojeda 1990). South of Maiquillahue Bay (39°S), intertidal fishes in pools are scarce and only some clinids and blennids remain, being *Calliclinus geniguttatus* the most conspicuous. *Myxodes virides*, *Tripterygion cunninghami* and *Scartichthys viridis* are also found in the rocky areas of the exposed Pacific coast down to Chiloé Island. In the area of Valdivia tide pool fishes of the Nototheniidae family, an abundant group in the southern channel region south of 45°, start to appear in intertidal pools. The more emblematic species in the intertidal habitats of the southern fjords south of 45° are the nototheniiforms *Harpagifer bispinis* and *Patagonothoten cornucola*, together with the zoarcid *Austrolychus deprecisseps*. The local intertidal fish assemblages do not contain more than 8 to 10 species in the fjord area (Moreno & Jara 1984). As yet, the information available on distribution of fish species is restricted to intertidal and shallow subtidal fishes (Ojeda et al. in press).

Latitudinal distribution of native species of birds, mammals, and reptiles associated to littoral environments along the Chilean coast are currently being investigated (Silva & Marquet unpublished data). Using published records these authors obtained distributional data for 93 species of birds, 25 mammals, and 14 reptiles registered as resident or occasional on the coast of Chile (no more than 10 km offshore). The general latitudinal pattern in species diversity (all taxa pooled) is non-linear. Total species richness increases with increasing latitude between 18 and 28° S and south of 50° S, but from 28° S the number of species decreases dramatically as latitude increases to 50°S. The highest species richness occurs between 25° and 30°S corresponding to the coastal area between Paposo and La Serena, where the number of species was as high as 80.

In general, latitudinal patterns in diversity vary among these taxa. Mammals show an increase in number of species with latitude, from 5 species around 20° S up to 19 species around 55° S, while reptiles species richness decreases progressively as latitude increases, from 8 species between 22° and 30°S to one species south of latitude 41°. Birds, on the other hand, show a more complex latitudinal richness pattern with several peaks and troughs. Richness reaches a peak of 65 species in north/central Chile, between 25° to 30° S. From this latitude to the south, richness decreases (33 species) until around 50° S and tends to increase further south. The latitudinal pattern in threatened species (vulnerable or endangered) shows also a non-linear pattern. It remains relatively high (> 10 species) in north/central Chile with a major peak of 13 species at around latitudes 35°- 40° S. Endemicity peaks at around latitude 30° S (5 reptile species). There are no endemic birds and only one endemic mammal species. The conservation status of seabirds as well as the identification of marine birds and mammals included in International Conventions have been discussed by Schlatter (1984) and Schlatter and Hucke-Gaete (1999) respectively. In an additional study, Schlatter and Simeoni (1999) recognized 109 species of marine birds associated to oceanic and costal areas in continental and insular Chile. Out of this total, 23 species (=21%) are included in some threat category.

These studies run short in term of representing the species diversity inhabiting coastal and

subtidal environments in Chile. Without doubt the total number of species, a large fraction of which are endemic, is substantial (specially towards subantartic areas, Viviani 1979, Santelices & Marquet 1998), as large as it is our current lack of knowledge of their conservation status and the need for a national system of Marine Protected Areas.

Patterns of community structure and processes affecting nearshore communities

The study of biological and physical processes structuring communities at one or a few sites has been the main focus of ecological research in Chile. Over the past two decades these findings have reached recognition as one of the best studied marine systems of the world, and examples of Chilean studies are starting to appear in basic ecological textbooks (e.g., Giller 1984, Putman 1994, Paine 1994, Raffaelli & Hawkins 1996, Barnes & Hughes 1999). However, this information comes from a relatively small number of study sites, and is mostly restricted to the intertidal zone. Recent reviews summarized much of the information available and presented the current view of our understanding about the dynamics of Chilean benthic nearshore systems (e.g., Santelices 1989, 1990, Castilla & Paine 1987, Vásquez & Buschman 1997, Castilla et al. 1993, MacLachlan & Jaramillo 1995). In this section, we draw from these reviews and other basic studies to present what we believe are the most important patterns and processes in the different systems. Our goal is twofold. First, whenever possible we want to identify key species and processes that for their impact on the rest of the community need special attention in conservation plans, and which could be used as indicators of the degree of intervention of the system. Secondly, we want to call attention to the major gaps in information in the different habitats, which either make it impossible to identify key components in the local system, or jeopardize the applicability of the ones we do identify as such.

In Chile there are two major and clear biases in the amount and intensity of the existent ecological information. First, most of the experimental work has been conducted on rocky and sandy intertidal zones, or shallow rocky subtidal habitats. Secondly, the great majority of the ecological studies have been conducted on a relatively small fraction of the coast, between about 30 and 39° S (Santelices 1990, Camus 1998). Thus, our account of the different systems is tainted by these limitations.

Intertidal and shallow subtidal rocky habitats

Wave exposed rocky intertidal areas are common habitats all along the Chilean coastline. In these systems the basic taxonomy of macroinvertebrates and macroalgae is generally well known. More intensive samplings and taxonomic and molecular work should turn up new species and clarify the status of many others, but no big changes in the total number of species are expected. There are some fairly specious groups of intertidal invertebrates whose taxonomic identification is particularly difficult and need revision, such as limpets of the genera Lottia, Scurria, Collisella and Nacella, and amphipods in general. A recent book about taxonomic identification of macroalgae has helped clarify the status of intertidal and shallow subtidal algal groups in central Chile (Hoffman & Santelices 1997). No equivalent exists for invertebrates. As for most ecological systems, it is difficult to determine the exact number of species that coexist in the intertidal zone. Local communities at exposed-rocky benches in central Chile are composed by some 30 to 60 macroscopic invertebrate species, both sessile and mobile (e.g., Marquet et al. 1990). This number does not consider the small sized species that inhabit almost exclusively within the mussel bed matrix or inside kelp holdfasts (Cancino & Santelices 1984, Vásquez, unpublished data, see below). Between 40 and 60 macroalgal species can be found in a given site, not taking into account microscopic forms or epiphytes (Camus 1998, Broitman and Navarrete, unpublished data). A fairly diverse assemblage of tidepool fishes conformed by 10 and up to 18 species is present at many sites in central Chile (Muñoz & Ojeda 1997). There is no information about latitudinal trends in species richness of local communities.

Zonation patterns have been extensively described for various localities (e.g., Alveal 1971, Santelices et al. 1977, Castilla 1981), most of them heavily affected by human collection. From Chiloé Island (ca. 43° S) towards the north, the kelp Lessonia nigrescens forms a characteristic belt at the lower end of the intertidal zone. Among the holdfasts of the large kelps there is either patches of algal turfs, mostly Gelidium spp. and other branched corticated algae, or patches of fleshy and calcified crustose algae. On rocky benches not directly exposed to breaking waves, the mosaic of algal turf and crustose algae can cover extensive areas of the low and mid-low intertidal zones. Along most of its range, from central Chile (about 30° S) to Magellan Strait, Lessonia shares the low intertidal zone with the bull kelp, Durvillaea antarctica. This latter spe-

cies is more prevalent to the south, and in areas south of Valdivia is relatively protected from human exploitation extending up into mid and even high intertidal zones. South of Chiloé, on the open coast of the fjords region, the scarce information available indicates that *Durvillaea* is relatively more abundant and prevalent than *Lessonia* (Dayton 1985). At about 20° S, *Lessonia* reaches its northernmost limit and the substratum is occupied mostly by encrusting coralline algal forms and high densities of herbivores. The mid intertidal zone of most sites in central and southern Chile, south of about 32° S, is dominated by beds of the mussel *Perumytilus purpuratus* (Castilla 1981). At some sites and on a more seasonal basis, a mixed mussel bed of *P. purpuratus* and *Semimytilus algosus* can extend down to the low intertidal zone and occupy the space among *Lessonia* plants, temporarily overgrowing the *Gelidium* spp. turf. When mussel beds are absent from the mid zone, the substratum is occupied by chthamaloid barnacles and corticated foliose algae (mostly *Mazzaella laminariodes*) and fleshy crustose algae (largely *Hildenbrandtia* spp. in central Chile and *Ralfsia* spp. in the South). In the mid zone of exposed fronts of Chiloé Island and in the low intertidal zone of semiprotected fronts, it is frequent to find juveniles and adults of *Austromegabalanus psittacus* (a large size barnacle) together with high densities of the muricid *Concholepas concholepas*. While in tidepools and channels of central Chile the black sea urchin, *Tetrapygus niger*, is probably the most important browser species, south of 39° S the only sea urchin present in the emergent substratum and intertidal pools is the red *Loxechinus albus*, which coexists with the former one in central Chile (Contreras & Castilla 1987, Moreno & Vega 1988).

North of about 32° S, where mussel beds are scarce, the mid zone is dominated by ephemeral algae (genera *Porphyra, Enteromorpha* and *Ulva*), fleshy crustose algae (mostly *Hildenbrandtia*) and bare rock. Mussel beds appear again as dominant components of the mid zone at some sites north of about 20°S and up to subtropical areas in Perú. On the shaded, more protected side of vertical walls the crustose alga *Codium dimorphum*, a thick and soft fleshy crust, can cover large areas of the mid intertidal landscape (Santelices et al. 1981). The high intertidal zone throughout the Chilean coast, down to the open coast of the Magellan region, is characterized by a band of the chthamaloid barnacles *Nothochthamalus scabrosus* and *Jehlius cirratus* and the seasonal appearance of ephemeral algae. Experimental evidence has shown that general zonation patterns described above can be substantially modified, directly or indirectly, by fishing. For instance, removal by humans of the muricid gastropod *Concholepas concholepas* allows mussel beds to extend into the lower intertidal zone (Durán &Castilla 1989), and removal of large keyhole limpets produces the extension of *Mazzaella laminarioides* well into the low intertidal (Moreno & Jaramillo 1983).

Based on the work conducted in the region between 32 and 36°S, and around 39°S, it is possible to identify critical species and processes in the intertidal system. First, there are two functional groups of overriding importance as species-engineers (Jones et al. 1994), which provide structural habitat for other species. In the mid intertidal zone, mussel beds (mostly *Perumytilus purpuratus*) provide a microhabitat for a large number of small sized species which are found only within the mussel bed matrix, as well as for species that are found elsewhere but either find refuge or recruitment sites in the mussel bed (Cancino & Santelices 1984, Castilla et al. 1989, Navarrete & Castilla 1990, Alvarado & Castilla 1996). These beds can cover more than 80% of the substratum at these tidal elevations and experiments have demonstrated that they are the dominant competitors for space (Paine et al. 1985). However, experiments have also demonstrated that, partly as a result of mussel larvae being unable to settle directly onto bare rock (Navarrete & Castilla 1993), the beds are very slow to recover from disturbance, particularly in the absence of recruitment mediators. A different pattern was found in southern Chile, where the recovery rate of *Perumytilus purpuratus* was very fast when herbivores and carnivores were excluded (Moreno et al. 1986). After the experimental exclusion of herbivores (*Fissurella picta*), *Perumytilus* recruited at increasing rates during 2 years, generating a matrix that facilitated mussel larval settlement. Thus, mussel beds in Central Chile are particularly sensitive to disturbance, while in southern Chile the response may be different depending on the species that are simultaneously disturbed.

The other important structural components in the low, rocky intertidal zone are the large kelps, *Lessonia nigrescens* and *Durvillaea antarctica*. These algae play two important roles as species-engineers. First because of their size and strong stipes, the plants create a special regime of physical disturbance, which is sufficient to prevent access from large herbivores (e.g., sea urchins) into the low and mid-low intertidal zones (Ojeda & Santelices 1984) and can substantially modify the water flow and wave forces for other algal and

invertebrate species that inhabit among the plants. Secondly, the holdfasts of these kelps, particularly *Lessonia* (see below), serve as a microhabitat to a large number of invertebrate species, many of which are rarely found in open areas (Cancino & Santelices 1984, Vásquez unpublished data). Besides mussels and kelps that are found along most of the coast of Chile, a special situation occurs within the Antofagasta Bay in northern Chile, where a dense bed of the giant tunicate, *Pyura praeputialis* monopolizes large areas of the mid and low intertidal zones (Clarke et al. 1999, Guiñez & Castilla in press). These beds also serve as a microhabitat to a large number of species, not commonly found elsewhere (Paine & Suchaneck 1983).

Several strong biological processes have been determined and experimentally quantified at sites in central Chile (33 °S) and around the area of Valdivia (41 °S). As in many other coasts of the world, top-down (trophic) factors play a major role in the regulation of local intertidal communities in Chile. Probably the strongest top-down force in these ecosystems is the intense human collection of invertebrates, algae and fish that can profoundly transform the landscape (Castilla et al. 1994, Branch & Moreno 1994, Castilla 1999). We will treat human impacts separately in the next section and will concern ourselves here with the more 'naturally intertidal' interacting species. There is a diverse arrange of vertebrate and invertebrate carnivore predators that feed on both mobile and sessile invertebrates (Castilla 1981, Castilla & Paine 1987, Navarrete & Castilla 1993, Branch & Moreno 1994, Muñoz & Ojeda 1997). Separate experiments have shown that many of these predators can have important effects on different prey populations, but so far there has been no experiments designed to quantify their effects in a comparable fashion (e.g., Navarrete & Menge 1996, Berlow et al. 1999). However, from the isolated studies it is now very clear that different species have very different impacts at the community level, suggesting a pattern more alike to a keystone type of predation than diffuse predation (e.g., Menge et al 1994, Navarrete & Menge 1996, Robles & Robb 1993). This means that it is possible to identify one or a small subset of species within the predatory guild, which have disproportionately strong effects on some community variable (Power et al. 1996, Allison et al. 1996). In central Chile, there are two carnivore species that appear to have a much stronger per capita effect than the rest of the carnivores with which they coexist. First, experimental removals of the sun star *Heliaster helianthus* from the mid intertidal zone led to a large reduction in the cover of mussel beds and a concomitant increase

in barnacle and ephemeral algal cover (Paine et al. 1985). This species can remove and consume several mussels at once, creating gaps in the mussel beds that can persist for months or years. Second, the exclusion of humans from a stretch of the coast (see below) revealed that the edible muricid gastropod *Concholepas concholepas*, which is kept at low densities by human collection in open (unprotected) areas, can completely decimate the mussel beds from the low, mid and even mid-high intertidal zones (Castilla & Durán 1985, Moreno et al. 1986, Durán & Castilla 1989, Castilla 1999). Because the dominant intertidal mussel in these beds, *P. purpuratus*, does not reach more than three to four cm in length, mussels cannot find a refuge in size from either *Heliaster* or *Concholepas*. It is not clear how strong are the direct and indirect interactions between these two predators, but certainly the strength should be modulated by the intensity of human collection of the gastropod. In the area of Valdivia, 840 km to the south, a comparable human exclusion experiment also showed that *Concholepas* can dramatically reduce the abundance of mussel beds, freeing space for other sessile species and triggering several indirect effects at different trophic levels (Moreno et al. 1986, Godoy & Moreno 1989). At these sites, there are no *Heliaster*, whose geographic distribution does not extend much beyond 36° S, and no other sea star seems to compensate for its predation pressure in the mid zone. The crabs of the genus *Acanthocyclus* can be very abundant at some sites in central and southern Chile (Navarrete & Castilla 1988, 1990) and their community-wide effect has yet to be quantified. In relatively wave-protected areas, the muricid predatory gastropod, *Acanthina unicornis* (= *Nucella calcar*) has been shown to heavily prey on mussel populations at mid-low intertidal levels, but they do not seem to be able to persistently control their tidal distribution (Moreno 1995). At the moment we cannot determine how much the impacts of *Concholepas* and *Heliaster* change north of about 32° S and south of Chiloé Island. Preliminary evidence for northern Chile does suggest that the overall impact of predation on major patterns of community structure might be very different to that in central Chile (Camus 1998). Recent studies by Vásquez et al. (1998) suggest that large-scale interannual perturbations, namely El Niño events, can have strong effects on local community dynamics and might modulate other biological interactions in northern Chile.

Regulatory top-down forces are not restricted to high trophic level predators. Experimental manipulations have shown that herbivores can con-

trol zonation patterns of macroalgae in the mid and low intertidal zones. In the low zone of central Chile, the balance between the algal turf and crustose (fleshy and calcareous) algae seems to be determined by herbivory (Ojeda & Santelices 1984, Santelices 1990). In turn, the abundance of herbivores is regulated to some extent by the whiplash effect of the large *Lessonia* plants. In relatively wave-protected channels and tidepools where *Lessonia* is naturally absent, herbivores reach high densities (particularly the black sea urchin *Tetrapygus niger*), and a blanket of pinkish calcareous algae (*Mesophyllum*) covers the low zone and extends into shallow subtidal areas (Santelices 1990). In exposed benches there is a diverse guild of herbivores, including several large chitons, key-hole limpets, sea urchins and herbivorous fish, but we have no information about their relative impacts. Herbivory is also intense at mid tidal elevations. The most abundant key-hole limpets are *Fissurella crassa* and *F. limbata* in central Chile, and *F. picta*, also followed by *F. limbata*, in southern Chile. Experimental manipulations in the Valdivia area showed that key-hole limpets can control the presence of the mid-intertidal belt of the alga *Mazzaella laminarioides* (Jara & Moreno 1984, Moreno et al. 1984). In central and northern Chile the *Fissurella* species are the largest herbivores and probably the most efficient mid littoral consumers (Oliva & Castilla 1986). Other species of limpets, *Siphonaria lessoni* and *Collisella* spp., are also found in the same habitat. These two species of limpets have small size, and exhibit changes in individual growth rate and in their distribution pattern when *Fisurella* spp. is present (Godoy & Moreno 1989). Again, these key-hole limpets are heavily exploited by humans, so their community-wide effects became apparent only after excluding humans from a stretch of the coast. The same key-hole limpets appear to have comparable effects in central Chile (Oliva & Castilla 1986). In southern Chile, there is also one herbivorous gastropod that can play an important role in community structure, the snail *Tegula atra*. This snail eats only filamentous ephemeral algae and ulvoids, and its vertical distribution tracks the abundance of this type of algae at mid and low intertidal zones, as well as the shallow subtidal, where it can clean the rocks of the turf of ephemerals. This facilitates the seasonal recolonization of the low intertidal and very shallow subtidal areas by *Macrocystes pyrifera* (Moreno & Sutherland 1982).

A typical landscape at low and mid intertidal levels in channels not directly exposed to breaking waves is the dominance of *Hildenbrandtia* spp. and other fleshy crustose algae with sparse barnacles and other sessile invertebrates. This pattern is observed even at areas with low densities of sea urchins and other herbivorous invertebrates. Recent experiments suggest that the culprit for this pattern is the blennioid fish *Scartichtys viridis*, which plays an important role in maintaining the low abundance of foliose macroalgae and the relatively high cover of brown and red crustose algae (Ojeda & Muñoz 1999). Rocky intertidal fishes of central Chile forage on a wide variety of species, including sessile and slow-moving (e.g., macroalgae, barnacle and gastropods) and active animals (e.g., decapods, isopods, amphipods, and small fishes). The intertidal fish assemblage is composed of three trophic groups: one guild consisting of five species of carnivorous (*Bovichthys chilensis, Gobiesox marmoratus, Auchenionchus variolosus, A. microcirrhis* and *Graus nigra*), a second guild of three species of microcarnivorous (*Myxodes viridis, Tripterygion cunninghami,* and *T. chilensis*), and a third guild of two species (the omnivore *Girella laevifrons* and the herbivore *Scartichthys viridis*; Muñoz & Ojeda 1997).

In Chile, the systematic study of recruitment (supply-side) as a factor structuring local, rocky shore communities is only beginning (e.g., Moreno et al. 1993, Gallardo et al. 1994, Carrasco & Carvajal 1996, Cañete et al. 1996). This situation holds also for other habitat types (e.g., sandy beaches, see below). We have virtually no information about the kinds of processes that regulate recruitment rates of any species along the coast, including the commercially exploited ones. Nor do we know if there are gradients of recruitment along the more than 4,000 km of open coast, or if particular sites could be classified as sources or sinks in terms of the population dynamics of some species. This information is critical in the design of marine reserve networks (Roberts 1998). Similarly, the relative importance of bottom-up processes in structuring the marine communities in the nearshore is lacking. Recently, Vásquez et al. (1998) documented that the frequency of upwelling appears not to be a determining factor of the diversity (species richness) of rocky littoral communities in northern Chile. Some general ideas about major oceanographic processes affecting nutrient supply to the coastal areas, or driving recruitment, as well as quantitative information on recruitment rates along large stretches of the coast is urgently needed.

Intertidal, soft-bottom habitats

Besides the common rocky intertidal areas, sandy beaches are common features along the Chilean coast, between Arica (ca. 19° S) and the exposed

coast of Chiloé Island (ca. 42° S). Microtidal estuaries (1-2 m of tidal range) are also represented, but only along the coast of south central Chile (ca. 35-41° S; Pino 1994[1]). Similarly, and even when salt marshes are found along the entire Chilean coast, they are more abundant at south central Chile. In the northern region, marshes occur primarily at areas located close to river outlets; further south (ca. 41-43° S), they also occur in inland marine waters such as that of the archipelagos. Most of the faunistic studies carried out in sandy beaches and intertidal estuarine flats deal primarily with benthic macroinfauna (Jaramillo 1978, 1982, 1987a and b), although local studies of the meiofauna inhabiting the very shallow sediments (about 1 cm deep) have been done (Clasing 1976).

Studies on the latitudinal distribution of species and abundance of the macroinfauna inhabiting sandy beaches showed that peracarids (primarily cirolanid isopods, *Excirolana* spp.) are dominant, in terms of species richness. The cirolanid isopod *Excirolana hirsuticauda* and the anomuran crab *Emerita analoga* are usually the most abundant taxa, being this crab the main contributor to intertidal biomass (Sánchez et al. 1982, Jaramillo 1978, 1982, 1987b, 1994, Jaramillo et al. 1998, Brazeiro et al. 1998). Studies carried out at different latitudes showed that the lower shore levels are usually occupied by *E. analoga* all along the Chilean coast. However, latitudinal changes in species composition are commonly observed at the upper intertidal zone (dry zone and drift line; Castilla et al. 1977, Hernández et al. 1998, Jaramillo 1987b, 1994). While the ghost crab *Ocypode gaudichaudii* and the cirolanid isopod *Excirolana braziliensis* are commonly found in the upper shore levels of northern Chile (ca. 19-23° S), the talitrid amphipod *Orchestoidea tuberculata*, the tylid isopod *Tylos spinulosus* and *E. braziliensis* are found in similar levels at north central Chile (ca. 28-30° S). On the other hand, *O. tuberculata* and *E. braziliensis* are typical inhabitants of sandy beaches of central and south central Chile (ca. 33-42° S). These studies also showed that the number of species of isopods (*Excirolana* and *Macrochiridothea*) is higher at sandy beaches located in south central Chile (ca. 40° S; Jaramillo 1982, Jaramillo 1987b). A higher number of taxonomic and ecological surveys carried out in sandy beaches of southern Chile (e.g.,

Jaramillo 1982, 1987b, Varela 1983) could explain the differences in species richness of peracarids along the Chilean coast. The influence of subantarctic waters on sandy beaches located in southern Chile may also explain the better representation of valviferan species of *Macrociridothea*, a typical taxon widely distributed on the southern tip of South America (cf. Moreira 1973). Recently, Brazeiro (1999) discussed patterns of community structure and distribution of the Chilean sandy beach macroinfauna and found that species with the widest range of distribution tend to be the most abundant.

In estuarine areas the macrofauna is dominated by different taxonomic groups in the upper (i.e., close to the limnetic areas) and middle reaches, as well as in the outlets (i.e., closest to the marine environment). The typical estuarine taxonomic groups in the upper reaches are Insecta (Diptera, Coleptera, Trichoptera, among others) and Oligochaeta (Naididae, Tubificidae; cf. García & Ojeda 1995). Polychaetes, followed by amphipods, are the dominant groups in the middle reaches (the most common species are *Prionospio (Minuspio) patagonica*, *Capitella capitata*, *Perinereis gualpensis* and the amphipod *Paracorophium hartmannorum*; Jaramillo et al. 1985, Quijón & Jaramillo 1993). At the estuarine outlets the macroinfauna is dominated by polychaetes (e.g., *Euzonus heterocirrus*), peracarid crustaceans (*Excirolana hirsuticauda*, *E. monodi* and *Macrochiridothea mehuinensis*) and bivalves (juveniles of *Mesodesma donacium*; Jaramillo et al. 1985). Latitudinal analyses of intertidal estuarine macroinfauna, as those cited above for the sandy beach macroinfauna, have not yet been conducted. There are not many studies on other biotic components of soft habitats such as meiofauna and salt marsh plants. The meiofauna inhabiting very shallow sediments (about 10 mm deep) in mud flats near Puerto Montt (ca. 41° S) was dominated by nematodes followed by ostracods and harpacticoid copepods (Clasing 1976). More than 60 species of vascular plants have been found in these habitats; *Sarcocornia fruticosa* and *Anagallis alternifolia* are the most frequent, while *Spartina densiflora* is common in marshes of south central Chile (San Martin et al. 1992, Ramírez et al. 1990).

Patterns of macroinfaunal communities inhabiting exposed sandy beaches of the Chilean coast have been associated to spatial and temporal variability of single physical factors such as mean grain size and water content of sands (Jaramillo 1987a, Jaramillo et al. 1996, Hernández et al. 1998) and to a composite index, the Dean's parameter, which describes the morphodynamic

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Pino M (1994) Geomorfología, sedimentología y dinámica de la circulación en estuarios micromareales del centro sur de Chile. Resúmen XIV Jornadas de Ciencias del mar, Puerto Montt, Chile: 106-107.

beach type (Jaramillo & McLachlan 1993, Jaramillo et al. 1998). In south central Chile, species richness, abundance and biomass of the macroinfauna increases from reflective to dissipative beaches (Jaramillo & McLachlan 1993). Similar results were found in sandy beaches of north and north central Chile (Jaramillo et al. 1998). These results suggest that similar factors (i.e., beach morphodynamics) might control the community structure of the Chilean macroinfauna, independent of geographic latitudes. However, recent findings (Jaramillo, unpublished data) showed a departure from that pattern, suggesting that other factors (e.g., seasonality) also affect species richness, abundance and biomass of the macroinfauna.

Predation by fish and birds has been suggested as important factors regulating macroinfaunal abundances of the Chilean sandy beach community (e.g., Jaramillo et al. 1980). Pequeño (1979) showed that *Eleginops maclovinus* feeds on *Emerita analoga* in sandy beaches of south central Chile. Whimbrels (*Numenius phaeopus*) and sanderlings (*Calidris* spp.) have also been observed consuming *Emerita analoga* in the swash zone of exposed beaches. However, experimental studies to test the effect of fish and bird predation on the benthic macroinfauna are not available. Experimental studies carried out on sandy beach species of the eastern USA showed that competition is indeed important in amphipod guilds (Croker & Hatfield 1980). Even when no such experimental studies have been carried out in Chile in sandy beaches, some evidence suggests that such kinds of interactions could be important. For example, the size-structure in *Emerita analoga* aggregations in the swash zone of sandy beaches, and the common inverse relationship between body size and abundance of this crab could be due to biological interactions (Jaramillo, unpublished data).

As for sandy beaches, the community structure of the intertidal estuarine macroinfauna has been mainly analyzed in relation to physical factors, such as water salinity gradients along estuaries and substratum characteristics (Bertrán 1984, 1989, Jaramillo et al. 1985, Donoso 1991, Quijón & Jaramillo 1993, 1996, Turner 1984). As it has been observed in other estuarine temperate areas (e.g., McLusky 1971), the finest and richest sediments in organic matter content support the highest abundances and biomasses, while sandy bottoms located closer to estuarine mouths support higher species richness (e.g., Bertrán 1984, Jaramillo et al. 1985). In estuarine areas of south central Chile epibenthic predation has been experimentally studied. Venegas (1992) observed a

significant increase in the abundance of the most abundant species of the intertidal macroinfauna of the Queule river estuary (the polychaete *Prionospio (Minuspio) patagonica*), when experimental areas were protected from predation by crabs, fishes and birds. Similarly, Velásquez (1987) found that the whimbrel *Numenius phaeopus* affects the population structure of its major prey, the polychaete *Perinereis gualpensis* Jeldes. The largest worms inhabit deeper sediment layers, escaping predation by whimbrells. Competition is probably an important factor structuring the intertidal soft-bottom communities, as it has been shown for polychaetes of the northern hemisphere (e.g., Levin 1981, 1982).

Subtidal, soft-bottom habitats

In comparison with intertidal habitats, the subtidal soft-bottom communities have been less studied. Most of the research in these systems is descriptive and mostly focuses on the following problems: (a) physical and chemical factors structuring the macroinvertebrate communities (not considering biological processes, or using experimental manipulations), (b) biogeochemical processes occurring in the sediments (especially related to massive prokaryotic sulphur bacterial mats such as *Thioploca* spp.; Fossing et al. 1995), and (c) environmental impact of anthropogenic activities in the soft-bottom communities. As in other systems, the majority of the studies are concentrated on a small fraction of the continental shelf (northern Chile: Antofagasta, central Chile: Valparaíso, south central Chile: Concepción and southern Chile: Punta Arenas) and have been conducted between 20 and 150 m deep. Thus, most of the existing information comes from upwelling ecosystems, and little is known from the fjords located between Chiloé and Cape Horn. These are important biases in the quantity and quality of the existing information. In this section, we present the most relevant patterns and processes in the different soft-bottom benthic systems based on previous studies and reviews (e.g., Arntz et al. 1991, Gallardo et al. 1995).

The farshore soft-bottom subtidal environment (ranging from about 30 to 200 m in depth) presents two special characteristics strongly associated with (1) upwelled waters (in northern and central Chile, Arntz et al. 1991), and (2) high level of habitat heterogeneity in the south (fjords and thousands of inner channels; Viviani 1979). Between Arica and Chiloé, and especially in central Chile, the basic taxonomy of dominant groups of macroinvertebrates is generally well known

(e.g., Annelida (Polychaeta), Wesenberg-Lund 1962, Hartmann-Schroeder 1962, Hartmann-Schroeder & Hartmann 1965, Carrasco 1974, 1976a,b, 1977, Rozbaczylo 1985 and Rozbaczylo & Salgado 1993; Mollusca (Solenogastra, Caudofoveata, Gastropoda and Bivalvia), Riveros-Zúñiga & Reyes 1950, Soot-Ryen 1959, Stuardo 1960, 1962, Ramorino 1968, Villarroel 1971, Marincovich 1973, Osorio et al. 1979, Osorio 1981, Ponder 1983 and De Castellanos 1992; Crustacea (Decapoda), Garth 1957 and Retamal 1981; Echinodermata (Ophiuroidea), Castillo 1968 and Larraín 1995). There are some groups of invertebrates whose taxonomic identification is particularly difficult and needs revision, such as Anthozoa, Nemertini, Nematoda, Oligochaeta, Pycnogonida, Cephalocarida, Cumacea, Amphipoda, Isopoda and Ostracoda. A recent taxonomic monograph about Chilean Protobranchia bivalves (as *Nucula, Ennucula, Propeleda, Tindariposis, Silicula, Yoldia, Yoldiella, Malletia, Tindaria* and *Acharax*) has helped clarify the status of deposit-feeder bivalves along the Chilean coast (Villarroel & Stuardo 1999). No equivalent work exists for the invertebrates of the meiofauna (e.g., Nematoda, Copepoda, Foraminifera) and microfauna (e.g., Ciliophora, Amoebida). More intensive samplings along the Chilean shelf (especially in the fjords area) could bring up new species, although major changes in the total number of species are not expected.

As for most ecological systems, it is difficult to determine the exact number of species that coexist in the soft-bottom communities. In general, local communities in northern and central Chile are composed by between 15 and 85 taxa of epi- and infaunal species >1 mm (e.g., Valdovinos 1998). There is no information for small-sized species of meiofauna and microfauna that inhabit within bed matrix of the sediments. In southern Chile, the number of species is clearly higher. A bathymetric trend in species richness of local macrobenthic communities, with maximum values in shallow waters, has been reported for northern (Jaramillo et al. 1998), central (Gallardo et al. 1995), and south central Chile (Valdovinos 1998). This negative bathymetric trend in species richness is explained by the effect of anoxic-hypoxic waters in deeper areas (see below). The fjord area of southern Chile shows the opposite trend (Di Geronimo et al. 1991), explained by the effect of a strong tidal current and mixohaline waters in shallow bottoms (Viviani 1979). However, more information is necessary to support this general trend and the underlying processes.

The soft-bottom communities of the upwelling ecosystem (northern and central Chile) have special characteristics such as the scarcity of large macroinfauna (>1.0 mm), high abundance of small macroinfauna (mainly polychaetes <1.0 mm), and the presence of massive prokaryotic sulfur bacterial mats (mainly *Thioploca* spp., Gallardo 1963, 1977a). The presence of large prokaryotic communities (*Thioploca* bottoms) has led to the suggestion that oxygen availability is the major structuring factor shaping benthic communities in this area (Gallardo 1963, 1968, 1977a, b, 1985, Hartmann-Schroeder & Hartmann 1965, Carrasco & Gallardo 1983, Arntz et al. 1985, 1991, Carrasco et al. 1988, Gallardo et al. 1995). In general, and from a taxonomic point of view, the macrofauna of central and northern Chile and the Peruvian shelves are very similar (Arntz et al. 1991). However, the abundance of macrofauna off Perú is lower than in central Chile by at least one order of magnitude (see Rowe 1971 and Arntz et al. 1991). The central Chile shelf seems to be a more favorable habitat for benthic colonization of macroinfauna because of the higher input of oxygen to the benthos during the autumn and winter seasons (Ahumada et al. 1983, Ahumada et al. 1991, Gallardo et al. 1995). In fact, the oxygenated waters affect positively the diversity, abundance and biomass of sublittoral benthos in the Peruvian continental shelf in inter-year cycles of the "El Niño" events (Tarazona 1984). The macroinfaunal benthos is clearly dominated in numbers by very small species of Polychaeta (e.g., up to $2 \cdot 10^3$ ind/0.1 m^2 and approximately 80% of the sample, Valdovinos 1998) and contains very few major taxa such as Crustacea (mainly Amphipoda), Mollusca (many Bivalvia and few Gastropoda), and others (e.g., Nemertea and Cnidaria; Carrasco & Gallardo 1983, Valdovinos 1998). Many important groups of macroinfaunal benthos are missing in northern and central Chile, when compared with the fjords ecosystem of southern Chile (Gallardo et al. 1995), the tropics or Antarctica (i.e., Gallardo et al. 1977).

Zonation patterns for the Arauco Gulf (Central Chile) have been extensively described and discussed by Valdovinos (1998, see more details of this work below in this paragraph), but other Chilean localities are not well known because of low spatial resolution in the samples and a poor characterization of the environment (e.g., granulometry, organic matter, contaminants). The soft bottoms of the Arauco Gulf exhibit shallow and intermediate depth patches closely associated with a deeper matrix, forming a complex mosaic in which patch number and configuration,

connectivity, boundary shapes, and overall het-
erogeneity operate to affect the flows of energy,
matter, and species. In this area, the wind plays an
important role in accentuating the differences
that exist between the seascape units. Distur-
bance pulses, such as storms and upwellings,
differentially affect the marine basin depending
on the localization of such events. Winter storms
affect shallow areas (<15 m), favoring the domi-
nance of a reduced number of opportunistic spe-
cies. Longshore currents produce erosion and
movement of the surface sediment, causing mor-
tality of smaller organisms but not of larger indi-
viduals that seek shelter deeper in the sediment.
The hypoxia-anoxia conditions generated during
the spring-summer upwellings affect specially
organisms residing in deeper zones of the basin
(>40 m) and favor the dominance of a reduced
number of opportunistic species with either (1) a
physiological range wide enough to support oxy-
gen depletion and/or (2) a life cycle synchronized
to such conditions. Diversity of the benthic
macrofauna, dominated by species with little tol-
erance to hypoxia-anoxia, reaches its maximum
in zones located at intermediate depths where
winter storms and spring-summer upwellings do
not have great effects. Abundance, biomass, spe-
cies richness, and dominance of guilds are non-
linear functions of the organic matter content of
the sediment in the Arauco Gulf; shallow sandy
areas, poor in organic matter, are dominated by
suspensivores, while the deposit-feeders domi-
nate in deeper, muddy sediments rich in organic
matter content. This observation suggests that the
distribution of guilds is fundamentally controlled
by food availability and by wind-driven perturb-
ing agents. It is not known if the pattern of species
abundance and the dominant factors affecting the
macroinfauna in this particular area may also
occur in other localities.

Biological processes affecting subtidal soft-
bottom communities have not yet been experi-
mentally quantified. It is possible that, as in many
other shelf coasts of the world, top-down factors
play an important role in the regulation of local
communities. In the soft-bottom of central Chile,
there are few carnivore species that appear to
have a much stronger effect than the rest of the
carnivores with which they coexist: juveniles of
various species of decapods, such as *Cancer
coronatus* Molina, 1782, *C. setosus* Molina, 1782
and *C. porteri* Rathbun, 1930 (all of them are
currently exploited), and some predatory poly-
chaetes errantia of large size, such as *Diopatra
chiliensis*, Quatrefáges, 1865 and *Glycera
americana* Leidy, 1865.

Identification of main human impacts affecting nearshore ecosystems

Several types of human impacts clearly affecting
nearshore ecosystems can be identified along the
coast of Chile, although the intensity, extent, and
persistence of these sources vary geographically
(Tables 3 and 4). The predominance of specific
activities in different regions is clear; mining
takes place mostly in northern Chile, industries,
forestry and agriculture are the main productive
activities in Central and Southern Chile, and
aquaculture peaks in the Austral Region. The
most important human impacts along the Chilean
coast, in terms of geographical extent and persis-
tence, are sewage discharges and the exploitation
of invertebrates and algae in rocky shores (Tables
3 and 4; Gross & Hajek 1998). The V Region has
the largest human population and consequently
the highest direct and indirect sewage discharges,
followed by the VIII Region, both in population
size and, pollution resulting from human settle-
ment (sewage and industry discharges). Although
the effect of seawage discharges on the structure
and functioning of coastal communities is not
well known, it is clear that fishing has a strong
effect on coastal ecosystems (see above). Areas
with smaller human population sizes on the coast
tend to have lower landing of both benthic inver-
tebrates and fish, although there is not a direct
relationship between coastal human population
size and landings.

The existing ecological information indicates
that in rocky intertidal and shallow rocky bot-
toms, the most important human impact is the
collection of invertebrates and macroalgae by
artisanal fishermen as well as occasional gather-
ers. Collection of invertebrates and macroalgae
for human consumption can be traced back to
hunter-gatherers (9,000 years ago) in northern
and central Chile (Llagostera 1979, Jerardino et
al. 1992). However the introduction of diving
technology and the access to new foreign markets
over the past few decades has produced an expo-
nential increase in exploitation rates (currently at
432,587 annual tons), which has led to symptoms
of overexploitation of the main target species.
Currently more than 22.000 divers and food-gath-
erers are exploiting benthic invertebrates, mostly
on the IV, V, VIII and X Regions (Table 3;
Moreno 2000). A chronic problem in the regula-
tion of invertebrate fisheries in Chile is the lack
of adequate enforcement of fisheries legislation,
partly because of the very long coastline and
sparseness of landing sites, but also because of
the lack of an efficient control of the artisanal
fisheries. Another problem is that, despite new

TABLE 3

Main human settlements (in cities and over the coast), fisheries landings, aquaculture production, rivers, seawage discharge and pollution in the 12 Administrative Regions of Chile (numbered from north to south). Biogeographic regions and latitudes are also listed

Principales asentamientos humanos (en cuidades y sobre la costa), desembarques, producción acuícola, ríos principales, descargas de aguas servidas y contaminación en las 12 Regiones Administrativas de Chile (de norte a sur). Se indican también las Regiones Biogegráficas y latitudes

Biogeographic Region	Region	Latitud (South)	Main cities >10.000 people located on the coast (*Main ports)	Coastal population (10^3 hab.)	Main rivers	Landings (1997) of main [a]benthic and [b]fish resources (10^3 ton)	Number of registered divers and food gatherers	Aquaculture production of [a]benthic and [b]fishes (ton)	Direct total seawage discharge from cities located on the coast	Indirect seawage discharge (from rivers, 10^3 m³ año)	Direct and indirect pollution from the industry (from rivers, in 10^3 m³ · año)
Peruvian or Chilean Province	I	18°30′ 21°30′	Arica and Iquique*	332	None	[a]8.28 [b]1,373.58	857	[a]117 [b]0	23,421	0	8,888
	II	21°30′′ 26°00	Tocopilla, Antofagasta* and Taltal	269	Río Loa	[a]29.90 [b]331.95	877	[a]184 [b]0	16,056	4,935	1,872
	III	26°00′ 29°10′	Caldera and Chañaral	31	Ríos Copiapó, Salado and Huasco	[a]92.82 [b]144.80	1076	[a]6,793 [b]0	1,486	9,621	14,761
	IV	29°10′ 32°15′	La Serena and Coquimbo*	229	Ríos Elqui, Limarí and Choapa	[a]57.69 [b]53.80	2036	[a]10,442 [b]41	14,562	6,165	8,496
	V	32°15′′ 33°50	Quintero, Concón, Valparaíso*, Viña del Mar and San Antonio*	691	Ríos La Ligua, Aconcagua, Marga-marga, Casablanca and Maipo	[a]14.94 [b]335.28	922	[a]133 [b]315	43,705	558,856	71,806
	VI	33°50′ 34°45′	All coastalcities <10.000	(Low)	Ríos Rapel and Nilahue	[a]1.16 [b]0.52	455	[a]0 [b]0	(Low)	23,139	47,012
	VII	34°45′ 36°00′	Constitución	30	Ríos Mataquito, Maule and Loanco	[a]1.98 [b]3.24	662	[a]0 [b]15	1,792	29,195	
	VIII	36°00′ 38°30′	Talcahuano (San Lota, Vicente)*, Lirquén*, Tomé, Penco, Coronel and Arauco	499	Ríos Itata, Andalién, Biobío, Lebu and Paicaví	[a]31.71 [b]3,302.58	3299	[a]7,365 [b]559	25,333	44,919	176,797
	IX	38°30′ 39°20′	All coastal cities <10.000	(Low)	Ríos Imperial and Toltén	[a]0.32 [b]0.65	368	[a]262 [b]50	(Low)	19,697	1,357
Transition zone	X	39°20′ 44°00′	Puerto Montt*, Ancud and Castro	166	Ríos Calle-Calle, Bueno and Maullín	[a]175.44 [b]231.97	8583	[a]101,569 [b]217,130	7,344	14,710	8,814
Magellanic Province	XI	44°00′ 49°30′	Aisén	35	Río Aisén (and many more small ones)	[a]4.69 [b]45.07	2434	[a]0 [b]26,323	?	2,565	607
	XII	49°30′ 56°00′	Puerto Natales and Punta Arenas*	135	Many small rivers	[a]42.02 [b]5.36	682	[a]0 [b]3,453	8,817	(Low)	64,046

fisheries legislation (Ley de Pesca y Acuicultura, D.S. N° 430, 1992), there has not been a concomitant development in the national system of marine protected areas that could serve as a buffer for exploited zones (Hastings & Botsford 1999, Castilla 1999).

On the rocky intertidal shore of central and southern Chile, the establishment of two marine reserves demonstrated the dramatic effects of the subsistence fisheries on the entire intertidal landscapes (Moreno et al. 1984, 1986, Castilla & Durán 1985, Oliva & Castilla 1986). We understand much less the ramifications of human exploitation on rocky subtidal areas, where most of the artisanal fishing takes place. We do know, however, that many of the species collected have the potential to play critical roles in those communities as predators or structural species. From the wide diversity of species collected by humans the ones whose collection has the potentially most harmful consequences for the rest of the community are: a) the muricid *Concholepas concholepas* (heavily collected intertidally and subtidally), b)

keyhole limpets of the genus *Fissurella* (also heavily collected intertidally and subtidally), c) kelps of the genus *Lessonia* (recently collected to feed exotic cultivated species such as abalone), d) the seastar *Heliaster helianthus* in central Chile (massive collections occur in spring and summer months), e) beds of *Pyura chilensis* in subtidal areas, which seems to act as engineer species for many other invertebrates. We have no ecological information about these beds, which are sometimes completely exterminated from large reefs, f) beds of mussels, *Aulacomya*, *Chorumytilus* and others, which provide habitat and recruitment sites for many other species.

The exploitation and use of sandy beaches is less diverse, and the effect of humans on the community structure less clear. For example, the clam *Mesodesma donacium* is the only invertebrate species widely fished in the surf zone and shallow subtidal areas of many exposed sandy beaches from Arica to Chiloé Island (Tarifeño 1980). This resource suffers a persistent human impact that may have affected natural popula-

TABLE 4

Main sources of human impact observed in the different administrative Regions of Chile

Principales tipos de impacto humano observado en las diferentes Regiones Administrativas de Chile

Main sources of human impact observed in the Chilean Coast	Administrative Regions of Chile											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Overexploitation of benthic resources	•	•	•	•	•	•	•	•	•	•	•	•
Introduced benthic species	•[1]		•[1]		•[1]				•[1]	•[1,2]		
Pollution by sewage discharges	•	•	•	•	•	•	•	•	•	•	•	•
Pollution by the fishing industry (organic discharges)	•	•		•	•	•		•		•		•
Pollution derived from aquaculture (Pacific salmon): organic matter, antibiotics, antiparasites										•	•	
Chemical pollution from different industries						•	•	•	•			•
Pollution from mining			•	•			•				•	
Pollution due to the use of anti-fouling in harbors and aquaculture			•		•	•		•		•		
Pollution from pest controls (agriculture)						•	•	•	•	•	•	
Pollution from pest controls (others)								•				
Oil spills from ships	•	•	•	•	•	•	•	•	•	•	•	•
Oil pollution (oil platforms)												•
Oil pollution (other sources)						•				•		
Dredging of main channels in Chilean Harbors			•			•	•		•		•	
Pollution from polluted rivers (several types)					•	•	•	•	•	•	•	
Construction of Port facilities			•			•	•		•		•	•

[1]Pacific Oyster (in the Chilean coast 3,203 tons are harvested annually)
[2]Red abalone (in the Chilean coast 1 ton is harvested annually)

tions since landings have decreased dramatically in the last 3 years (see Jaramillo et al. 1994). However, the effect of persistent (or occasional, see below) removal of *Mesodesma* on the sandy beach community is unknown.

In contrast to the geographically extensive invertebrate and macroalgal fisheries, other human activities are concentrated in some regions, among them aquaculture, copper and iron mining, discharges of organic matter from the fishing industry and chemical pollutants from industry and agriculture (Tables 3 and 4). At present, aquaculture targets two groups of species in specific regions along the coast of Chile: natives and introduced. Among the native ones, *Argopecten purpuratus* constitutes most of the emerging industry taking place in the IV Region, but the potential for aquaculture of other native invertebrate species is being investigated in Chile (e.g., clam, limpet, trumulco, sea urchin, Chilean hake). Introduced species are also cultured in Chile (e.g., Pacific salmon), or are planned to be cultured based on current experimental projects (e.g., Pacific halibut, hiromi, abalone). Probably the most striking case of aquaculture of introduced species is the Pacific salmon, that fluorished in southern Chile in the last decade (Table 3 and 4) and now amounts to 43% of the total income from fish products perceived by the country. Despite the fact that the Fishing and Aquaculture Law explicitly indicates that aquaculture activities should not affect the ecosystem, little has been done in this respect. Furthermore, the introduction of species for aquaculture was allowed in the new legislation. The presence of free salmon in the south (escaped from pens), the intensive use of antibiotics and other chemicals to control salmon parasites (but also affecting molting of crustaceans in general), and severe eutrophication of the system are among the many impacts of salmon aquaculture that have not yet been evaluated. Due to escapes of salmon from pens and the ranching activities since the early 80's, four species of salmon can be found in the north patagonian region of Chile: *Salmo salar* (Atlantic Salmon), *Oncorhynchus tshawytscha* (Chinook), *O. kisuch* (Coho), and *O. mykiss* (Rainbow trout). The Chinook is known to have wild populations in some rivers and at sea, the Rainbow trout shows wild populations in almost all the Chilean rivers, and the escaped Coho salmon has established wild populations in recent years in the Aysen rivers and fjords (Soto et el. 1997). One of the major potential disturbances related to these introductions, through direct or indirect effects, is the replacement of high trophic-level native predators; the effects on the rest of the natural communities are still unknown. The emerging industry of abalone (and also sea urchin aquaculture) has contributed to the local decimation of the brown algae *Lessonia* spp. populations. *Lessonia* spp. is used as the main food item for both cultured species and its extraction can have severe consequences in coastal habitats where these macroalgae are dominant structural species (see above). Although aquaculture of both native and introduced species is currently concentrated in a few regions, it could extend to the rest of the country in the near future with the incorporation of new species.

Another localized human activity is the copper and iron mining that has been taking place for several decades in northern Chile. For instance, in northern Chile (I-III Regions) the average concentration of copper in seawater and sediments is three times higher than in the rest of the country, and well above the international standards (Hernández 1998). Other heavy metals, such as Hg and Pb also show higher concentrations in northern Chile, while the concentration of Cadmium in sediments is higher in the XI and XII (Hernández 1998). In all cases strong spatial variation in the concentration of heavy metals has been found (Hernández 1998). In the case of Antofagasta Bay, major steps to avoid pollution at the MEI production site over the last years have brought levels of copper concentration back to normal (Hernández 1998). Recent studies showed that the two most important mining activities in the country have caused dramatic ecological impacts on intertidal and subtidal marine environments; copper tailing produces more ecological perturbation than iron (Vásquez et al. 2000). Although reports of the effect of pollutants on the macroinfauna in sandy beaches are limited, a significant effect of mine tailings on macroinfaunal density and biomass has also been shown (Chañaral, ca. 26° S; Castilla 1983). Other studies showed that solid and liquid waste (from mining, but also from human settlements) released into the sea disrupt the distribution and abundance of brown algae populations (Castilla & Nealler 1978, Vásquez & Guerra 1996, Vásquez et al. 1999).

Some human activities can have intense impact on the nearshore community only during short periods of time, although the actual effect on the marine community might be long lasting. Among them are vacationers, oil spills, dredging, and ballast seawater. Oil spills do have an affect on macroinfaunal density and biomass in sandy beaches (ca. 32° S; Castilla et al. 1977), and affect survival of marine birds and mammals. Occasional exploitation of sandy beach invertebrates such as *M. donacium* occurs in summer

time, by beach visitors. Fishing effort exerted by beach visitors is comparable to the artisanal fishery (De Ruyck & Soares, unpublished data); however, experimental studies did not show any significant effect of human exclusion on macroinfaunal abundance in a sandy beach of south central Chile (Mehuin, ca. 39° S, Jaramillo et al. 1996). Construction of new roads that allows easy access to coastal areas may increase the number of visitors to the intertidal zone and their impact on these ecosystems. To date, human impact is low in some areas such as in intertidal estuarine flats of south central Chile. However, in some of these estuaries, large domestic vertebrates such as cows and pigs from nearby farming communities produce occasional, but large mechanical disturbances, although the actual effect has not been quantified. Similarly, mechanical disturbance by fishing boats on the mud flats is unknown.

So far there are no written reports of marine invertebrate or fish species introduced to Chile (other than related to aquaculture activities). It is possible that the circulation pattern along the coast of Chile does not favour successful colonization of exotic species, but with increasing frequency of international trade the potential for species introduction increases. Although there are regulations for ballast seawater, enforcement is not always achieved and a variety of species could be introduced, especially in major ports and bays. The European heron (Cornelius, Marquet & Navarrete, unpublished data) is probably one of the examples of introduced species that is definitely using the intertidal zone, although its impact on the benthic community is still unknown.

The use of indicators to assess the actual impact of the different human activities on nearshore communities is desirable, but difficult to achieve. Although some variables of human impact can be easily quantified (e.g., copper levels, or *Escherichia coli*), the actual impact on the system is not easy to assess. However, the current knowledge of the rocky intertidal system and the main factors structuring the community between 33 and 41° S provided the grounds for developing indicators of severe human exploitation (Moreno, unpublished data). Among others, the following indicators of severe human exploitation were recognized:

1. Size distributions of edible invertebrates are truncated in the larger size classes (mainly for *Fissurella* spp. and *Concholepas concholepas*) in all types of intertidal habitats impacted by humans (Moreno et al. 1984, Oliva & Castilla 1986, Castilla & Durán 1985, Moreno et al. 1986, Durán & Castilla 1989).

2. High cover of *Mazzaella laminarioides* and *Ulva* spp. in the midlittoral of protected and semiprotected rocky shores is found when herbivores have been removed by humans (Moreno et al. 1984, Oliva & Castilla 1986). The high cover of these two algal species is a good indicator only in extended rocky shore areas, but can not be used in the limits between rocky and sandy beaches where the same effect is apparently produced by sand abrasion.

3. Large plants of *Durvillaea antarctica* are present only in the very low intertidal or shallow subtidal rocks of exposed fronts, less accessible to humans, and absent from protected and semi protected benches where humans exploitation is high (Castilla & Bustamante 1989, Bustamante & Castilla 1990).

These are the most easily perceived effects of humans in rocky intertidal communities along central and southern Chile. The distribution of intertidal species and the environmental conditions in northern Chile and the fjord region differ from the systems where experimental human exclusion studies were conducted. Thus, the indicators proposed above can only be of use between 33 and 41 °S. Indicators of human use for the rest of the country are also needed, especially for northern Chile where exploitation of intertidal communities is more pronounced (Table 3).

Other indicators of human impact (specifically of iron and copper mining and of sewage discharges) are the presence and abundance of *Lessonia trabeculata* (subtidal) and *L. nigrescens* (intertidal) and the community associated with their holdfasts. Tailing from copper mining appears to cause more ecological perturbations than that from Fe mining in northern Chile (Vásquez et al. 1999). In severe cases of contamination (e.g., 2 km from copper mining effluents), the macroalgae themselves may disappear or be found in bad condition, with no macroinvertebrates species inside or nearby the holdfasts (Vásquez et al. 1999). Similar ecological damages have been documented for rocky and sandy intertidal communities in northern Chile (El Salvador, Castilla & Nealler 1978). At lower pollution levels, *Lessonia* survival increases, and the holdfast community (diversity of species in the holdfast-microcosm) provides a sensitive method to assess copper contamination (Vásquez & Vega unpublished data). If proven efficient for other latitudes, this indicator could be used to assess human impact in other regions of Chile. Another indicator of pollution is the extensive dominance in the entire intertidal zone by the green alga *Enteromorpha* in polluted areas. *Enteromorpha compresa* from Caleta Palito, one of the highest

copper-enriched coastal localities in northern Chile, tolerates high copper concentration constituting the only species of algae in areas with mining discharge influence (Correa et al 1996).

INTRUMENTS, NEEDS AND GUIDELINES FOR MARINE CONSERVATION

Although the establishment of marine conservation policies takes into consideration scientific, social, economic, and legal criteria, we think that biological and ecological principles should guide the identification of priority geographic regions for conservation. We do not claim that the other criteria are not important, simply that they should play a critical role only after the questions of what needs to be conserved and where to concentrate conservation efforts have been addressed based on biological considerations. From this perspective, we present and discuss in this section the (1) main instruments for marine conservation used worldwide, (2) basic needs for marine conservation in Chile, and (3) guidelines for marine conservation based on the current knowledge about the ecology and biogeography of the nearshore ecosystem in Chile.

Instruments for Marine Conservation

The current crisis of the marine environment (loss of biodiversity, habitat alteration, extensive declines in population sizes, pollution) was partly contained several decades ago in terrestrial systems by the designation of national parks and reserves which protect biotic and abiotic resources. In the marine environment the use of protected areas (MPA) is relatively new, but the number of MPAs worldwide is increasing dramatically. MPAs are being used to protect endangered species and critical life history stages, maintain biodiversity, spawning biomass of exploited species, and intra-specific genetic diversity, protect specific habitats, improve yield, and also for educational purposes. However, the sudden interest in the creation of MPAs is driven more by the collapse of fisheries than by the state of biodiversity. Nevertheless, major efforts have also been directed to the creation of MPAs as reservoirs of biodiversity, and currently MAPs are the main instruments for marine conservation. We think that, as in terrestrial systems, the major goal of MPAs should be the protection of biodiversity (e.g., species and habitat diversity, ecological processes). From this perspective, the selection

of potential sites for sitting MPAs and the total area to be protected are critical.

There is little empirical evidence to suggest how much should be conserved in the marine system. The Wold Conservation Union (IUCN) has proposed a goal of 20 % of the world´s coastline (IUCN 1992), but it is no clear what is the foundation behind this figure. Other authors have suggested different target areas for protection, ranging from 10 % of the total range of a population (based on the fishery principle of protecting a fraction of the spawning biomass) to 40% of the spawning stock for species particularly vulnerable to fisheries (Mace 1994). Recently Lauck et al. (1998) suggested that reserves covering about 30% of the fishing grounds are needed to maintain stocks at target levels, considering intermediate levels of uncertainty in the system. These figures come from MPAs designed mostly for fisheries purposes. However, it is clear that much of these estimations do not have scientific basis, and there is little agreement on how much should be protected.

Regarding site selection, the best documented process in the marine system involves the application of ecological criteria, and for this purpose several types of ranking schemes have been used (Kelleher & Kenchington 1992, Odendaal et al. 1995, Salm & Price 1995). These rankings include criteria such as diversity, productivity, representativity of the biogeographic regions, status of the species and habitat, extent of human use, etc. Hockey & Branch (1997) suggested to consider the middle/edge system in selecting sites for MPAs. While areas of higher diversity are at the edge, placing a MPA in the middle of a biogeographic region would have positive effects, since higher abundance and reproductive success should be expected in the center of species ranges. Furthermore, negative effects, due to variations in the ranges of distribution caused by climate changes, would be avoided. Within a biogeographic region, a range of habitat types (e.g., sandy beaches, rocky shores, estuaries, different conditions of wave exposure, etc.) and especially vulnerable habitats need to be incorporated (Hockey & Branch 1997). Ballantine (1997) discussed not only the criterium of representativiness but also the replication and connectivity among MPAs. It is also important to consider whether the area includes exploited species and its "permeability" to adjacent areas. Finally, the conditions of the selected area are not trivial; a pristine area, or at least one that is not heavily impacted, is preferable. After biological criteria have been applied, general consideration about the feasibility of placing a marine reserve within the range of

areas of interest needs to be evaluated (i.e., external threats, conflicts of interest, costs of establishing and maintaining a MPA). For instance, management and enforcement of marine reserves established adjacent to terrestrial reserves may be more easily achieved (Attwood et al. 1997, Hockey & Branch 1997). The additional benefit of having a MPA adjacent to terrestrial reserves is the eradication of problems related to land use. Efforts also need to be made to consider regional and international regulations.

Besides the considerations of the total area to be protected and the target regions for MPAs, the design of the network is also of great importance. The factors contributing to the success or failure of MPAs are difficult to decipher, and very often the failure has been attributed to inadequate management or enforcement. However, the design is also likely to affect the success of the MPA. A number of concepts, which are being applied to MPAs in terrestrial systems, deserve attention; the SLOSS debate (Simberloff 1988) and the connectivity between MPAs are at the center of the discussion on reserve design. As yet, the dichotomy in the design of MPAs (e.g., size) stems from the intended purpose, although this situation may change as more evidence becomes available. The debate concerning the edge effects has consequences on the transfer of propagules (or other life history stages), and also pollutants, across reserve boundaries. This issue is probably of greatest importance for fisheries reserves, where spillover to fishing areas needs to be assured (Attwood et al. 1997). However, spacing and reserve size is also of major importance for MPAs created as reservoirs of biodiversity, although until now contradictory results have been found (McNeil & Fairweather 1993). The reality is that little can be said regarding optimum MPA network design based on scientific evidence, and the experience gained from a MPA network may not necessarily be effective in other geographic areas since the design is strongly dictated by the biology of the species or communities that need to be protected, and the local oceanographic conditions (Nowlis & Roberts 1997).

The instruments related to the protection of aquatic areas have existed in Chile since 1960. The concept of marine protected area, and the need to establish them, is present in eight Chilean laws and four decrees. In addition, Chile is party to a number of international conventions which promote the creation of MPAs for different purposes. Three categories of protection are recognized: (1) areas for management and exploitation of benthic resources, (2) marine reserves, and (3) marine parks. Each of these have a different set of

objectives as well as management and conservation actions (Morales & Ponce 1997). According to Morales & Ponce (1997), the legal framework for the implementation of marine protected areas is substantial; however, the mechanisms for the implementation need yet to be developed. As yet, most efforts have been directed toward the creation of partially protected areas for fisheries purposes (Management and Exploitation Areas, MEA), one Marine Reserve (as a genetic reserve of the overexploited Northern scallop *Argopecten purpuratus;* Morales & Ponce 1997) and only recently three submarine parks have been created at Eastern Island by the Subsecretaria de Marina. Legally these protected areas are not Marine Parks (but Coastal and Marine Protected Areas, because only the Fisheries Administration has the mechanisms to create Marine Parks). In addition, there are other types of protected areas (marine concessions; Castilla 1986, 1996). Considering the basic information needed for site selection, designation of total area to be protected, and the design of the interconnected network, in the next two sections we discuss the basic needs to implement such a MPA network in Chile, and propose some guidelines.

Basic Needs

In this section we will outline the basic needs for marine conservation plans in Chile derived from our overview. However, we recognize that there are other needs in the legal system and social aspects that need to be considered, and those we will briefly discuss. The following are among the biological and ecological needs we identified:

1. Some gaps in information regarding the taxonomy and large-scale patterns of species distribution, for some taxonomic groups. We think that more taxonomic and molecular work may help clarify the status of some species and also show the existence of new species. However, since no large variations in the total number of species are expected, the current large-scale patterns of species distribution may not substantially change in the future.

2. An urgent need of studies addressing the causal factors generating the patterns of species distribution observed, especially in southern Chile. This information is needed for all taxonomic groups, since different diversity patterns are observed for different taxa.

3. A need to organize the existing biological and ecological information using some criteria (e.g., larval ecology). This work would require the join efforts of a team of recognized marine scientists from Chile, but unfortunately, this type of project is not a strong candidate for funding in

the Chilean research funding system. Along the same line, a team of recognized scientists could play a critical role in determining the criteria for site selection, evaluation, and management of MPAs. This strategy was used in South Africa, where the task group reviewed not only the status of marine conservation and evaluated existing marine reserves, but also proposed action plans.

4. A need to classify the conservation status of species and identify particular groups of species that need to be considered separately in a network of marine protected areas. For instance, data on minimum viable population size are available only for 15 of the 101 exploited marine species in Chile (Moreno 2000). For most exploited species stock assessments are not regularly conducted, and information on genetic diversity is non-existing.

5. A deficiency in information about life history of most species. Modes of development (ranging from direct development to long planktonic life) affect the replenishment patterns of marine populations, and this single factor could greatly affect the design and effectiveness of MPAs.

6. A necessity in information about coastal currents in order to better understand possible ways of larval transport in the nearshore, and its effect on population and community dynamics. As yet, most oceanographic studies have been conducted on the continental shelf, and little has been done in coastal waters.

7. A need for more information about community structure and ecosystem functioning, especially highlighting the effect of human impact; currently this information comes only from very few geographic regions. More information about community structure for other areas of the coast is needed, particularly considering the strong differences in temperature, circulation patterns, habitat heterogeneity, species composition, as well as the effect of upwelling and El Niño along the 4000 km of coastline. Experimental work has been mostly conducted on rocky intertidal shores, and more information about other types of systems is needed (e.g., soft-bottoms).

8. A need for more studies to assess the actual effect of upwellings on coastal community dynamics; upwellings are a major oceanographic component of the Chilean ecosystem.

9. That indicators of human impact need to be developed for more systems and expanded for rocky shores to northern and southern Chile. The indicators currently available are based on studies conducted in a few geographic regions, and it is unclear whether those indicators can be used in other areas of the country.

10. The need to evaluate the frequency, extent and effects of pollution, fisheries, storms, oil spills, and other environmental factors. Insurance factors have been proposed as a way to qualitatively assign these risks. Records on most of these factors have not yet been compiled, and in many cases, the information is widespread or not available in Chile. For instance, the effect of fishing on the whole ecosystem (e.g., removal of large or key predators, bycatch) or habitat fragmentation (e.g., benthic fisheries) has not yet been evaluated.

11. A need to evaluate the effect of species introduced for aquaculture purposes on local biodiversity and ecosystem functioning (local, but also potential for dispersal). This imposes a major constraint on the success of MPAs as reservoirs of biodiversity (e.g, salmonids in Southern Chile).

12. A need to analyze, adopt/modify/extend to local conditions (ecological, social) the criteria proposed for site selection (e.g., Salm & Price 1995).

In addition, we recognize other needs that may have an effect on any marine conservation strategy in Chile. It is a priority to quickly establish an efficient system for the implementation, management and enforcement of MPAs. It is also a priority to provide the national agency interested in marine conservation the tools to create MPAs as reservoirs of biodiversity (e.g., CONAMA), rather than relying on agencies interested in MPAs only for management purposes. Additional research fundings (e.g., sectorial programs) may have an enormous impact on the quality and amount of information that can be obtained in relatively short time. It may also help to achieve a higher level of involvement of scientists in conservation, including outreach programs. Educational programs directed to conservation in general, and especially to marine conservation, need to be implemented in Chile. We think that social pressure for more immediate conservation measures may result through educational programs. Finally, we think that the bureaucratic system in Chile does not favor the possibility of debate about conservation issues. For instance, the general public does not have easy access to public information (e.g., stock assessment of exploited species). Access to such information is important because conservation groups could do independent analysis, and generate informative/educative debates.

Guidelines for Marine Conservation in Chile

Since the dispersed efforts to create a network of MPAs in Chile have not yet yielded results, we

think that future plans could be benefited from the incorporation of the experience gained in other geographic areas of the world. For instance, major efforts in defining priority areas for conservation in Chile need to be taken, rather than following the alternative, opportunistic approach of sitting MPAs in the less conflicting sites or sites not yet occupied by MEAs or assigned for aquaculture purposes. For instance, the spatial arrangement of the more than 220 MEAs requested so far (Darío Rivas, pers. comm.) responds to the opportunistic requirement of fishermen unions, and does not respond to a coordinated plan of the fisheries´ administration to allow for interspaced no-take zones. In fact, the wide spread of MEAs along the coast of Chile poses serious problems to the potential sitting of MPAs since in some regions (e.g., IV and V) virtually the whole coast has already been assigned to MEAs. We think that MEAs are an excellent management strategy for benthic resources, and they could complement any conservation plan, but caution should be exerted to balance the possible "competition" for suitable sites between MPAs for conservation and management purposes.

The need to preserve species and ecological processes along the Chilean coast has already been discussed (e.g., Castilla 1976, 1986; Ormazábal 1993), and potential sites have even been suggested. Ormazábal (1993) suggested to incorporate the littoral zone adjacent to the exist-

ing coastal National Parks. Actually, many sites identified for the conservation of the biodiversity in Chile (terrestrial flora and fauna; Muñoz et al. 1996) could be extended to intertidal or shallow subtidal areas, since they are located on the coast and cover both biogeographic regions. We think that Ormazábal´s proposal (1993) is a plausible step that does not necessarily exclude a future marine conservation plan with specific objectives. In fact, there are already 11 protected areas in the National System of protected areas (National Park, National Reserve, or National Monument) that include a section of sea bottom (Table 5) and 10 more that are adjacent to the coast, or include coastal areas, extendeding along the coast of Chile. However, we agree with Castilla (1996) that the design of a marine reserve network cannot be completely accommodated to terrestrial conservation plans and needs to take into account the latitudinal variation in species diversity and ecosystem processes (Castilla 1996). In addition, the size of the resulting MPAs, the orientation, and the spacing between them may not allow exchange of propagules or adult stages.

As it has been proposed for Chile (Castilla 1996) and for other areas (e.g., South Africa, Hockey & Branch 1994, Hockey & Branch 1997), we think that a MPA network needs to be designed in such a way that (1) biogeographic regions are well represented (including Oceanic Islands), (2) unique or special oceanographic sys-

TABLE 5

Units of the National System of Protected Areas that include a section of the sea bottom, and of the National System of Wild Protected Areas of Chile (SNAPE) adjacent to the coast or that include coastal area. NM indicates National Monument, NR National Reserve, and NP National Park

Unidad del Sistema Nacional de Areas Protegidas que incluye una sección de fondo marino y del Sistema Nacional de Areas Silvestres Protegidas adyacentes a la costa, o que incluyen una sección de área costera. NM indica Monumento Nacional, NR Reserva Nacional y NP Parque Nacional

Units of the National System of Protected Areas that include sections of sea bottom	Units of the National System of Wild Protected Areas of Chile (SNAPE) adjacent to the coast or that include coastal areas
Isla Magdalena (NP)	Pan de Azucar (NP)
Laguna San Rafael (NP)	Llanos de Chile (NP)
Bernado O´Higgins (NP)	Bosque Fray Jorge(NP)
Alberto M. de Agostini (NP)	Archipielago Juan Fernandez (NP)
Cabo de Hornos (NP)	Rapa Nui (NP, already established)
Las Guaitecas (NR)	Chiloe (NP)
Katalalixar (NR)	Isla Gamblin (NP)
Alacalufes (NR)	Pinguino de Humboldt (NR)
La Portada (NM)	Laguna Torca (NR)
Cinco Hermanas (NM)	Isla Cachagua (NM)
Los Pingüinos (NM)	

tems within a biogeographic region are protected, and (3) all habitats are well represented (this includes different habitat types as well as wave exposures). Additional priority areas may need to be established to protect endangered species. Based on our overview and ongoing studies, we think that the two biogeographic regions identified by most authors need to be represented in a network of MPAs in Chile. Diversity is definitely higher south of 40-45 °S (although not for all taxonomic groups), but high spots of diversity should not be the only issue in site selection in this case because species composition changes dramatically north and south of this latitude. The decision of establishing a MPA in Chiloé Island is important because of the high diversity of this area, but it should be kept in mind that this area represents the edge of the distribution of most species. Therefore, at least one large (although replication within a region is desirable) MPA needs to be placed south of 45 °S, which should include fjords and channels, as well as protected and exposed coasts. Special attention to the potential impact of salmon aquaculture and escapees on no-take zones needs to be taken. Preliminary modeling results suggest that optimum spacing of MPAs depends on the dispersal ability of the target species (Tuck & Possingham 2000). Ongoing studies also suggest that several small reserves seem to work better for species with long planktonic life, while large reserves seem to be preferable for species with direct development (Hastings & Botsford, unpublished data). The Humboldt Region presents a simplified situation from this perspective because species with planktonic larvae are predominant, and because at any given latitude the mean range size of species does not change, regardless of modes of development (Fernández, unpublished data). The Magellan area presents the most difficult scenario for the design of MPAs to assure connectivity, because it combines about the same proportion of species with direct development, planktotrophic, and lecitotrophic larvae, and the range sizes vary on average between 10 and 40 degrees (Fernández, unpublished data; range sizes in the sea seem to be related to the potential for dispersal of larval stages). Although diversity does not change for most known taxa within the Humboldt Region, we think that two groups of large MPAs (reservoirs of diversity and ecological processes) should be considered, one in the northern region (north of 30 °S) and one south of 30 °S. Several authors have consistently suggested a small discontinuity in species richness, recruitment of intertidal species, and also in ß diversity in intertidal rocky and sandy beach communities at about 30° S

(Santelices 1980, Camus 1998, Brazeiro 1999, Navarrete & Fernández, unpublished data). North of about 30 °S there is also a discontinuity in the diversity of native species of birds, mammals, and reptiles associated to littoral environments, and endemicity peaks. Within the Humboldt region, the effect of upwellings and El Niño event as large-scale oceanographic processes need to be considered. A good representativity of habitat types in each MPA is desirable.

Castilla (1996) emphasized that MPAs should also meet educational purposes. We also believe that education is very important, but to meet this goal small MPAs could be used and site selection of large MPAs do not need to take into consideration the vicinity of major population settlements and educational centers. In our opinion, near-pristine sites should be preferably selected to avoid highly deteriorated habitats due to anthropic influence. Marine concessions managed by Chilean Universities could serve for educational purposes, through some incentives. There are currently five Marine Concessions assigned each to the University of Arturo Prat (Huiquique; I Región), Universidad Católica del Norte (La Herradura, IV Región), Universidad de Valparaíso (Montemar, V Región), Pontificia Universidad Católica de Chile (Las Cruces, V Región) and Universidad de Concepción (Dichato, VIII Región). The actual goal and current state of these Marine Concessions is unclear in most cases (except for the reserve of Las Cruces), however the situation could change if special incentives are offered to maintain these areas as pristine in exchange for educational services. Other coastal universities may also be considered for this plan.

There are no doubts about the deterioration of the coastal and the nearshore ecosystems in Chile. Despite that the economy of the country depends enormously on the sea, conservation actions have not yet been a priority in Chile. As yet, all the efforts have been directed to obtain the best, short term benefit from the ocean; for instance fractions of the high economic returns of some activities (e.g., salmon aquaculture, sea urchin fishery) have not been used to evaluate their impact on the marine ecosystem, and to compensate/mitigate for those actions. Only recently the last of the four priorities of the Fisheries Administration, set conservation plans, started to receive attention although currently most efforts come from the CONAMA. This overview shows that there is substantial (although not complete) knowledge about the nearshore ecosystem, and this information could be used to design a conservation plan, if Chile is going to use the instruments available in its legal system and meet its international com-

promises promoting the creation of MPAs as reservoirs of biodiversity in the near future.

LITERATURA CITADA

AHUMADA R, A RUDOLPH & V MARTINEZ (1983) Circulation and fertility of water in Concepcion Bay, Chile. Estuarine, Coastal and Shelf Science 16: 95-105.

AHUMADA R, P MATRAI & N SILVA (1991) Phytoplankton biomass distribution and relationship to nutrient enrichment during an upwelling event off Concepcion bay, Chile. Boletín de la Sociedad de Biología de Concepción (Chile) 62: 7-19.

ALLISON G, BA MENGE, J LUBCHENCO & SA NAVARRETE (1996) Predictability and uncertainty in community regulation: consequences of reduced consumer diversity in coastal rocky ecosystems. In: Mooney HA, JH Cushman, E Medina, OE Sala & ED Schulze (eds) Functional roles of biodiversity: 371-392. A global perspective. Wiley Press.

ALLISON G, J LUBCHENCO & M CARR (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8: S79-S92.

ALVARADO JL & JC CASTILLA (1996) Tridimensional matrices of *Perumytilus purpuratus* on intertidal plataforms with varying wave forces in central Chile. Marine Ecology Progress Series 133: 135-141.

ALVEAL K (1971) El ambiente costero de Montemar y su expresión biológica. Revista de Biología Marina (Valparaíso) 14: 85-119.

ARAYA-VERGARA JF (1976) Reconocimiento de tipos e individuos geomorfológicos regionales en la costa de Chile. Información Geográfica (Chile) 23: 9-30.

ARNTZ WE, LA FLORES, M MALDONADO & G CARBAJAL (1985) Cambios de los factores ambientales, macrobentos y bacterias filamentosas en la zona de mínimo de oxígeno frente al Perú durante "El Niño" 1982-1983. In: Arntz WE, A Landa & J Tarazona (eds) "El Niño" y su impacto en la fauna marina: 65-77. Boletín Instituto del Mar del Perú.

ARNTZ WE, J TARAZONA, VA GALLARDO, LA FLORES, & H SALZWEDEL (1991) Benthic communities in oxygen defficient shelf and upper slope areas of the Pervian and Chilean coast, and changes caused by El Niño. In: Tyson RV & TH Pearson (eds) Modern and ancient continental shelf anoxiaVol. 58: 131-154. Geological Society Special Publication Edition.

ATTWOOD CG, JM HARRIS & AJ WILLIAMS (1997) International experience of marine protected areas and their relevance to South Africa. South African Journal of Marine Science 18: 311-332.

BALLANTINE WJ (1997) Design principles for systems of «no-take» marine reserves. Fisheries Centre, University of British Columbia, Vancouver. 18 pp.

BARNES RSK & RN HUGHES (1999) An introduction to marine ecology. Third Edition. Blackwell Science, London. 286 pp.

BERLOW EL, SA NAVARRETE, C BRIGGS, BA MENGE & M POWERS (1999) Quantifying variation in strengths of species interactions. Ecology 80: 2206-2224.

BERTRAN C (1984) Macroinfauna intermareal en un estuario en el sur de Chile (estuario del río Lingue, Valdivia). Studies on Neotropical Fauna and Environment 19: 33-46.

BERTRAN C (1989) Zonación y dinámica temporal de la macroinfauna intermareal en el estuario del río Lingue (Valdivia, Chile). Revista Chilena de Historia Natural 62: 19-32.

BOLTOVSKOY E (1964) Provincias zoogeográficas de América del sur y su sector antártico según los foraminíferos bentónicos. Boletín Instituto de Biología Marina de Mar del Plata 7: 93-99.

BRANCH GM & CA MORENO (1994) Intertidal and subtidal grazers. In: Siegfried WR (ed) Rocky shores: Exploitation in Chile and South Africa Vol.103: 75-100. Ecological Studies Edition, Springer-Verlag.

BRATTSTRÖM H & A JOHANSSEN (1983) Ecological and regional zoogeography of the marine benthic fauna of Chile. Sarsia 68: 289-339.

BRAZEIRO A (1999) Community patterns in sandy beaches of Chile: richness, composition, distribution and abundance of species. Revista Chilena de Historia Natural 72: 93-105.

BRAZEIRO A, ROZBACZYLO N & FARIÑA JM (1998) Distribución espacial de la macrofauna en una playa expuesta de Chile central: efectos de la morfodinámica intermareal. Investigaciones Marinas (Valparaíso) 26: 119-126.

BUSTAMANTE RH & JC CASTILLA (1987) The shell-fishery in Chile: an anlysis of 26 years of landings (1960-1985). Biologia Pesquera (Chile) 16: 79-97.

BUSTAMANTE RH & JC CASTILLA (1990) Impact of human exploitation on populations of the intertidal southern bull-kelp *Durvillaea antarctica* (Phaeophyta, Durvilleales) in central Chile. Biological Conservation 52: 205-220.

CAMUS PA (1998) Estructura espacial de la diversidad en ensambles sésiles del intermareal rocoso en Chile centro-norte: la diversidad local como un resultado de determinantes multiescala. Tesis de Doctorado, Departamento de Ecología, P. Universidad Católica de Chile, Santiago. 262 pp.

CANCINO J & B SANTELICES (1984) Importancia ecológica de los discos adhesivos de *Lessonia nigrescens* Bory (Phaeophyta) en Chile central. Revista Chilena de Historia Natural 57: 23-33.

CAÑETE J, VA GALLARDO, R GUIÑES, F CARRASCO & M BALTAZAR (1996) Observaciones sobre la migración y distribución vertical de megalopas de *Peuroncodes monodon* en la plataforma continental frente a bahía San Vicente. Gayana Oceanología (Chile) 4: 56-68.

CARCELLES AR & SI WILLIAMSON (1951) Catálogo de los moluscos marinos de la provincia magallánica. Revista del Instituto Nacional de Investigación de Ciencias Naturales 2: 225-383.

CARRASCO F (1974) Spionidae (Polychaeta) provenientes de la Bahía de Concepción y lugares adyacentes. Boletín de la Sociedad de Biología de Concepción (Chile) 48: 185-201.

CARRASCO F (1976a) Larvas de la familia Spionidae (Polychaeta) en el plancton de la Bahía de Concepción, Chile. Gayana Zoología (Chile) 38: 1-63.

CARRASCO F (1976b) Paraonidae (*Aricidea pigmentata n.sp.*), Magelonidae y Oweniidae (Annelida, Polychaeta) en bahía Concepción, Chile. Boletín de la Socieda de Biología de Concepción (Chile) 50: 113-121.

CARRASCO F (1977) Polychaeta (Annelida) de Bahía de Concepción, Chile. Familias Orbiniidae, Cirratulidae, Cossuridae, Capitellidae y Ampharetidae, con la descripción de tres especies y una subespecie nuevas. Boletín de la Sociedad de Biología de Concepción (Chile) 51: 67-92.

CARRASCO FD & VA GALLARDO (1983) Abundance and distribution of the macrobenthic infauna of the Gulf of Arauco, Chile. Int Revue ges Hydrobiol 68: 825-838.

CARRASCO F & M CARBAJAL (1996) Reclutamiento de Macroinfauna bentónica en un área influenciada por surgencias costeras: Bahía de Concepción, Chile. Gayana Oceanología (Chile) 4: 169-181.

CARRASCO F & M CARBAJAL (1996) Reclutamiento de Macroinfauna bentónica en un área influenciada por surgencias costeras: Bahía de Concepción, Chile. Gayana Oceanología (Chile) 4: 169-181.

CARRASCO FD, VA GALLARDO & S MEDRANO (1988) Sublittoral macrobenthic faunal assemblages of two nearby embayments from central Chile. Int Revue ges Hydrobiol 73: 441-455.

CASTILLA JC (1976) Parques y reservas marítimas: Creación, probables localizaciones y criterios básicos. Medio Ambiente (Chile) 2: 70-80.

CASTILLA JC (1979) Características bióticas del Pacífico Sur-Oriental, con especial referencia al sector chileno. Revista de la Comisión Permanente del Pacífico Sur 10: 167-182.

CASTILLA JC (1981) Perspectivas de investigación en estructura y dinámica de comunidades intermareales rocosas de Chile central. II. Depredadores de alto nivel trófico. Medio Ambiente (Chile) 5: 190-215.

CASTILLA JC (1983) Environmental impact in sandy beaches of copper mine tailings at Chañaral, Chile. Marine Pollution Bulletin 14: 459-464.

CASTILLA JC (1986) ¿Sigue existiendo la necesidad de establecer Parques y Reservas Marinas en Chile. Ambiente y Desarrollo 2 (Chile): 53-63.

CASTILLA JC (1988) Earthquake-caused coastal uplift and its effects on rocky intertidal kelp communities. Science 242: 440-443.

CASTILLA JC (1996) La futura Red Chilean de Parques y Reservas Marinas y los conceptos de conservación, preservación y manejo en la legislación nacional. Revista Chilean de Historia Natural 69: 253-270.

CASTILLA JC (1999) Coastal marine communities: trends and perspectives from human-exclusion experiments. Trends in Ecology and Evolution 14: 280-284.

CASTILLA JC & E NEALLER (1978) Marine environtal impact due to mining activities of El Salvador Cooper Mine, Chile. Marine Pollution Bulletin 9: 67-70.

CASTILLA JC & LR DURAN (1985) Human exclusion from the rocky intertidal zone of central of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos 45: 391-399.

CASTILLA JC & M FERNANDEZ (1998) Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. Ecological Applications 8: S124-S132.

CASTILLA JC & OLIVA D (1990) Ecological consequences of coseismic uplift on the intertidal kelp belts of *Lessonia nigrescens* in central Chile. Estuarine, Coastal and Shelf Science 31: 45-56.

CASTILLA JC & RH BUSTAMANTE (1989) Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillaea antarctica* (Phaeophyta, Durvilleales). Marine Ecology Progress Series 50: 203-214.

CASTILLA JC & RT PAINE (1987) Predation and community organization on Eastern Pacific, temperate zone, rocky intertidal shores. Revista Chilena de Historia Natural 60: 131-151.

CASTILLA JC, C LUXORO & SA NAVARRETE (1989) Galleries of the crabs *Acanthocyclus* under intertidal mussel beds: their effect on the use of primary substratum. Revista chilena de Historia Natural 62: 199-204.

CASTILLA JC, GM BRANCH, & A BARKAI (1994) Exploitation of two critical predators: the gastropod *Concholepas concholepas* and the rock lobster *Jasus lalandii*. In: Siegfried WR (ed) Rocky Shores: Exploitation in Chile and South Africa Vol. 103: 101-130. Ecological Studies Edition, Springer-Verlag, Berlin, Germany.

CASTILLA JC, M SANCHEZ & O MENA (1977) Estudios ecológicos en la zona costera afectada por contaminación del Northern Breeze. I Introducción general y comunidades de playas de arena. Medio Ambiente (Chile) 2: 53-64.

CASTILLA JC, SA NAVARRETE & J LUBCHENCO (1993) Southeastern Pacific Coastal Environments: Main Features, Large-Scale Perturbations, and Global Climate Change. In: Mooney H, E Fuentes & B Kronberg (eds) Earth System Responses to Global Change 13: 167-188. Academic Press Inc.

CASTILLO JG (1968) Contribución al conocimiento de los ofiuroídeos chilenos. Gayana Zoología (Chile) 14: 78.

CLARKE M, V ORTIZ & JC CASTILLA (1999) Does early development of the Chilean tunicate *Pyura praeputialis* (Heller 1978) explain restricted distribution of the species? Bulletin of Marine Science 65: 745-754.

CLASING E (1976) Fluctuaciones anuales de la meiofauna en la marisma de Chinquihue (Puerto Montt, Chile). Studies on Neotropical Fauna and Environment 11: 179-198.

COMTE D, SK EISEMBERG, E LORCA, M PARDO, L PONCE, R SARAGONI, SK SINGH & G SUAREZ (1986) The 1985 central Chile earthquake: a repeat of previous great earthquakes in the region? Science 233: 449-453.

CONTRERAS S & JC CASTILLA (1987) Feeding behavior and morphological adaptations in two sympatric sea urchin species in central Chile. Marine Ecology Progress Series 38: 217-224.

CORREA JA, P GONZALEZ, P SANCHEZ, J MUÑOZ & MC ORELANA (1996) Copper-algae interactions: inheritance or adaptations? Environmental Monitoring and Assesment 40: 41-54.

CROKER R & E B HATFIEDLS (1980) Space partitioning and interactions in a intertidal sand burrowing amphipod guild. Marine Biology 61: 79-88.

CSUTI B, S POLASKY, PH WILLIAMS, RL PRESSEY, JD CAMM, M KERSHAW, AR KIESTER, B DOWNS, R HAMILTON, M HUSO & K SAHR (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. Biological Conservation 80: 83-97.

DALL WH (1909) Report on a collection of shells from Peru with a summary of the litoral marine mollusca of the Peruvian zoological province. Proocedings of the U.S. National Museum. 37: 147-294.

DAVIS GE (1989) Designated harvest refugia: The next stage of marine fishery management in California. CalCOFI Reports 30: 53-58.

DAYTON PK (1985) The structure and regulation of some South American kelp communities. Ecological Monographs 55: 447-468.

DAYTON PK, SF THRUSH, MT AGARDY & RJ HOFMAN (1995) Environmental effects of marine fishing. Aquatic Conservation: Marine and Freshwater Ecosystems 5: 205-232.

DE CASTELLANOS ZA (1992) Catálogo descriptivo de la malacofauna marina magallánica: Neogastropoda, Buccinulidae y Nassaridae. CIC, Provincia de Buenos Aires. Comisión de Investigaciones Científicas, Argentina 8: 27 pp.

DELL RK (1971) The marine mollusca of the Royal Society Expedition to southern Chile, 1958-1959. Records of the Dominium Museum. 7: 155-233.

DI CASTRI E & E HAJEK (1976) Bioclimatología de Chile. Vicerectoría Académica, Universidad Católica de Chile, Santiago, Chile. 128 pp.

DI GERONIMO S, S PRIVITERA, C VALDOVINOS (1991) Molluskan thanatocoenoses of the Magellan Straits. Memorie di Biologia Marina e di Oceanografia 19: 505-208.

DOBSON AP, JP RODRIGUEZ, WM ROBERTS & DS WILCOVE (1997) Geographic distribution of endangered species in the United States. Science 275: 550-553.

DONOSO E (1991) Distribución y estructura comunitaria de la macroinfauna intermareal en dos estuarios del sur de Chile. Tesis Universidad Austral de Chile (Pedagogía en Biología, Química y Ciencias Naturales). 33 pp.

DUGAN JE & GE DAVIS (1993) Application of marine refugia to coastal fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 50: 2029-2042.

DURAN LR & JC CASTILLA (1989) Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. Marine Biology 103: 555-562.

ENFIELD DB (1989) El Niño past and present. Reviews in Geophysics. 27: 159-187.

FOSSING H, VA GALLARDO, BB JOERGENSEN, M HUETTEL, LP NIELSEN, H SCHULZ, DE CANFIELD, S FORSTER, RN GLUD, JK GUNDERSEN, J KUEVER, NB RAMSING, A TESKE, B THAMDRUP & O ULLOA (1995) Concentration and transport of nitrate by the mat-forming sulphur bacterium *Thioploca*. Nature. 374: 713-715.

GAINES SD & J LUBCHENCO (1982) A unified approach to marine plant-herbivore interactions II. Biogeography. Annual Review in Ecology and Systematics 13: 11-138.

GALLARDO VA (1963) Notas sobre la densidad de la fauna bentónica sublitoral del norte de Chile. Gayana Zoología (Chile) 10: 3-15.

GALLARDO VA (1968) Observaciones sobre la fauna bentónica del Golfo de Arauco. Boletín de la Sociedad de Biología de Concepción (Chile) 40: 145-160.

GALLARDO VA (1977a) Large benthic microbial communities in sulfide biota under Peru-Chile subsurface countercurrent. Nature 268: 331-332.

GALLARDO VA (1977b) On the discovery of a large microbial community living in the soft bottoms of the continental shelf of Chile and Peru. Anales del Instituto de Investigaciones Marinas, Pta Betín (Colombia) (Supplemento 1): 23-30.

GALLARDO VA (1984) Revisión actualizada a 1983 de la contaminación marina proveniente de fuentes terrestres en le región del pacífico sudeste (Colombia, Chile, Ecuador, Panamá y Perú). Revista de la Comisión Permanente del Pacífico Sur 14: 19-173.

GALLARDO VA (1985) Efecto del fenómeno de "El Niño" sobre el bentos sublitoral frente a Concepción, Chile. In: Arntz W, A Landa & J Tarazona (eds) "El Niño": su impacto en la fauna marina, Callao Perú: 79-85. Boletín del Instituto del Mar del Perú, Perú.

GALLARDO VA, FD CARRASCO, R ROA & JI CAÑETE (1995) Ecological patterns in the benthic macrobiota across the continental shelf off Chile. Ophelia 40: 167-198.

GALLARDO VA, J CASTILLO, MA RETAMAL, A YAÑEZ, HI MOYANO & JG HERMOSILLA (1977) Quantitative studies on the soft-bottom macrobenthic communities of shallow Antarctic bays. In: Llano G (ed) Adaptations within Antarctic ecosystems: 361-387. Gulf Publishing Houston.

GALLARDO VA, JI CAÑETE, S ENRIQUEZ BRIONES, M BALTAZAR & R ROA (1994) Preliminary notes on the recruitment of *Pleuroncodes monodon* (H. Milne Edwards, 1837), (Decapoda, Galatheidae) on the continental shelf off central Chile. Journal of Crustacean Biology 44: 665-669.

GARCIA V & C OJEDA (1995) Estructura del bentos en áreas con enriquecimiento orgánico en el complejo estuarial de los ríos Calle-Calle, Valdivia y Cruces. Tesis de Licenciatura en Biología Marina, Universidad Austral de Chile, Valdivia. 31 pp

GARTH J (1957) The Crustacea Brachyura Decapoda of Chile. Reports of the Lund University Chile Expedition 1948-1949 N° 29: 1-34.

GILLER PS (1984) Community structure and the niche. Outline Studies in Ecology, Chapman & Hall. 175 pp.

GODOY C & CA MORENO (1989) Indirect effects of human exclusion from the rocky intertidal in southern Chile: a case of cross-linkage between herbivores. Oikos. 54: 101-106.

GONZALEZ E, E VILLOUTA & G DANERI (1997) Diagnóstico y análisis para el diseño de un sistema nacional de reservas marinas. FIP 96-52. 115 pp.

GROSS P & E HAJEK (1998) Indicadores de calidad y gestión ambiental. Alfabeta Artes Gráficas, Santiago. 221 pp.

GUIÑEZ R & JC CASTILLA (in press) An allometric tridimentional model of self thiming for a gregarious tunicate. Ecology.

HARTMANN-SCHROEDER G & G HARTMANN (1965) Zur Kenntnis des Sublitorals der chilenisehen Kuste unter besonderer Berucksichtigung der Polychaeten und Ostracoden (Mit Bemerkungen über den Einfluss sauerstoffarmer Stroemungen aufdie Besiedlung von marinen Sedimenten). Mitt hamb zool Mus Inst suppl 62: 1-384.

HARTMANN-SCHROEDER G (1962) Zur Kenntnis des Eulitorals der chilenischen Pazifikkuste und der argentinischen Kuste Sudpatagoniens unter besonderer Berucksichtigung der Polychaeten und Ostracoden. Tl. II. Die Polychaeten des Eulitorals. Mitt Hamburg Zool Mus Inst suppl 60: 57-167.

HASTINGS A & LW BOTSFORD (1999) Equivalence in yield from marine reserves and traditional fisheries management. Science 284: 1537-1538.

HERNANDEZ C (1998) Análisis espacio-temporal de la concentración de cobre disuelto y total en Punta Coloso, Antofagasta. In: Arcos D (ed) Minería del cobre, ecología y ambiente costero: 317-331. Editora Anibal Pinto SA, Chile

HERNANDEZ C, SH CONTRERAS, JA GALLARDO & JM CANCINO (1998). Estructura comunitaria de la macroinfauna a lo largo de una playa arenosa de Chile central: Lenga, Bahía de San Vicente. Revista Chilena de Historia Natural 71: 303-311.

HOCKEY PAR & GM BRANCH (1994) Conserving marine biodiveristy on the African coast: implications of a terrestrial perspective. Aquatic conservation: marine and freshwater ecosystems 4: 345-362.

HOCKEY PAR & GM BRANCH (1997) Criteria, objectives and methodology for evaluating Marine Protected Areas in South Africa. South African Journal of Marine Science 18: 369-383.

HOFFMANN A & B SANTELICES (1997) Flora marina de Chile. Ediciones Universidad Católica de Chile. 434 pp.

JARA F & CA MORENO (1984) Herbivory and structure in a midlittoral rocky community: a case in the southern Chile. Ecology 65: 28-38.

JARAMILLO E (1978) Zonación y estructura de la comunidad macrofaunística en playas de arena del sur de Chile (Mehuín, Valdivia). Studies on Neotropical Fauna and Environment 13: 71-92.

JARAMILLO E (1982) Taxonomy, natural history and zoogeography of sand beach isopods from the coast of southern Chile. Studies on Neotropical Fauna and Environment 17: 175-194.

JARAMILLO E (1987a) Community ecology of chilean sandy beaches. Ph.D. Dissertation, University of New Hampshire, Durham, NH, USA. 216 pp.

JARAMILLO E (1987b) Sandy beach macroinfauna from the Chilean coast: zonation patterns and zoogeography. Vie et Milie 37: 165-174.

JARAMILLO E (1994) Patterns of species richness in sandy beaches of South America. South . African Journal of Zoology 29: 227-234.

JARAMILLO E & A MCLACHLAN (1993) Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. Estuarine, Coastal and Shelf Science 37: 615-624.

JARAMILLO E, F CARRASCO, P QUIJON, M PINO & H CONTRERAS (1998) Distribución y estructura comunitaria de la macroinfauna bentónica en la costa del norte de Chile. Revista Chilena de Historia Natural 71: 459-478.

JARAMILLO E, H CONTRERAS & P QUIJON (1996) Macroinfauna and human disturbance in a sandy beach of south-central Chile. Revista Chilena de Historia Natural 69: 655-663.

JARAMILLO E, M PINO, L FILUN & M GONZALEZ (1994) Longshore distribution of *Mesodesma donacium* (Bivalvia: Mesodesmatidae) on a sandy beach of the south of Chile. The Veliger 37: 192-200.

JARAMILLO E, S MULSOW & R NAVARRO (1985) Intertidal and subtidal macroinfauna in the Queule river estuary. Revista Chilena de Historia Natural 58: 127-137.

JARAMILLO E, W STOTZ, C BERTRAN, J NAVARRO, C ROMAN & C VARELA (1980) Actividad locomotriz de *Orchestoidea tuberculata* (Amphipoda, Talitridae) sobre la superficie de una playa arenosa del sur de Chile (Mehuín, Provincia de Valdivia). Studies on Neotropical Fauna and Environment. 15: 9-33.

JERARDINO A, JC CASTILLA, JM RAMIREZ & N HERMOSILLA (1992) Early coastal subsistence patterns in central Chile: A systematic study on the marine-invertebrate fauna from the site of Curaumilla-1. Latin American Antiquity 3: 43-62.

JONES CG, JH LAWTON & M SCHACHAK (1994) Organism as ecosystem engineers. Oikos 69: 373-386

KELLEHER G & R KENCHINGTON (1992) Guidelines for Establishing Marine Protected Areas. World Conservation Union (IUCN), Gland, Switzerland. 79 pp.

KNOX GA (1960) Litoral ecology and biogeography of the southern oceans. Proceedings of the Royal Society of London, Series B, 152: 577-624.

LANCELLOTTI D & JA VASQUEZ (1999) Biogeographical patterns of benthic invertebrates in the southeastern Pacific littoral. Journal of Biogeography 26: 1001-1006.

LARRAIN A (1995) Biodiversidad de equinodermos chilenos: Estado actual del conocimiento y sinópsis biosistemática. Gayana Zoología (Chile) 59: 73-96.

LAUK T, CV CLARK, M MANGEL & GR MUNRO (1998) Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8: 572-578.

LEVIN LA (1981) Dispersion, feeding behaviour and competition in two spionid polychaetes. Journal of Marine Research 39: 99-117.

LEVIN LA (1982) Interference interactions among tube-dwelling polychaetes in a dense infaunal assemblage. Journal of Experimental Marine Biology and Ecology 65: 107-119.

LLAGOSTERA A (1979) 9700 years of maritime subsistence on the Pacific: an analysis by means of bioindicators in the north of Chile. American Antiquity 44: 309-324.

LUBCHENCO J, GW ALLISON, SA NAVARRETE, BA MENGE, JC CASTILLA, O DEFEO, C FOLKE, O KUSSAKIN, T NORTON & AM WOOD (1995) Coastal systems. In: Heywood VH & RT Watson (eds) Global biodiversity assessment: 370-381. United Nations Environmental Programme, Cambridge.

MACE PM (1994) Relationship between common biological reference points used as thresholds and targets of fisheries management strategies. Canadian Journal of Fisheries and Aquatic Sciences 51: 110-122.

MACLACHLAN A & E JARAMILLO (1995) Zonation on sandy beaches. Oeanography and Marine Biology Annual Review 33: 305-335.

MARINCOVICH L Jr (1973) Intertidal mollusks of Iquique, Chile. Natural History Museum of Los Angeles County, Science Series 16: 1-49.

MARQUET PA, SA NAVARRETE & JC CASTILLA (1990) Scaling population density to body size in rocky intertidal communities. Science 250: 1125-1127.

MCLUSKY D (1971) Ecology of estuaries. Heinemnn Educational Books Ltd., London. 144 pp.

MCNEIL SE & PG FAIRWEATHER (1993) Single largo or several small marine reserves? An experimental approach with seagrass fauna. Journal of Biogeography 20: 429-440.

MENGE BA, EL BERLOW, C BLANCHETTE, SA NAVARRETE & SB YAMADA (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64: 249-286.

MORALES CE & F PONCE (1997) Parques marinos y reservas en la ley general de pesca y acuicultura: desafíos para su establecimiento y aplicación. Estudios Oceanológicos (Chile) 16: 19-26.

MOREIRA P (1973) Species of *Macrochiridothea* Ohlin, 1901 (Isopoda, Valvifera) from Southern Brazil, with notes on remaining species of the genus. Boletím do Instituto Oceanografico do Sao Paulo (Brasil) 22: 11-47.

MORENO CA (2000) Areas marinas y borde costero. In: Brzovic PF & M Romaggi (eds) Estado del medio ambiente en Chile-1999: 245-286. Universidad de Chile, Santiago.

MORENO CA & E JARAMILLO (1983) The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. Oikos 41: 73-76.

MORENO CA & HF JARA (1984) Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fueguian Islands, Chile. Marine Ecology Progress Series 15: 99-107.

MORENO CA & JP SUTHERLAND (1982) Physical and biololgical processes in *a Macrocystis pyrifera* community near Valdivia. Oecologia 55: 1-6.

MORENO CA & R VEGA (1988) Valor científico de las reservas marinas costeras: un ejemplo de estudio ecológico con poblaciones intermareales de *Loxechinus albus* (Molina). Informe Unesco Ciencias Mar 47: 124-134.

MORENO CA (1995) Macroalagae as a refuge from predation for recruits of the mussel *Choromytilus chorus* (Molina 1782) in southern Chile. Journal of Experimental Marine Biology and Ecology 191: 181-193.

MORENO CA, GA ASENCIO & S IBAÑEZ (1993) Patrones de asentamiento de *Concholepas concholepas* (Brugière) (Mollusca:Muricidae) en la zona intermareal rocosa de Valdivia, Chile. Revista Chilena de Historia Natural 66: 93-101.

MORENO CA, JP SUTHERLAND & HF JARA (1984) Man as a predator in the intertidal zone of southern Chile. Oikos 42: 155-160.

MORENO CA, K LUNECKE & MI LOPEZ (1986) The response of an intertidal *Concholepas concholepas* population (Gastropoda; Muricidae) to protection from man in southern Chile and its effects on benthic sessile assemblages. Oikos 46: 359-364.

MUÑOZ AA & FP OJEDA (1997) Feeding guild structure of a rocky intertidal fish assemblage in central Chile. Environmental Biology of Fishes 49: 471-479.

MUÑOZ M, H NUÑEZ & J YAÑEZ (1996) Libro rojo de los sitios prioritarios para la conservación de la diversidad biológica en Chile. Impresora Creces Ltda, Santiago. 203 pp.

NAVARRETE SA & JC CASTILLA (1988) Resource partitioning between intertidal predatory crabs: interference and refuge utilization. Journal of Experimental Marine Biology and Ecology 143: 101-129.

NAVARRETE SA & BA MENGE (1996) Keystone predation: interactive effects of two predators on their main prey. Ecological Monographs 66: 409-429.

NAVARRETE SA & JC CASTILLA (1990) Resource partitioning between intertidal predatory crabs: interference and refuge utilization. Journal of Experimental Marine Biology and Ecology 143: 101-129.

NAVARRETE SA & JC CASTILLA (1993) Predation by Norway rats in the intertidal zone of central Chile. Marine Ecology Progress Series 92: 187-199.

NORSE EA, ed (1993) Global marine biological diversity: A strategy for building conservation into decision making. Island Press, Washington, DC.

NOWLIS JS & CM ROBERTS (1997) You can have your fish and eat it too: theoretical approaches to marine reserve design. Proceedings of the 8th International Coral Reef Symposium 1996, 2:1907-1910.

ODENDAAL ET FJ, M KROESE & J AOMANANA (1995)
The strategic plan for the management of the coastal
zone of the Masoala Peninsula, Madagascar. Eco-
Africa Environmental Consultants, Cape Town. 214
pp.

OJEDA FP, FA LABRA & AA MUÑOZ (2000) Biogeo-
graphical patterns of Chilean littoral fishes. Revista
Chilena de Historia Natural 73:

OJEDA FP & AA MUÑOZ (1999) Feeding selectivity of
the herbivorous fish *Scartichthys viridis*: effects on
macroalgal community structure in a temperate in a
temperate rocky intertidal coast. Marine Ecology
Progress Series 184: 219 - 229.

OJEDA FP & B SANTELICES (1984) Invertebrate com-
munities in holdfasts of the kelp *Macrocystis pyrifera*
from southern Chile. Marine Ecology Progress Series
16: 65 - 73.

OLIVA D & JC CASTILLA (1986) The effect of human
exclusion on the population structure of key-hole
limpets *Fissurella crassa* and *F. limbata* on the coast
of central Chile. Marine Ecology 7: 201-217.

ORMAZABAL C (1993) The conservation of biodiversity
in Chile. Revista Chilena de Historia Natural 66: 383-
402.

OSORIO C (1981) Caudofoveata y Solenogastra de Chile.
Boletín de la Sociedad de Biología de Concepción
(Chile) 52: 115-128.

OSORIO C, J ATRIA & S MANN (1979) Moluscos marinos
de importancia económica en Chile, Biología Pesquera
(Chile) 11: 3-47.

PAINE RT (1994) Marine rocky shores and community
ecology: an experimentalist's perspective. Ecology
Institute, Oldendorf/Luhe, Germany. 152 pp.

PAINE RT & TH SUCHANEK (1983) Convergence of
ecological processes between independently evolved
competitive dominants: A tunicate-mussel compari-
son. Evolution 37: 821-831.

PAINE RT, JC CASTILLA & J CANCINO (1985) Pertur-
bation and recovery patterns of starfish-dominated
intertidal assemblages in Chile, New Zealand, and
Washington State. American Naturalist 125: 679-
691.

PAULY D, V CHRISTIANSEN, J DALSGRAARD, R
FROESE & F TORRES JR (1998) Fishing down ma-
rine food webs. Science 279: 860-863.

PEQUEÑO G (1979) Antecedentes alimentarios de
Eleginops maclovinus (Valenciennes, 1830)
(Teleostomi: Nototheniidae), en Mehuín, Chile. Acta
Zoológica Lilloana (Argentina) 35: 207 -230.

PICKARD GL (1971) Some physical oceanographic fea-
tures of inlets of Chile. Journal of Fisheries Reseach
Board of Canada 28: 1077-1106.

PONDER WF (1983) Rissoaform gastropods from the
Antartic and Sub-Antarctic. British Antarctic Survey.
Scientific Reports. 108: 1-96.

POWER ME, D TILMAN, JA ESTES, BA MENGE, WJ
BOND, S MILLS, G DAILY, JC CASTILLA, J
LUBCHENCO, & RT PAINE (1996) Challenges in
the quest for keystones. BioScience 46: 609-620.

PRENDERGAST JR, RM QUINN & JH LAWTON (1999)
The gaps between theory and practice in selecting
nature reserves. Conservation Biology 13: 484-492.

PRENDERGAST JR, RM QUINN, JH LAWTON, BC
EVERSHAM & DW GIBBONS (1993). Rare species,
the coincidence of diversity hotspots and conserva-
tion strategies. Nature 365: 335-337.

PRESSEY RL, CJ HUMPHRIES, CR MARGULES, RI
VANE-WRIGHT & PH WILLIAMS (1993) Beyond
opportunism: Key principles for systematic reserve
selection. Trends in Ecology and Evolution 8: 124-
128.

PUTMAN RJ (1994) Community Ecology. Chapman &
Hall, London. 177 pp.

QUIJON P & E JARAMILLO (1993). Temporal variabil-
ity in the intertidal macroinfauna in the Queule river
estuary, south-central Chile. Estuarine, Coastal and
Shelf Science. 37: 655-667.

QUIJON P & E JARAMILLO (1996). Seasonal vertical
distribution of the intertidal macroinfauna in an estu-
ary of south-central Chile. Estuarine, Coastal and
Shelf Science 43: 653-663.

RAFFAELLI D & S HAWKINS (1996) Intertidal ecology.
Chapman & Hall, London. 356 pp.

RAMIREZ C, C SAN MARTIN & D CONTRERAS (1990)
Ecosociología de las marismas litorales del centro-
sur de Chile. Agro Sur (Chile) 18: 104-112.

RAMORINO L (1968) Pelecypoda del fondo de la Bahía
de Valparaíso. Revista de Biología Marina, Valparaíso
13: 175-285.

RAY GC (1991) Coastal-zone biodiversity patterns.
BioScience 41(7): 490-498.

RETAMAL MA (1981) Catálogo ilustrado de los crustáceos
decápodos de Chile. Gayana Zoología (Chile) 44: 1-
110.

RIVEROS-ZÚÑIGA F & JG REYES (1950) Catalogo
descriptivo de los Venéridos chilenos. Revista de
Biología Marina, Valparaíso 2: 28 pp.

ROBERTS CM (1998) Sources, sinks and tge design of
marine reserve networks. Fisheries 23: 16-19.

ROBLES C & J ROBB (1993) Varied carnivore effects and
the prevalence of intertidal algal turfs. Journal of Experi-
mental Marine Biology and Ecology 166: 65-91.

ROBLES F, E ALARCON & A ULLOA (1974) Water
masses in the northern Chilean zone and their varia-
tion in a cold period (1967) and warm periods (1969,
1971-1973) In: Reunión de Trabajo sobre el Fenómeno
de El Niño: 1-68. COI, Guayaquil.

ROWE GT (1971) Benthic biomass and surface productiv-
ity. In: Coslow JD (ed) Fertility of the sea: 441-454.
Gordon & Breach Science Publishers, NY.

ROY K, D JABLONSKI & V VALENTINE (1998) Marine
latitudinal diversity gradients: test of causal hypoth-
eses. Proceedings of the National Academy of Sci-
ence USA 95: 3699-3702.

ROZBACZYLO N & P SALGADO (1993) Poliquetos
Spionidae de fondos blandos submareales de la Bahía
de Valparaíso, Chile (Annelida: Polychaeta). Estudios
Oceanológicos (Chile) 12: 17-28.

ROZBACZYLO N (1985) Los anélidos poliquetos de Chile
- Indice sinonímico y distribución geográfica de
especies. Monografías Biológicas (P. Universidad
Católica de Chile) (Chile) 3: 1-284.

SALM RV & A PRICE (1995) Selection of marine pro-
tected areas. In: Gubbay S (ed) Protected Areas:
principles and techniques for management: 15-31.
Chapman & Hall, London.

SAN MARTIN C, D CONTRERAS, J SAN MARTIN & C RAMIREZ (1992) Vegetación de las marismas del centro-sur de Chile. Revista Chilena de Historia Natural 65: 327-342.

SANCHEZ M, JC CASTILLA, O MENA (1982) Variaciones verano-invierno de la macrofauna de arena en playa Morrillos (Norte Chico, Chile). Studies on Neotropical Fauna and Environment 17: 31-49.

SANTELICES B (1980) Phytogeographic characterization of the temperate coast of Pacific South America. Phycologia 19: 1-12.

SANTELICES B (1989) Algas marinas de Chile. Distribución. Ecología. Utilización. Diversidad. Ediciones Universidad Católica de Chile. 399 pp.

SANTELICES B (1990) Patterns of organization of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. Hydrobiologia 192: 35-57.

SANTELICES B (1991) Littoral and sublittoral communities of continental Chile. In: Mathieson AC & PH Nienhius (eds) Intertidal and littoral ecosystem. Ecosystem of the world 24: 347-369. Elsevier.

SANTELICES B & PA MARQUET (1998) Seaweeds, latitudinal diversity patterns, and Rapoport's rule. Diversity and Distribution 4: 71-75.

SANTELICES B, J CANCINO, S MONTALVA, R PINTO & E GONZALEZ (1977) Estudios ecológicos en la zona costera afectada por contaminación del «Northern Breeze». II. Comunidades de playas de rocas. Medio Ambiente (Chile) 2: 65-83.

SANTELICES B, S MONTALVA & P OLIGER (1981) Competitive algal community organization in exposed intertidal habitats from central Chile. Marine Ecology Progress Series 6: 267-276.

SCHLATTER R (1984) Status and conservation of seabirds in Chile. En Status and conservation of the World's seabirds. In: JP Croxall, PG Evans & RW Schreiber (eds) ICBP Technical publication 2:261-269.

SCHLATTER R & R HUCKE-GAETE (1999) Importancia de la cooperación internacional para la conservación de aves y mamíferos marinos presentes en Chile. Estudios Oceanológicos (Chile) 18:13-24.

SCHLATTER R & A SIMEONE (1999) Estado del conocimiento y conservación de las aves en mares chilenos. Estudios Oceanológicos (Chile) 18: 25-33.

SEBENS KP & RT PAINE (1979) Biogeography of anthozoans along the west coast of South America: habitat, disturbance, and prey availability. In: Proceedings of the International Symposium of Marine Biogeography and Evolution of South Hemisphere 137: 219-237. New Zealand, Department of scientific and industrial research. Information Series.

SIMBERLOFF D (1988) The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19: 473-511.

SMENOV VN (1977) Biogeographical latitudinal- zonal nomenclature of coastal marine biota. Oceanology 17: 710-718.

SOOT-RYEN T (1959) Pelecypoda. Reports of the Lund University Chile Expedition 1948-49 Lunds Univ Arsskrift N° 5: 1-86.

SOTO D, F JARA & CA MORENO (1997) Evaluación de salmonidos de vida libre existentes en las aguas interiores de las Regiones X y XI. Informe Final FIP 95-31. 98 pp.

STEVENS GC (1989) The latitudinal gradient in geographic range: how so many species coexist in the tropics. American Naturalist 133: 240-256.

STEVENS GC (1996) Extending Rapoport's rule to Pacific marine fishes. Journal of Biogeography 23: 149-154.

STRUB T, J MESIAS, V MONTECINOS, J RUTLLANT & S SALINAS (1998) Coastal ocean circulation off western south america. Coastal segment (6,E). In: Robinson AR & KH Brink (eds) The Sea, Volume 11. John Wiley & Sons Inc.

STUARDO J (1960) La familia Glycymeridae (Bivalvia) en Chile. Revista de Biología Marina, Valparaíso 10: 133-143.

STUARDO J (1962) Caecum chilense, nuevo molusco para Chile. Gayana Zoología (Chile) 5: 3-9.

STUARDO J (1964) Distribución de los moluscos marinos litorales en latinoamérica. Boletín del Instituto de Biología Marina de Mar del Plata 7: 79-91.

TARAZONA J (1984) Modificaciones de la infauna bentónica de una bahía con deficiencia de oxígeno durante El Niño 1982-83. Revista de la Comisión Permanente del Pacífico Sur 15: 223-238.

TARIFEÑO E (1980) Studies on the biology of the surf clam Mesodesma donacium (Lamarck, 1818) (Bivalvia: Mesodesmatidae) from Chilean sandy beaches. Ph.D. Thesis, University of California, Los Angeles. 277 pp.

TUCK GN & HP POSSINGHAM (2000) Marine protected areas for spatially structured exploited stocks. Marine Ecology Progress Series 192: 103-118.

TURNER A (1984) Zonación y estratificación de la macroinfauna intermareal del estuario del río Queule (IX Región, Chile). Medio Ambiente (Chile) 7: 29-36.

VALDOVINOS C (1998) Patrones de distribución espacial de la macrofauna bentónica sublitoral en el Golfo de Arauco (Chile central). Tesis para optar al grado de Doctor en Ciencias Mención Zoología Universidad de Concepción, Chile. 327 pp.

VALENTINE JW & D JABLONSKI (1983) Larval adaptations patterns of brachiopods diversity in space and time. Evolution 37: 1052-1061.

VARAS E & FP OJEDA (1990) Intertidal fish assemblages of the central Chilean coast: diversity, abundance and trophic patterns. Revista de Biología Marina, Valparaíso 25: 59-70.

VARELA C (1983) Anfípodos de las playas de arena del sur de Chile (Bahía de Maiquillahue, Valdivia). Studies on Neotropical Fauna and Environment 18: 25-52.

VASQUEZ JA & A BUSCHMANN (1997) Herbivory-kelp interactions in subtidal Chilean comunities: a review. Revista Chilena de Historia Natural 70: 41-52

VASQUEZ JA & N GUERRA (1996). The use of seaweeds as bioindicators of natural and anthropogenic contaminants in northern Chile. Hydrobiologia 326/327: 327-333.

FERNANDEZ ET AL.

VASQUEZ JA, PA CAMUS, & FP OJEDA (1998) Diversidad, estructura y funcionamiento de ecosistemas costeros rocosos del norte de Chile. Revista Chilena de Historia Natural 71: 479-499.

VASQUEZ JA, JM VEGA, B MATSUHIRO & C URZUA (1999) The ecological effects of mining discharges. on subtidal habitats dominated by macroalgae in northern Chile: population and community level studies. Hydrobiología 398/399: 217-229.

VASQUEZ JA, B MATSUHIRO, MA VEGA, LM PARDO & D VELIZ (2000) The effects of mining pollution on subtidal habitats of northern Chile: population and community level studies. International Journal of Environment and Pollution 13: 453-472.

VELASQUEZ C (1987) Depredación por aves migratorias sobre la macroinfauna intermareal de fondos blandos en el estuario del río Queule (IX Región, Chile). Tesis de Magister en Ciencias Mención Zoología. Universidad Austral de Chile. 73 pp.

VENEGAS C (1992) Depredación epibentónica como factor organizador de la macroinfauna intermareal en el estuario del río Queule, IX Región, Chile. Tesis de Magister en Ciencias Mención Zoología, Universidad Austral de Chile. 34 pp.

VILLARROEL M & J STUARDO (1999) Protobranchia (Mollusca: Bivalvia) chilenos recientes y algunos fósiles. Malacologia 40: 113-229.

VILLARROEL M (1971) Taxonomía y distribución de los Protobranquiados chilenos recientes y de algunos fósiles. Tesis de Licenciado en Biología, Universidad de Concepción, Chile. 227 pp.

VIVIANI CA (1979) Ecogeografia del litoral chileno. Studies on Neotropical Fauna and Environment 14: 65-123.

WESENBERG-LUND E (1962) Polychaeta Errantia. Reports of the Lund University Chile Expedition (43) Acta University Lund 57(12): 1-139.