Revista Chilena de Historia Natural
73:625-641 2000

Biogeographic patterns of Chilean littoral fishes

Patrones biogeográficos de los peces litorales de Chile

F. PATRICIO OJEDA[1], FABIO A. LABRA[1] & ALEJANDRO A. MUÑOZ [2]

[1]Departamento de Ecología, Facultad de Ciencias Biológicas, P. Universidad Católica de Chile, Casilla 114-D, Santiago, Chile, e-mail: pojeda@genes.bio.puc.cl
[2]Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

ABSTRACT

In this study, we analyzed the biogeographic patterns of the Chilean littoral fish fauna, including latitudinal trends in teleost and chondrichthyan fish species richness, their distribution range patterns, and their level of endemism, both to the Chilean coast and the Southeastern Pacific. We determined the number and percentage of fish taxa within four different groups based on their biogeographic affinities. This was done, both for teleost and chondrichthyan fishes, at the species, genus and family level. In order to recognise the existence of biogeographic regions, we applied cluster and ordination analyses to the distribution data, using objective bootstrapping techniques at the three taxonomic levels used. We found that littoral fish diversity remains fairly constant along the coast down to around 40° S, declining south of this latitude. We detected two biogeographic regions along the Chilean coast, with a break between them at 40° S. These results lend support to previously recognized biogeographic provinces or faunistic units. These two biogeographic regions are a reflection of the mixed origin of the Chilean littoral ichthyofauna, consisting of northern warm-temperate fishes of subtropical origin and southern cold-temperate fishes of subantarctic origin. While the percentage of fishes endemic to the Chilean coast is not high (18%), a large percentage of teleost species inhabiting Chilean littoral waters are endemic to the Southeastern Pacific (44%). Dispersal and evolutionary history, rather that other factors, seem to explain the observed patterns of distribution of this particular fish fauna. This study represents a necessary first step towards understanding the biogeography of Southeastern Pacific marine fishes.

Key words: Marine biogeography, littoral fishes, endemism, Southeastern Pacific Ocean, latitudinal diversity patterns.

RESUMEN

En este estudio, analizamos los patrones biogeográficos de los peces litorales chilenos, incluyendo las tendencias latitudinales en riqueza de especies de peces teleosteos y condrictios, sus rangos de distribución, y nivel de endemismo, tanto para la costa de Chile, como para el Pacífico Suroriental. Determinamos el número y porcentaje de taxa de peces pertenecientes a cuatro grupos según sus afinidades biogeográficas. Esta asignación a grupos se hizo al nivel de especie, género y familia, tanto para teleosteos como condrictios. Con el fin de determinar la existencia de regiones biogeográficas, utilizamos análisis de conglomerados y ordenación en conjunto con técnicas de aleatorización, para los tres niveles taxonómicos estudiados. Se determinó que la diversidad de peces litorales se mantiene relativamente constante a lo largo de la costa, hasta alrededor de los 40° S, disminuyendo hacia el sur. Detectamos dos regiones biogeográficas a lo largo de la costa chilena, con un quiebre entre ellas a los 40° S. Estos resultados apoyan la existencia de las provincias biogeográficas o unidades faunísticas reconocidas previamente en la literatura. Estas dos regiones biogeográficas reflejan el origen mixto de la ictiofauna litoral chilena, la que consiste de especies de peces de origen subtropical y subantartico. Aunque el porcentaje de peces endémicos a la costa chilena es bajo (18%), un alto porcentaje de las especies de teleosteos presentes en aguas chilenas es endémico al Pacífico Suroriental (44%). Procesos relacionados con fenómenos de dispersión y la historia evolutiva de los componentes de esta fauna explicarían de mejor manera los patrones de distribución observados más que otros factores sugeridos en la literatura. Este estudio representa un primer paso hacia una mejor comprensión de la biogeografía de los peces marinos del Pacífico Suroriental.

Palabras clave: Biogeografía marina, peces litorales, endemismo, Océano Pacifico Suroriental, patrones de diversidad latitudinal.

INTRODUCTION

One of the most striking geographic features of the mainland Chilean coast is its long latitudinal extension covering almost 4.200 km. This coast has another peculiar characteristic: from Arica (18°20'S) to the northern part of Chiloé Island (ca. 41° 45'), the coastline is an almost continuos straight line, fully exposed to the prevailing south-southwesterly winds (Thomas et al. 1994, Strub et al. 1998). On the other hand, the coast from Chiloé to Cape Horn (ca. 56°) is highly fragmented with a large number of islands and channels known as the Chilean archipelago region. All these characteristics may explain why this coast has largely attracted the attention of scientists interested in biogeography. As a consequence of this, an important number of studies have analyzed the distribution patterns of several marine floristic and faunistic groups along the Chilean coast (e.g. Balech 1954, Sebens & Paine 1979, Santelices 1980, Jaramillo 1982, Brattström & Johanssen 1983, Brattström 1990). Most of these studies have suggested biogeographical units based on distributional breaks of selected numbers of marine groups (primarily invertebrates). Despite the fact that most of these biogeographic studies have used different criteria and methodology for selecting their target groups and data analysis (Camus, in press), two faunistic groups have generally been recognized along the Chilean coast, a northern warm-temperate region to the north of 42° S and a southern cold-temperate region to the south of 42° S (Balech 1954, Briggs 1974). A transitional area between 30 and 42° S, where a mixing of both faunas occurs, has also been proposed (Dahl 1960, Dell 1971, Brattström & Johanssen 1983). However, the number of biogeographical units (regions, provinces or districts), as well as their limits or boundaries are still under discussion (see Lancellotti & Vásquez 1999, Camus, in press).

Even though the Chilean nearshore ichthyofauna has received increasing attention in recent years (Moreno & Jara 1984, Varas & Ojeda 1990, Lloris & Rucabado 1991, Pequeño & Lamilla 1995, Pequeño et al. 1995, Muñoz & Ojeda 1998, Berríos & Vargas 2000, Angel & Ojeda, in press, Quijada & Cáceres 2000), few studies have attempted to elucidate biogeographical aspects of this important component of the littoral fauna along the extensive Chilean coastline (Sielfeld & Vargas 1999, Pequeño 1999).

In this paper, we analyze the latitudinal distribution patterns of littoral marine fishes occurring along the Chilean coast based on available literature. The main aims of the present paper were:

(a) to determine latitudinal trends in the number of littoral fish taxa, at the level of species, genus and family occurring along the Chilean coast. (b) to construct latitudinal distribution maps of these fishes with the purpose of identifying groups of taxa with different biogeographic affinities along the Chilean coast. (c) to determine the level of endemism of teleost and chondrichthyan littoral fish species at two spatial scales: endemic to the south-eastern Pacific Ocean and to Chilean waters (18 - 56° S). (d) Then, by using cluster analyses and ordination techniques on distribution data of littoral teleost and chondrichthyan fishes, we test the most generalized hypothesis emerging from previous biogeographical studies. This hypothesis states that the Chilean littoral marine fauna is composed of two biogeographic regions, a northern warm-temperate region and a southern cold-temperate region, with a boundary between them located at 42°S, and a transitional region within the warm-temperate region stretching from 30-33° S southwards (Brattström & Johanssen 1983).

MATERIAL & METHODS

Littoral fish species distribution database

We obtained information on the latitudinal distribution of marine teleost and chondrichthyan fish species inhabiting Chilean littoral waters from a wide literature source (see Appendix I), based on the species lists published by Pequeño (1989, 1997). We followed the taxonomic nomenclature and classification of fish taxa used by Nelson (1994) and Eschmeyer (1998). Fish species registered in small fishery catches in recent years were also included (SERNAP 1996, 1997, 1998). We also included our unpublished data base of species collected in subtidal and intertidal waters on the northern and central Chilean coast (Ojeda, unpublished data).

Criteria for littoral fish species selection and definition of latitudinal distribution zones

We included fish species that have been captured from subsurface waters down to a maximum depth of 60 m, thus excluding deep-water species and all oceanic fishes that have not been recorded within this depth range. The analysis included fish species inhabiting subtidal waters as well as those have been found in intertidal habitats. We did not consider oceanic island fish species (i.e, Easter Island, Juan Fernández Archipelago, and Sala & Gómez Island; see Yañez-Arancibia, 1975; Randall & Cea-Egaña, 1984; Sepúlveda, 1987). We also excluded from the present study those species that have only been registered in Chilean Antarctic Territorial waters (Pequeño 1989), as well as warm water fishes associated with El Niño events off the coast of northern Chile (Kong et al. 1985).

We divided the Chilean coast into 2° latitudinal sections from 18 to 56° S, determining the presence or absence of each fish taxa at the species, genus and family levels within each segment of coastline as reported in the literature. Discontinuous distributions of any species, genus or family were assumed to be owing to lack of published ichthyiological records in the areas where these were apparently absent, and a continuous distribution was assumed for the analysis.

Biogeographic analyses

We determined latitudinal trends in the number of species, genera and families of teleost and chondrichthyan fishes as well as in the total number of fish species along the Chilean coast. The latitudinal distribution range of each fish species, genus and family was represented using distribution maps. These maps allowed us to identify possible biogeographic groups of taxa based on shared latitudinal distribution patterns along the Chilean coast. The number of taxa in these groups was quantified in order to determine their relative contribution to the total number of fish taxa. The groups recognised were: northerly distributed taxa, with distribution ranges from 18 down to as far south as 40° S; widespread taxa with distribution ranges along the entire Chilean coastline; southerly distributed taxa ranging from 56 °S northwards up to 38-40° S. Finally, we distinguished narrowly distributed taxa, located anywhere along the Chilean coastline, but whose distribution range within the Chilean coast did not exceed 10°.

The degree of similarity in fish taxa present between pairs of 2° latitudinal sections along the coast of Chile was calculated using Jaccard's coefficient of similarity based on presence/absence of fish taxa. To determine the existence of biogeographic regions, we carried out a cluster analysis on these pairwise Jaccard similarity values. The algorithm used was an unweighted pair-group method using arithmetic averages, (UPGMA) (Krebs 1999). We then applied bootstrapping techniques to objectively determine the level of taxonomic similarity of individual coastal segments at which biogeographic regions could be recognised. For this, we reshuffled the original presence/absence data 1000 times, obtaining pseudo values of similarity, which were then pooled to construct a frequency distribution histogram. We compared our observed similarity values with the generated frequency distribution, and considered those values that exceeded the 95th percentile as corresponding to greater similarity in taxonomic composition than that expected by chance alone (Manly 1991). Existence of biogeographic regions was also determined through nonmetric multidimensional scaling based on Jaccard similarity matrices, where similar sections are clustered by an ordination technique (Manly 1991, Clarke and Ainsworth 1993). Both these analyses were done for teleosts and chondrichthyans at the species, genus and family levels.

RESULTS

Latitudinal trends in number of fish taxa

We registered a total of 162 fish species, in 114 genera and 66 families in Chilean littoral waters. The number of fish species remains fairly constant between the northern Chilean coast (18° S) and the northern parts of southern Chile (approx. 38-40° S), with a mean of 104 ± 3 species (mean ± SD; range 98-109 species) (Fig. 1). Maximum species richness occurs between 32 and 34° S (109 species), corresponding to ca. Valparaíso. South of 40° S, we observed a sharp drop in the total number of species (74 ± 7, mean ± SD.; range 66-82 species), increasing only slightly between 54 and 56° S. A similar pattern is found when only teleost fishes are considered (Fig. 1). On the other hand, chondrichthyan species richness is substantially lower throughout the Chilean coast, averaging 21 ± 1 and 14 ± 2 north and south of 40°S, respectively (mean ± SD, ranges: 20-22 and 11-17 species), but also decreasing from 40° S southward (Fig. 1). When we considered higher taxonomic categories (genus and family), a similar pattern was observed in the number of taxa, with a decrease from 40° S southward, both in teleosts and chondrichthyans (Fig. 2a and b).

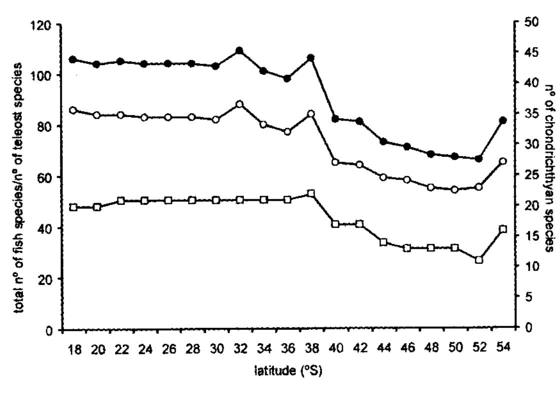

Fig. 1. Total number of fish species, and number of teleost and chondrichthyan species inhabiting littoral marine waters along the coast of Chile.

Patrones latitudinales en el número total de especies de peces, y número de especies de teleosteos y condrictios que habitan aguas litorales marinas en la costa de Chile.

Biogeographic patterns

Four groups with different biogeographic affinities could be recognized according to the distribution ranges of Chilean littoral teleost fishes (n = 133), while only three could be detected amongst chondrichthyans (n = 28) (Fig. 3). The first one includes species with a northern distribution range occurring in Chilean waters from 18° S (northern limit of the Chilean coast) to latitudes ranging between 20 and 40° S, representing 38 and 18% of total number of teleost (n = 50) and chondrichthyan (n = 5) fish species, respectively (Fig. 3). Fish species in this group include the teleosts *Aplodactylus punctatus*, *Scartichthys viridis*, *Labrisomus philippii*, *Kyphosus analogus*, *Cheilodactylus variegatus* and *Hemilutjanus macrophtalmos* and chondrichthyans such as *Triakis maculata,* and *Sphyrna zygaena* among others.

The second group is composed of widespread species found along the entire Chilean coast (18-56°). This group represents 23 and 32 % of the total number of teleost (n = 31) and chondrichthyan (n = 9) species, respectively (Fig. 3). Examples of species found in this group are the teleosts *Paralichthys microps*, *Sebastes capensis*, *Gobiesox marmoratus*, *Sicyases sanguineus*, *Genypterus chilensis* and *Pinguipes chilensis*, and the chondrichthyans *Schroederichthys chilensis, Callorhynchus callorhynchus* and *Mustelus whitneyi*.

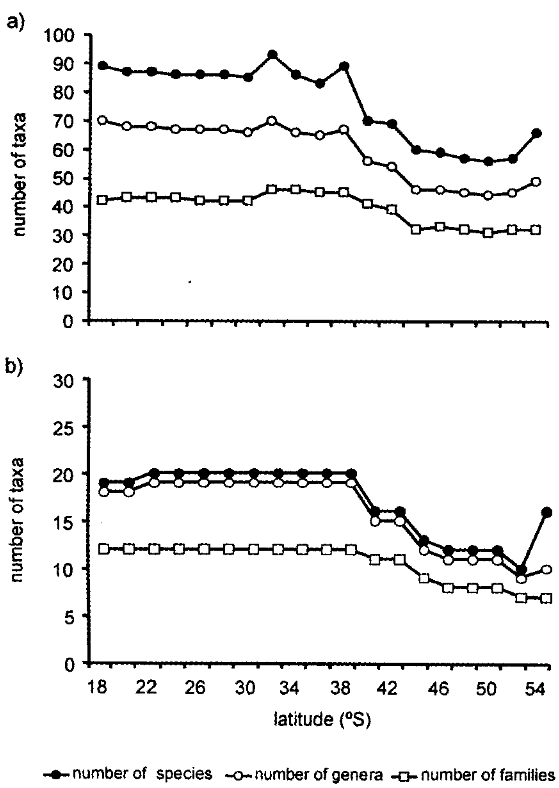

Fig. 2. Total number of a) teleost and b) chondrichthyan fishes, at the level of species, genus and family, found in littoral marine waters along the Chilean coast.

Patrones latitudinales en el número de a) teleosteos y b) condrictios al nivel de especie, género y familia en aguas litorales marinas en la costa de Chile.

Species that in Chilean littoral waters have narrow distribution ranges form a third group consisting of 17% of the total number of teleosts (n = 22). Distributional ranges of the representatives of this group do not exceed 10° in latitude (Fig. 3). Examples of species found in this group are the teleosts *Auchenionchus variolosus*, *Bovichthys chilensis*, *Calliclinus nudiventris*, *Myxodes ornatus*, *Scartichthys crapulatus*, *Kyphosus analogus* and *Nexilosus latifrons*.

We defined a fourth group formed by species with a southerly distribution range, consisting of fishes occurring from 56° S northwards to not further north than 38-40° S (e.g., the teleosts *Harpagifer bispinnis*, *Careproctus crassus*, *Cottoperca gobio*, *Patagonotothen sima* and *P. wiltoni*, and chondrichthyans *Bathyraja griseocauda* and *B. magellanica*), This group accounts for 26% (n = 34) and 21% (n = 6) of the total number of teleosts and chondrichthyans, respectively. All these chondrichthyan species also have a restricted distribution range along the southern Chilean coast (Fig. 3).

Analysis at the genus and family levels yielded the same four biogeographic groups among teleost fishes (Fig. 4). Northerly-distributed taxa include the genera *Anisotremus*, *Kyphosus* and *Labrisomus*, as well as the families Aplodactylidae, Kyphosidae, Pomacentridae, amongst others, representing 35 and 19% of the total number of teleost genera (n = 32) and families (n = 10), respectively (Fig. 4). Taxa with broad distribution ranges include the genera *Aphos*, *Thyrsites*, and *Gobiesox*, and the families Sciaenidae, Gobiesocidae, Pinguipedidae and Scorpaenidae among others. Genera and families in this group account for 31 and 65% of the total number of teleost genera (n = 29) and families (n = 35), respectively (Fig. 4).

Narrowly distributed taxa of teleost fishes include the genera *Nexilosus*, *Bovichthys* and *Ilucoaetes* and the families Gadidae and Harpagiferidae, accounting for 15 (N=14) and 6% (N=3) of the total respectively. Southerly distributed taxa include *Careproctus*, *Heterogobius* and *Patagonotothen*, and the families Channichthidae, Liparidae and Zoarcidae. These taxa account for

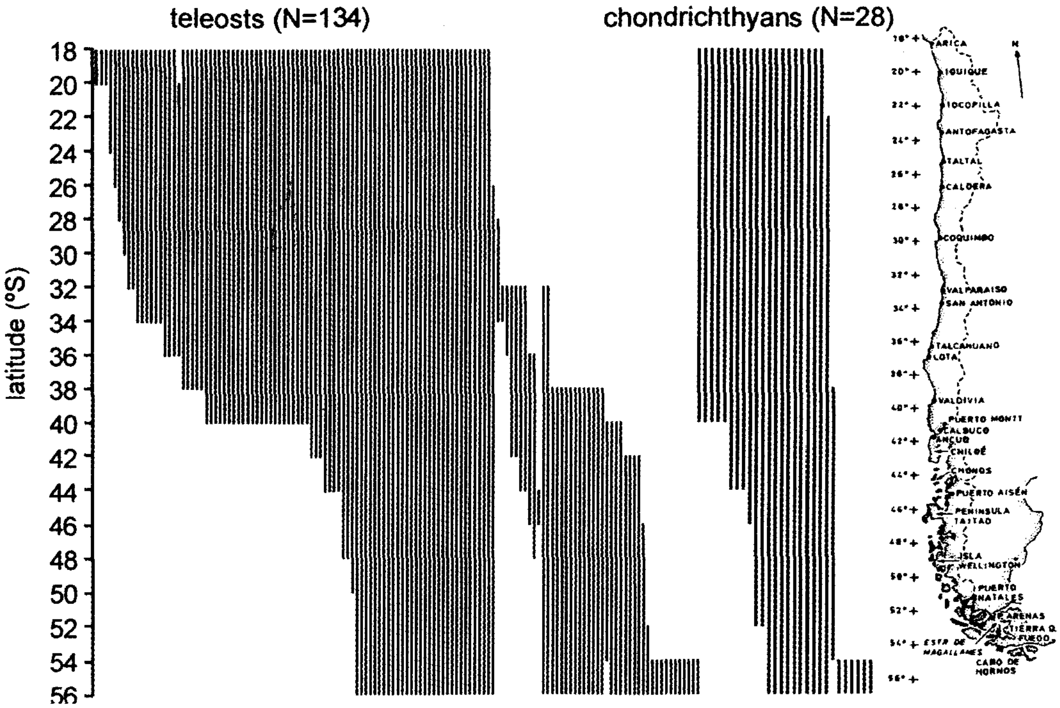

Fig. 3. Distribution ranges of littoral teleost and chondrichthyan species found along the Chilean coast. Each bar represents the distribution of a single species.

Rangos de distribución de especies litorales de teleosteos y condrictios a lo largo de la costa de Chile. Cada barra representa la distribución de una especie.

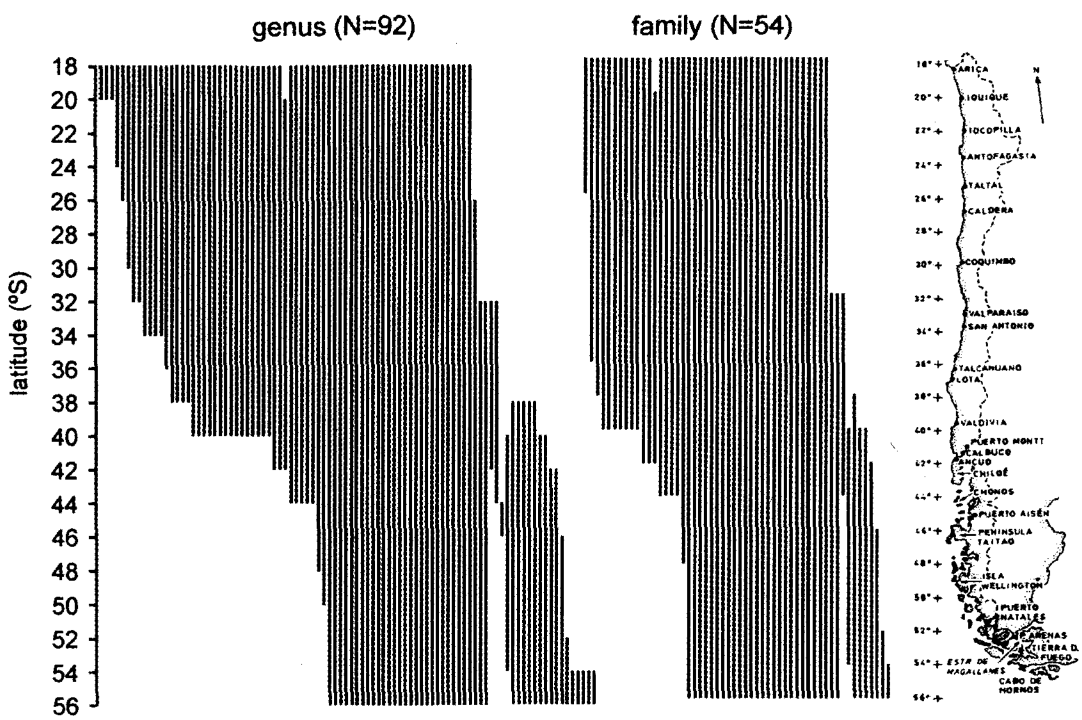

Fig. 4. Distribution ranges of teleost genera and families represented in littoral waters along the Chilean coast. Each bar represents the distribution of a single teleost genus or family.

Rangos de distribución de géneros y familias de teleosteos representados en aguas litorales a lo largo de la costa de Chile. Cada barra representa la distribución de un género o familia.

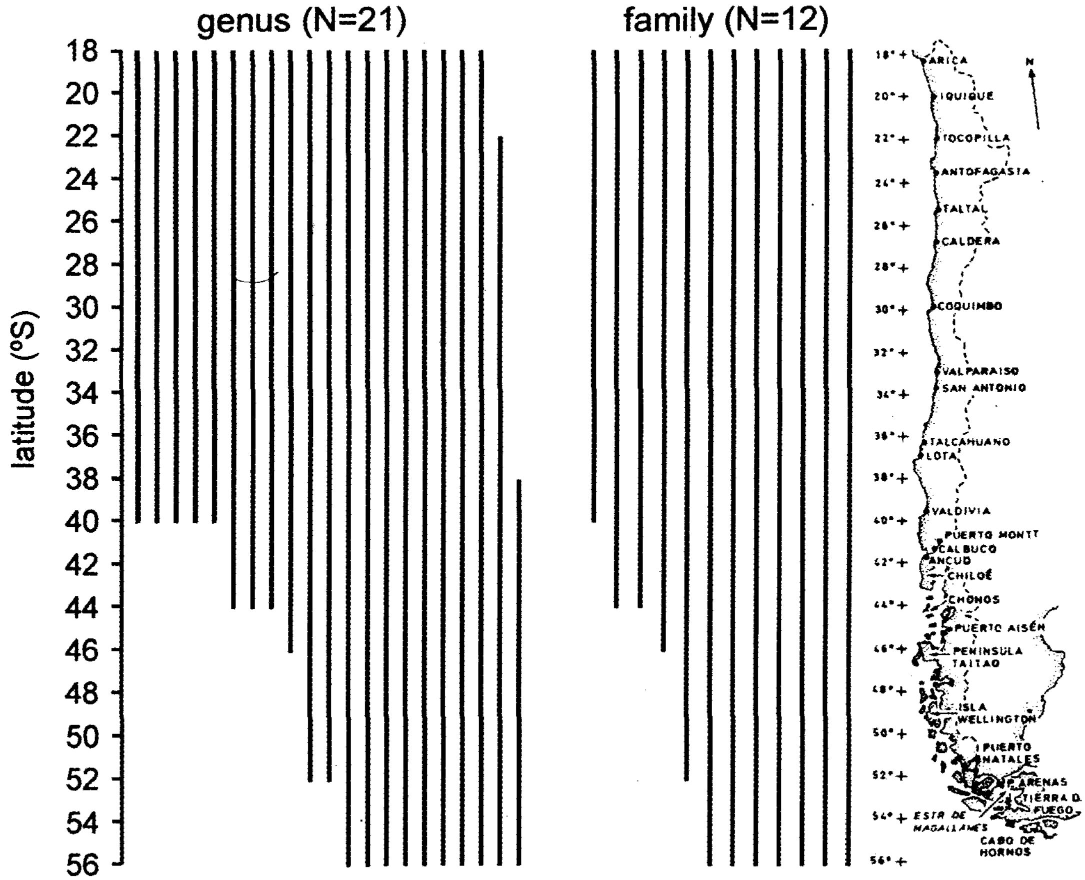

Fig. 5. Distribution ranges of chondrichthyan genera and families represented in littoral waters along the Chilean coast. Each bar represents the distribution of a single chondrichthyan genus or family.

Rangos de distribución de géneros y familias de condrictios representados en aguas litorales a lo largo de la costa de Chile. Cada barra representa la distribución de un género o familia.

17 (n = 16) and 16% (n = 9) of the total number of teleost genera and families, respectively (Fig. 4).

At the genus and family levels, chondrichthyans could be separated into three and two groups, respectively. The first group comprising northerly distributed taxa includes five genera (24%) (*Heptranchias, Centroscyllium, Sphyrna, Triakis* and *Carcharodon*) and one family (8%) (Sphyrnidae) which ranged from 18° S down to not further than 40° S (Fig. 5). The second group, comprised of widespread taxa found along the entire Chilean coastline, includes the genera *Galeorhinus*, *Lamna* and *Schroederichthys* and the families Carcharhinidae, Lamnidae and Rajidae, accounting for 48 (n = 10) and 58% (n = 7) of the total number of chondrichthyan genera and families, respectively (Fig. 5). There were no narrowly distributed chondrichthyan genera and families. Only one chondrichthyan genus, *Bathyraja*, had a southerly distribution, representing 5% of the total number of chondrichthyan genera.

Levels of endemism

Of the total number of littoral teleost fishes occurring in Chilean waters, 18 species (13%) are endemic to the Chilean coast (see Appendix 1), while 59 species (44%) are endemic to the Southeastern Pacific Ocean (i.e., restricted to littoral waters between 0 and 56° S). On the other hand, of the total of 28 chondrichthyan species found along the Chilean littoral waters, only 2 of them (*Triakis maculata* and *Schroederichthys chilensis*; 7%) are endemic to the Southeastern Pacific Ocean, with none being endemic to Chilean waters.

Biogeographic regions

Application of an UPGMA cluster analysis on data on the distribution of teleost fishes at the species, genus and family levels indicated two statistically significant latitudinal biogeographic regions along the Chilean coast: one ranging from

18 to 40° S, and the other from 40 to 56° S (Fig. 6a, c, and e). Ordination of the data through nMDS corroborated the existence of these two biogeographic groups (Figs. 6 b, d, and f). However, within the northern region it is possible to distinguish two subunits at the level of species, genus and family: one ranging from 18 to 32° S, and another from 32 to 40°S (Figs. 6a, c, and e). Similarly, within the southern region there are two groups, one from 40 to 44°S and another from 44 to 56°S (Figs. 6a, c, and e). The northernmost and southernmost groups of latitudes reflect the presence of subtropical and subantarctic species, while the latitudes from 32 to 40° S show a mixture of species from the north and south (Figs 3 and 6a).

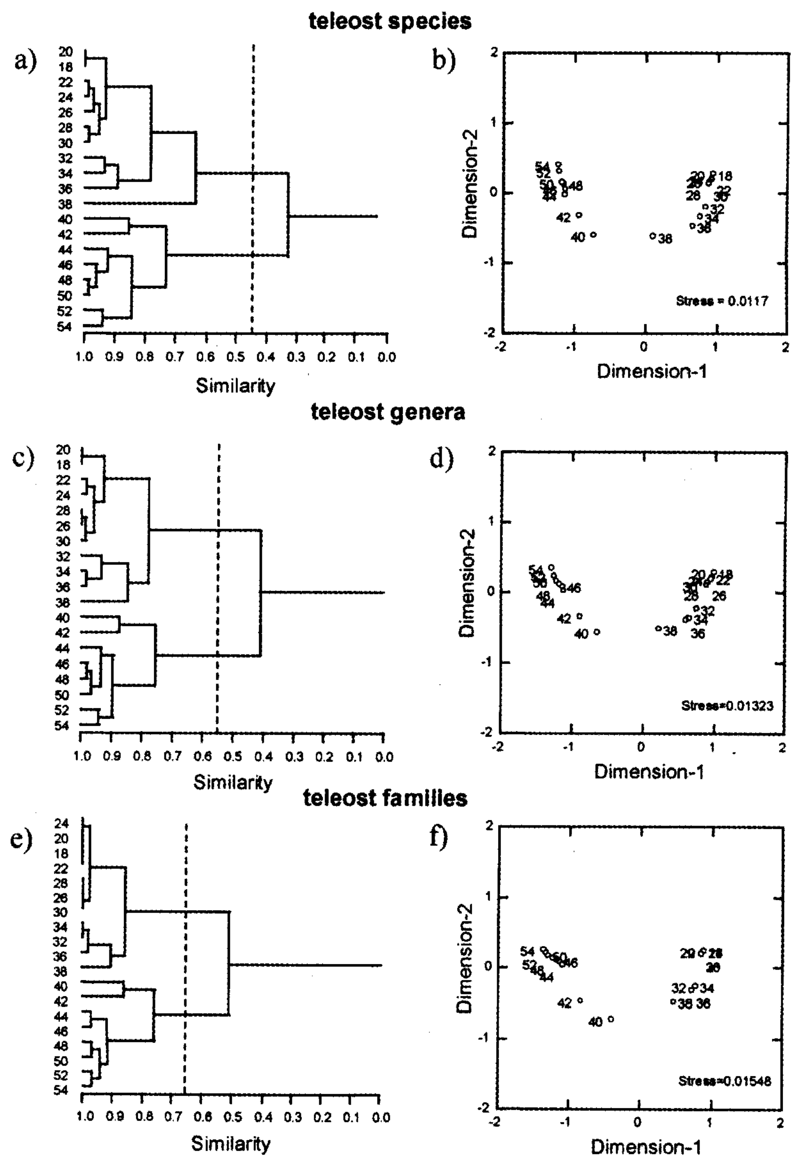

Fig. 6. Latitudinal similarity phenograms and nMDS ordinations based on the presence or absence of teleost fishes at the level of species (a and b), genus (c and d) and family (e and f). Dotted lines indicate the level of similarity between pairs of latitudinal sections at which significant biogeographic regions could be recognized in the phenograms after application of a bootstrapping procedure. Insets indicate Kruskal stress values for nMDS configuration.

Dendrogramas y ordenaciones de nMDS basadas en la presencia o ausencia de teleosteos al nivel de especie (a y b), género (c y d) y familia (e y f). Las líneas punteadas indican el nivel de similitud entre pares de secciones latitudinales al que pudieron distinguirse regiones biogeográficas significativas en los dendrogramas luego de aplicar un procedimiento de aleatorización. Valores de stress de Kruskal se indican en el reçuadro inserto en los gráficos de ordenación de nMDS.

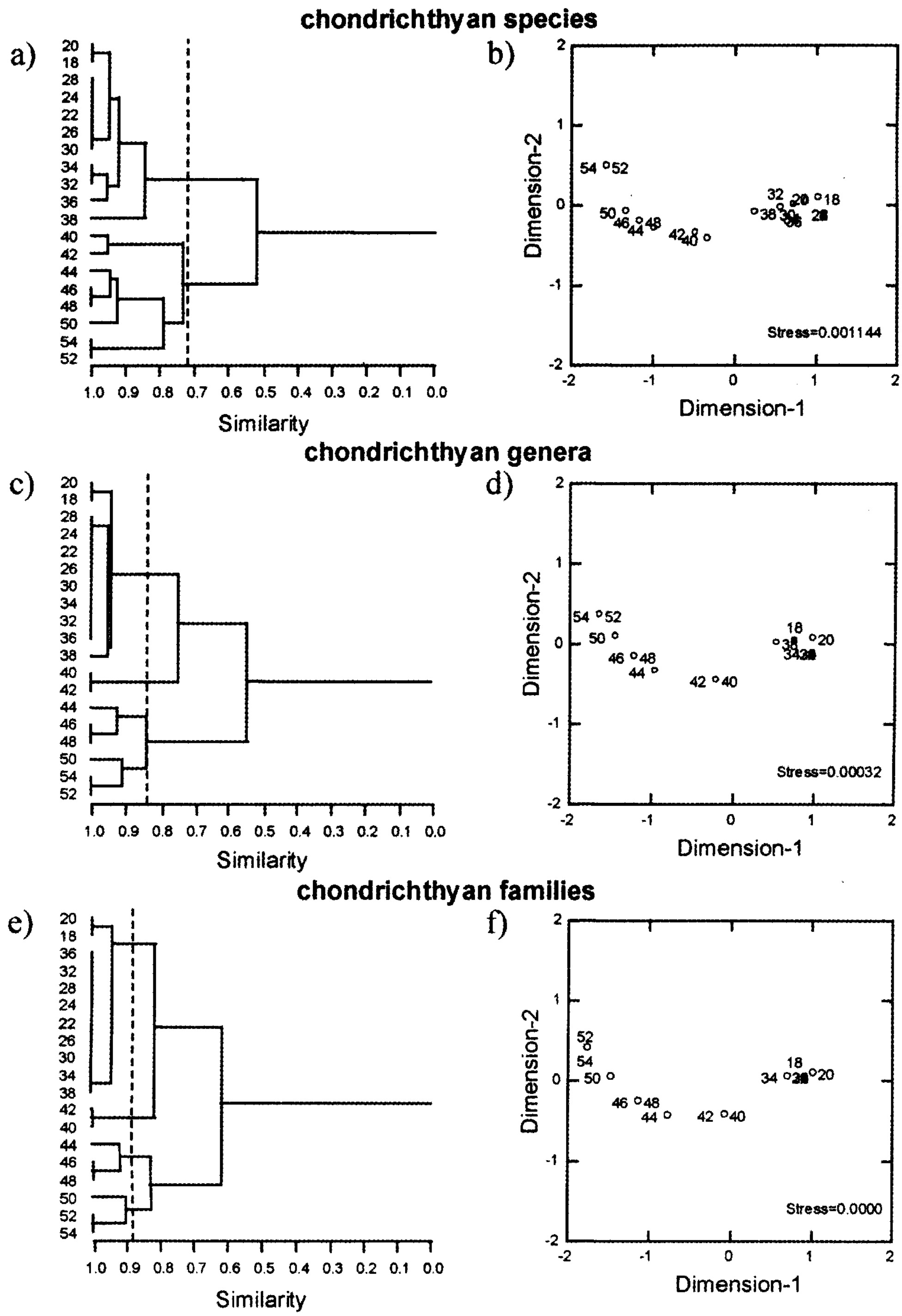

Fig. 7. Latitudinal similarity phenograms and nMDS ordinations based on the presence or absence of chondrichthyan fishes at the level of species (a and b), genus (c and d) and family (e and f). Dotted lines indicate the level of similarity between pairs of latitudinal sections at which significant biogeographic regions could be recognized in the phenograms after application of a bootstrapping procedure. Insets indicate Kruskal stress values for nMDSconfiguration.

Dendrogramas y ordenaciones de nMDS basadas en la presencia o ausencia de condrictios al nivel de especie (a y b), género (c y d) y familia (e y f). Las líneas punteadas indican el nivel de similitud entre pares de secciones latitudinales al que pudieron distinguirse regiones biogeográficas significativas en los dendrogramas luego de aplicar un procedimiento de aleatorización. Valores de stress de Kruskal se indican en el recuadro inserto en los gráficos de ordenación de nMDS.

Analysis of distribution data of chondrichthyan fishes at the species level revealed the existence of two biogeographic regions: 1) a northern region ranging from 18 to 40° S, and 2) a southern region from 40 to 56° S (Fig.7a), although application of the ordination techniques also showed the existence of a narrow region from 54 to 56° S (Fig. 7b). On the other hand, at the genus level, four zones were identified, the first one ranging from 18 to 40° S, and three southern regions: 40 to 44° S, 44 to 50° S and 50 to 56° S. (Fig.7c and d). At the family level, four regions were also recognized: a northern region ranging from 18 to 40° S, and three southern regions: 40 to 44° S, 44 to 50° S and 50 to 56° S (Fig.7e and f).

Biogeographic affinities

Having established two statistically significant latitudinal biogeographic regions along the Chilean coast: a northern warm-temperate region (18 - 40° S) and a southern cold-temperate region (40 - 56° S), we analyzed the biogeographic affinities of those teleost species occurring within the northern warm-temperate region whose southern distribution ends at 40° S and of those occurring within the southern cold-temperate region whose northern distribution limit lies at 40° S. Our results show that of the 50 teleost species with a northerly distribution range (from 18 to 40° S), 8 (16%) are exclusively found in Chilean waters (i.e., up to 18° S), 31 (62%) extend their distribution ranges further north (between 18 and 0° S), and 12 (24%) occur further north than 0°, thus prolonging their distribution range to the Northeastern Pacific. The later two groups include fishes belonging to Blenniidae, Gobiesocidae, Kyphosidae, Pomacentridae, Serranidae, among others. Of the total of 34 teleost species with a southerly distribution (from 40 to 56° S), 29 of them (85%) are also found in Argentinian waters, while only 5 species (15%) are endemic to this southern cold temperate region. The former group includes representatives of Zoarcidae, Nototheniidae, Harpagiferidae and Liparidae.

DISCUSSION

Latitudinal patterns in composition and number of species

Diversity of littoral fish species along the Chilean coast presents three clear cut latitudinal patterns: a fairly constant number of species from 18 to approximately 40° S, a sharp drop in species richness south of this latitude, and a marked increase in number of species in the southernmost part of Chile between 54 and 56°. The first break in fish diversity roughly coincides with the southernmost portion of continental Chile, where a major change in topography, climate and hydrography occurs southward. The second break in diversity is determined by the appearance of endemic subantarctic teleosts and chondrichthyans such as Zoarcidae and Rajidae, respectively.

A similar pattern has been observed both in terms of the total number, as well as littoral and shallow water benthic invertebrate species (Brattström & Johanssen 1983), except for the rise in species diversity at 54º S. In contrast, the total number of species of sublittoral benthic invertebrates and macroalgae increases steadily towards the south of Chile (Santelices 1980, Brattström & Johanssen 1983, Lancelloti & Vásquez 2000). In macroalgae, this pattern results from a southward increase in the contribution of species of subantarctic origin (Santelices, 1980). The drop in diversity southward of 42º S has often been attributed to the lack of adequate sampling in this area (e.g., Brattström & Johanssen 1983, Lancelloti & Vásquez 2000, Camus, in press). However, the intensive ichthyological research conducted in the southernmost regions of Chile clearly demonstrates that this is not the case for littoral fishes (e.g., Moreno & Jara 1984, Lloris & Rucabado 1991, Pequeño & Lamilla 1995, Pequeño et al. 1995, Pequeño 1999).

On the other hand, our results do not concur with those reported by Sielfeld & Vargas (1999) regarding the number of ichthyogeographical sectors occurring between 42 and 57º S, which approximately correspond to our south cold temperate region (40-56º S). Within this biogeographic region we identify two teleost subgroups: one from 40 to 44º S and another from 44 to 56º S at all taxonomic levels analysed. In contrast, these authors recognised three sectors: a "northern sector" (42 to 46-47º S), an "intermediate sector" (47-48 to 51º S), and a "southern sector" (52 to 56º S). However, their results can be challenged because of their subjectivity in recognising fish associations (i.e., 30% similarity). In another recent study, Pequeño (1999), who analysed the littoral fishes occurring in the Chilean fjords between 47 and 52º S, suggests that the southern zone of South America should be recognised as one ichthyogeographic unit that probably extends towards the Atlantic including the Falkland Islands.

Levels of endemism

Few teleost species occur exclusively in Chilean littoral waters (18 species representing 13% of the total number of teleosts), while no chondrichthyan species are endemic to Chile at this level. In contrast, 44% of the 133 teleost species occurring along the Chilean coast are endemic to the Southeastern Pacific coast (i.e., 59 species). Thus, at this spatial scale, the level of endemism of teleosts occurring in Chilean littoral waters is very high. However, only 7% of chondrichthyans (represented by 2 shark species) are endemic to the Southeastern Pacific, a result that is not surprising given that most sharks are widely distributed throughout the world (Compagno 1984a, b).

Biogeographic Regions

Our analysis of latitudinal distribution patterns of Chilean marine teleost littoral fishes suggested the existence of two main biogeographic regions along the coast of Chile, 1) a warm-temperate region stretching from 18 to 40° S, and 2) a cold-temperate region ranging from 40 to 56° S. These two regions were identified irrespective of the taxonomic level considered, (i.e., species, genus or family). Similarly, the analysis of distribution patterns of chondrichthyan fishes indicated the same biogeographic regions. However, a subdivision of the cold-temperate region into different sub-regions was suggested, depending on the taxonomic level studied. These two main biogeographic regions are reflections of marked latitudinal differences in composition and number of fish taxa as shown in the distribution maps and cluster analyses.

The biogeographic regions identified in this study for Chilean marine littoral fishes correspond to previously recognized provinces or faunistic components based on distribution patterns of benthic invertebrates (Briggs 1974, Brattström & Johanssen 1983), but do not concur with those described by Santelices (1980, 1989) for marine macroalgae. Santelices (1980) distinguished a very broad phytogeographic region stretching from northern Peru (5° S) to southern Chile (53° S), and a narrow region (54–55° S) consisting of the area of the Magellan Strait and Cape Horn.

Confirming earlier results, Brattström & Johanssen (1983) recognized two main regions, a northern warm-temperate region and a southern cold-temperate region, meeting at 42° S, and coinciding with the sharp change in topography from Chiloé Island southwards (see Brattström & Johanssen 1983 and references therein). However, recent work on benthic macroinvertebrates has challenged this view, identifying a loosely defined transitional area ranging from 30-33° S to 35-48° S (Lancellotti & Vásquez 1999), thus rejecting the hypothesis of the existence of a major break around 42° S. However, we believe that their results are an artifact of the low level of resolution used, especially in the southern part of Chile (e.g., their Magellan Strait zone).

Biogeographic affinities of littoral fishes

Based on the analysis of latitudinal trends in the number of fish taxa, distribution maps, and the results of the cluster analysis and biogeographic affinities of the different groups conforming this fish fauna, we propose that the littoral fish fauna is clearly composed of two groups of different origins: a warm-temperate group of fish species of tropical and sub-tropical origin, belonging to the Peruvian province, and a cold-temperate group of species of subantarctic origin, belonging to the Magellanic province. The coastal fish fauna occurring from 30 to 42° S (central Chile) is a mixture of subantarctic, subtropical, pan-oceanic and a few endemic fish species, as correctly suggested by Mead (1970). In this sense, this is a transitional zone where both faunas occur.

In this transitional zone, the relative number of species in each group changes along the coast of Chile, with the greatest changes occurring between 32 and 44° S. In this zone there is a gradual replacement of northern teleost species by endemic species restricted to the south-central coast and southern species. This replacement results in the biogeographic differences that give rise to the regions discussed above. Among chondrichthyans, the biogeographic differences are due to the steady drop in the number of northern species southwards of 40° S.

The causes of latitudinal gradients in species diversity have been debated over the last years, with criticism being directed to circular hypotheses, or lack of consistent correlations between diversity and potential causal factors such as latitudinal ranges, area and productivity among others (see Rhode 1992, Rhode et al. 1993). Tests of causal hypotheses of marine latitudinal diversity gradients for marine prosobranch gastropods have found that western Atlantic and eastern Pacific Oceans show similar patterns in diversity, and that these patterns cannot be explained by latitudinal differences in species range-length (Rappoport´s rule), species-area effects or recent geologic histories (Roy et al. 1998). In that study, diversity was found to correlate significantly with solar energy input, represented by average sea surface temperature, which was hypothesized to be related to productivity. The implication of this is that diversity would be an evolutionary outcome of trophodynamic processes inherent in ecosystems, and not just a byproduct of physical geographies. On the other hand, Moreno et al. (1979) proposed an ecological hypothesis to explain the latitudinal changes in the diversity of littoral fishes. They observed greater community diversity in the central coast and proposed that this latitudinal variation was due to a more complex environmental matrix consisting of kelp forests at lower latitudes. However, their study was based on the analysis of only two localities, one in central Chile and the other further south.

We believe, however, that the explanation to the latitudinal pattern of coastal Chilean fish diversity found in this study, as well as why there are so few fish species here in comparison to tropical regions, together with the level of endemism observed along the Chilean coast, lies in the analysis of processes related to dispersal and evolutionary history of the different components that conform this coastal fish fauna. Most of the littoral Chilean fish fauna is composed of modern Perciform species (c.a. 65%). Perciforms originated in the Indo-Pacific, dispersing along the tropics to the eastern Pacific, and later extending polewards to cold waters of both hemispheres (Myers 1941). Because of their tropical origin, it has been strongly suggested that there has not been sufficient time for Perciforms to adapt to the cold environment found at lower latitudes (Mead 1970). This interplay of dispersal and evolutionary origin may well explain the observed decline in fish diversity southwards, and why the Chilean coastal fauna is so depauperate. In fact, Mead (1970) has pointed out that the cold temperate Chilean coast is the geographical endpoint of this radiation, and it is the place most distant from several sources of fish fauna. Another fact that clearly supports this explanation deals with the phenomenon of fish herbivory along Chilean cold temperate waters. It has been suggested that fish herbivores, which are advanced percoid forms, and a very diverse group in the tropics (Sale 1991) have not yet radiated into cold-temperate waters (Mead 1970). Recent studies suggest this is the case, since the number of herbivore fish species sharply declines towards the poles (Horn 1989, Horn & Ojeda 1999). Along the Chilean coast, this number declines from six in the northern Chilean coast to three in the central Chilean coast to none at all south of Concepción (37° S). (Miranda 1967, Ojeda et al. 1990[1]).

In conclusion, this study shows a steady decline in littoral fish diversity southward of 40° S. Analysis of distribution ranges of fishes indicates two biogeographic regions along the Chilean coast, with a break at 40° S, supporting previously recognized biogeographic provinces or faunistic components. These regions reflect the mixed origin of Chilean littoral fishes. While the percentage of fishes endemic to the Chilean coast is not high (18%), a high percentage of teleost species inhabiting Chilean littoral waters are endemic to the Southeastern Pacific (44%). Dispersal and evolutionary history rather that other factors seem to explain the observed patterns of distribution of this particular fish fauna. This study represents a first step towards understanding the biogeography of Southeastern Pacific marine fishes.

ACKNOWLEDGMENTS

We dedicate this paper to the memory of Dr. Patricio Sánchez (1928-1999), a founder of modern marine biology in Chile, who stimulated the study of zoology, biogeography, and ecology by many of the new generations of marine scientists in Chile. This study was mainly funded by FONDAP O & BM N° 3 and FONDECYT 1990154 grants to F.P.O. F.A.L. is currently funded by a DIPUC doctoral fellowship and A.A.M. acknowledges a CONICYT doctoral fellowship.

LITERATURE CITED

ANGEL A & FP OJEDA (in press) Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. Marine Ecology Progress Series.

BERRIOS V & ME VARGAS (2000) Estructura del ensamble de peces intermareales de la costa rocosa del norte de Chile. Revista de Biología Marina y Oceanografía (Chile) 35: 73-81.

BALECH E (1954) División zoogeográfica del litoral sudamericano. Revista de Biología Marina (Valparaíso) 4: 184-195.

BRATTSTRÖM H & A JOHANSSEN (1983) Ecological and regional zoogeography of the marine benthic fauna of Chile. Report no. 49 of the Lund University Expedition 1948-1949. Sarsia 68:289-339.

BRATTSTRÖM H (1990) Intertidal ecology of the northernmost part of the Chilean archipelago. Report no. 50 of the Lund University Expedition 1948-1949. Sarsia 75: 107-160.

BRIGGS JC (1974) Marine zoogeography. McGraw-Hill Co., New York. 475 pp.

---

[1] OJEDA FP, I KONG, AG BENAVIDES, LS FUENTES & C CACERES (1990) Peces herbívoros de la costa norte-centro de Chile: desentrañando mitos y realidades. Resúmenes X Jornadas Ciencias del Mar, Santiago, Chile. 73 pp.

CACERES CW, AG BENAVIDES & FP OJEDA (1993) Ecología trófica del pez herbívoro *Aplodactylus punctatus* (Pisces: Aplodactylidae) en la costa centro-norte de Chile. Revista Chilena de Historia Natural 66: 185-194.

CAMUS P (in press) Biogeografía marina de Chile continental. Revista Chilena de Historia Natural.

CERVIGON F, G PEQUEÑO & CA MORENO (1979) Descripción de *Calliclinus nudiventris* nov. sp y notas adicionales sobre *C. geniguttatus*. (Pisces: Clinidae) de Chile. Medio Ambiente 4: 40-50.

CHIRICHIGNO N (1974) Clave para identificar los peces marinos del Perú. Instituto del Mar del Perú. Informe N° 44. Callao. 387 pp.

CHIRICHIGNO N (1982) Catálogo de especies marinas de interés económico actual y potencial para america latina. Parte 2. Pacífico Centro y Sur Oriental. INFOPESCA, FAO. PNUD, SIC 18212. ROMA. 588 pp.

CLARKE KR & M AINSWORTH (1993) A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92: 205-219.

COLLETTE B & C NAUEN (1983) FAO Species Catalogue. Vol. 2. Scombrids of the World. Fao Fisheries Synopsis N° 125, Vol. 2, 137 pp.

COMPAGNO LJV (1984a) FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 1. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis N° 125, Vol. 4, Part 1, 249 pp.

COMPAGNO LJV (1984b) FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 2. Carcharhiniformes. FAO Fisheries Synopsis N° 125, Vol. 4, Part 2 pp.

DAHL E (1960) The cold temperate zone in Chilean seas. Proceedings of the Royal Society of London, series B 152: 631-633.

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

FARIÑA JM & FP OJEDA (1993) Abundance, activity, and trophic patterns of the redspotted catshark, *Schroederichthys chilensis*, on the Pacific temperate coast of Chile. Copeia 1993: 545-549.

ESCHMEYER WN, ed (1998) Catalog of Fishes. California Academy of Sciences, San Francisco. 2095 pp.

FOWLER HW (1951) Analysis of the fishes of Chile. Revista de Historia Natural (1947-1949), 51-53: 263-326.

HERNANDEZ C, R GALLEGUILLOS & C OYARZUN (2000) Diferenciación genética de *Merluccius gayi gayi* y *Merluccius gayi peruanus* (Pisces, Merluciidae) y antecedentes paleogeográficos de su área de distribución. Revista Chilena de Historia Natural 73: 23-29.

HORN MH (1989) Biology of marine herbivorous fishes. Oceanography and Marine Biology Annual Review 27: 167-272.

HORN MH & FP OJEDA (1999) Herbivory. In: Horn MH, KLM Martin & MA Chotkowski (eds) Intertidal Fishes, Life in two worlds: 197-222. Academic Press, San Diego.

INZUNZA AJ & G PEQUEÑO (1988) Aspectos trofico-adaptativos y reafirmación de dos especies en el género *Calliclinus* Gill 1860 (Osteichthyes, Clinidae). Boletín de la Sociedad de Biología, Concepción (Chile) 59: 69-93.

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

KONG I, J TOMICIC & J ZEGERS (1985) Ictiofauna asociada al fenómeno "El Niño" 1982-1983 en la zona norte de Chile. Investigaciones Pesqueras (Chile) 32: 215-224.

KREBS CJ (1999) Ecological Methodology. Second Edition. Addison-Welsey Educational Publishers, Menlo Park. 620 pp.

LANCELLOTTI DA & JA VASQUEZ (1999) Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. Journal of Biogeography 26: 1001-1006.

LANCELLOTTI DA & JA VASQUEZ (2000) Zoogeografía de macroinvertebrados bentónicos de la costa de Chile: contribución para la conservación marina. Revista Chilena de Historia Natural 73: 99-129.

LLORIS D & J RUCABADO (1991) Ictiofauna del Canal Beagle (Tierra de Fuego), aspectos ecológicos y análisis biogeográfico. Publicaciones especiales Instituto Español de Oceanografía n° 8, Ministerio de Agricultura, Pesca y Alimentación, Madrid. 182 pp.

MANN G (1954) La vida de los peces en aguas chilenas. Universidad de Chile; Ministerio de Agricultura, Chile. 342 pp.

MANLY BFJ (1991) Multivariate Statistical Methods. A Primer. 1st Edition Chapman & Hall. London. 159 pp.

MEAD GW (1970) A History of South Pacific Fishes. In: Scientific Exploration of the South Pacific. National Academy of Sciences. Standard Book N° 309-017556: 236-251. National Academy of Sciences, Washington D.C.

MENNI RC, RA RINGUELET & RH ARAMBURU (1984) Peces marinos de la Argentina y Uruguay. Editorial Hemisferio Sur, Buenos Aires. 359 pp.

MIRANDA O (1967) Calendario Ictiológico de San Antonio. 1. Enumeración de la comunidad de Peces, mediante la red de tres telas, en un hábitat rocoso. Biología Pesquera (Chile) 2: 3-49.

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

MORENO CA, WE DUARTE & JH ZAMORANO (1979) Variación latitudinal del número de especies de peces en el sublitoral rocoso: una explicación ecológica. Archivos de Biología y Medicina Experimental 12: (Chile) 169-178.

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 AA & FP OJEDA (1998) Guild structure of carnivorous intertidal fishes of the Chilean coast: implications of ontogenetic dietary shifts. Oecologia 114: 563-573.

MYERS GS (1941) The fish fauna of the Pacific Ocean, with special reference to zoogeographical regions and distribution as they affect the international aspects of the fisheries. Proceedings Sixth Pacific Congress 3: 201-210.

NAVARRO J & G PEQUEÑO (1979) Peces litorales de los archipiélagos de Chiloé y Los Chonos, Chile. Revista de Biología Marina (Valparaiso). Departamento de Oceanología, Universidad de Chile 16: 255 - 309.

NELSON JS (1994) Fishes of the world, 3nd Edition, Wiley Interscience, New York, 600 pp.

NUÑEZ L & JA VASQUEZ (1987) Observaciones tróficas y de distribución espacial de peces asociados a un bosque submareal de *Lessonia trabeculata*. Estudios Oceanológicos 6: 79-85.

OJEDA FP (1983) Distribución latitudinal y batimétrica de la ictiofauna demersal del extremo austral de Chile. Revista Chilena de Historia Natural 56: 61-70.

OJEDA FP (1989) Nuevos antecedentes sobre *Gymnothorax modesta* (Kaup) 1860 (Osteichthyes; Muraenidae) y comentarios sobre las especies de murenas de la costa de Chile. Estudios Oceanológicos (Chile) 8: 61- 65.

OJEDA FP & S AVILES (1987) Peces oceánicos Chilenos. In: Castilla JC (ed) Islas Oceánicas Chilenas: conocimiento científico y necesidades de investigaciones: 247-270. Ediciones Universidad Católica de Chile, Santiago.

OJEDA FP & JM FARIÑA (1996) Temporal variations in the abundance, activity and trophic patterns of the rockfish, *Sebastes capensis* off the coast of the central Chilean coast. Revista Chilena de Historia Natural 69: 205-211.

OYARZUN F & G PEQUEÑO (1989) Sinopsis de Blenniidae de Chile (Osteichthyes; Perciformes). Gayana Zoología (Chile) 53: 3-40.

PEQUEÑO G (1977) El género *Galeorhinus* en Chile (Elasmobranchii: Triakidae). Revista de Biología Marina (Valparaíso) 16: 183-188.

PEQUEÑO G (1989) Peces de Chile. Lista sistemática revisada y comentada. Revista de Biología Marina, Valparaíso 24: 1-132.

PEQUEÑO G (1997) Fishes of Chile. Reviewed and annotated checklist: Addendum. Revista de Biologia Marina y Oceanografia (Chile) 32: 77-94.

PEQUEÑO G (1999) Peces del crucero CIMAR-FIORDO 2, a los canales patagónicos de Chile, con consideraciones ictiogeográficas. Ciencia y Tecnología del Mar (Chile) 22: 165-179.

PEQUEÑO G & J LAMILLA (1995). Peces intermareales de la costa de Llanquihue (Chile): composición taxonómica, abundancia relativa y gradiente de distribución longitudinal. Revista de Biología Marina (Valparaíso) 30: 7-27.

PEQUEÑO G, J LAMILLA, D LLORIS & J RUCABADO (1995) Comparación entre las ictiofaunas intermareales de los extremos austral y boreal de los canales Patagónicos. Revista de Biología Marina (Valparaíso) 30: 155-177.

QUIJADA PA & CW CACERES (in press) Patrones de abundancia, composición trófica y distribución espacial del ensamble de peces intermnareales de la zona centro-sur de Chile. Revista Chilena de Historia Natural. 73.

RANDALL JE & A CEA-EGAÑA (1984) Native names of Easter Island fishes, with comments on the origin of the Rapa-nui people. Occasional Papers of Berenice Pauahi Bishop Museum 25: 1-16.

RHODE K (1992) Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65: 514-527.

RHODE K, M HEAP & D HEAP (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. American Naturalist 142: 1-16.

ROY K, D JABLONSKI, JW VALENTINE & G ROSENBERG (1998) Marine latitudinal diversity gradients: Tests of causal hypothesis. Proceedings of the National Academy of Sciences, USA 95: 3699-3702.

SALE PF (1991) The ecology of fishes on coral reefs. Academic Press, San Diego. 754 pp.

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, Santiago. 399 pp.

SEBENS KP & RT PAINE (1979) Biogeography of anthozoans along the west coast of South America: habitat, disturbance, and prey availability. Proceedings International Symposium of Marine Biogeography and Evolution of the Southern Hemisphere 2: 219-237.

SEPULVEDA JI (1987) Peces de las Islas Oceánicas Chilenas. In: Castilla JC (ed) Islas Oceánicas Chilenas: conocimientos científicos y necesidades de investigaciones: 227-245. Ediciones Universidad Católica de Chile, Santiago.

SERNAP (1996) Anuario Estadístico de Pesca. 1996. Ministerio de Economía, Fomento y Reconstrucción, Servicio Nacional de Pesca (SERNAP) (ed). 224 pp.

SERNAP (1997) Anuario Estadístico de Pesca. 1997. Ministerio de Economía, Fomento y Reconstrucción, Servicio Nacional de Pesca (SERNAP) (ed). 306 pp.

SERNAP (1998) Anuario Estadístico de Pesca. 1998. Ministerio de Economía, Fomento y Reconstrucción, Servicio Nacional de Pesca (SERNAP) (ed). 283 pp.

SIELFELD W & M VARGAS (1999) Review of marine fish zoogeography of Chilean Patagonia (42° - 57°S). Scientia Marina 63 (Suplement 1): 451-463.

STEPHENS JS & VG SPRINGER (1974) Clinid fishes of Chile and Peru, with descriptions of a new species, Myxodes ornatus from Chile. Smithsonian Contributions to Zoology 159: 1-24.

STEPIEN CA (1990) Population structure, diets, and biogeographic relationships of a rocky intertidal fish assemblage in central Chile: high levels of herbivory in a temperate system. Bulletin of Marine Science 47: 598-612.

STRUB PT, JM MESIAS, V. MONTECINO, J RUTLANDT & S. SALINAS (1998) Coastal ocean circulation off western South America. In: Robinson AR & KH Brink (eds) The sea. Vol. II. The global coastal ocean: 273-313. John Wiley & Sons, New York.

THOMAS AC, F HUANG, PT STRUB & C JAMES (1994) Comparison of the seasonal and interannual variability of phytoplankton pigment concentrations in the Perú and California Current system. Journal of Geophysic Research 99: 7355-7370.

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.

WILLIAMS JT (1990) Phylogenetic relationships and revision of the Blenniid fish genus Scartichthys. Smithsonian Contributions to Zoology 492: 1–30.

YAÑEZ-ARANCIBIA L (1975) Zoogeografía de la fauna ictiológica de la Isla de Pascua (Easter Island). Anales del Centro de Ciencias del Mar y Limnología (México) 2: 29-52.

Invited Editor J.C. Castilla

APPENDIX 1

List of teleost and chondrichthyan fish species inhabiting littoral marine waters along the coast of Chile on which the biogeographic analysis was based. The latitudinal distribution range of each fish species and the literature sources from where this information was gathered are indicated

Species	Family	Distribution range	Literature source
cartilaginous fishes			
Alopias vulpinus	Alopiidae	18-44	4,6,7,15,40
Callorhynchus callorhynchus	Callorhynchidae	18-56	4,15,16,33,34,35,40
Prionace glauca	Carcharhinidae	18-56	5,8,15,33,34,35,40
Cetorhinus maximus	Cetorhinidae	18-52	4,7,40
Heptranchias perlo	Hexanchidae	18-40	5,7,15,28
Hexanchus griseus	Hexanchidae	18-44	5,7,15,28,40
Notorynchus cepedianus	Hexanchidae	18-46	5,7,40
Charchodon charcharias	Lamnidae	18-44	7
Isurus oxyrinchus	Lamnidae	18-52	5,7,33,34,35,36,40
Lamna nasus	Lamnidae	18-56	5,7,15
Bathyraja brachiurops	Rajidae	38-54	5,40
Bathyraja griseocauda	Rajidae	54-56	14,40
Bathyraja magellanica	Rajidae	54-56	14,40
Bathyraja scaphiops	Rajidae	54-56	14,40
Psammobatis rudis	Rajidae	54-56	14
Psammobatis scobina	Rajidae	22-56	14,15,40
Raja chilensis	Rajidae	54-56	14
Raja flavirostris	Rajidae	18-56	14,15,16,40
Raja trachyderma	Rajidae	54-56	14,40
Cephaloscilium ventriosum	Scyliorhinidae	18-40	5,8
Schroederichthys bivius	Scyliorhinidae	18-56	5,8,14,40
Schroederichthys chilensis	Scyliorhinidae	18-56	5,8,9,24
Sphyrna zygaena	Sphyrnidae	18-40	5,40
Squalus acanthias	Squalidae	18-56	7,14,40
Squatina armata	Squatinidae	18-44	7,24
Galeorhinus galeus	Triakidae	18-56	5,7,27,40
Mustelus whitneyi	Triakidae	18-56	5,8,15,24,33,34,35,40
Triakis maculata	Triakidae	18-40	5,8,15,24
teleost fishes			
Agonopsis chiloensis	Agonidae	18-56°	14,15,17,20,28,29,40
Aplodactylus punctatus	Aplodactylidae	18-40°	2,4,5,15,16,21,24,34,36
Austromenidia nigricans	Atherinidae	38-56°	5,14,17,29,40
Odonthestes regia	Atherinidae	18-56°	1,5,16,20,24,29,34,35
Aphos porosus	Batrachoididae	18-56°	4,5,15,16,18,24,36,38
Hypsoblennius sordidus	Blenniidae	18-48°	18,20,26,29,36,37,38
Scartichthys gigas	Blenniidae	18-40°	1,24,36,39
Scartichthys viridis	Blenniidae	18-36°	1,16,18,24,36,37,38,39
Scartichthys crapulatus	Blenniidae	28-34°	39
Bovichthys chilensis	Bovichthyidae	32-42°	15,16,18,19,20,24,37,38
Cottoperca gobio	Bovichthyidae	38-56°	5,14,17,40
Brama australis	Bramidae	18-56°	33,34,35
Parona signata	Carangidae	18-50°	33,34,35,40
Decapterus macrosoma	Carangidae	18-20°	5
Selene peruviana	Carangidae	18-40°	5
Trachionotus paitensis	Carangidae	18-20°	5
Seriola mazatlana	Carangidae	18-28°	4,15,24,33,34,35
Seriola lalandi	Carangidae	18-40°	5,40
Trachurus murphyi	Carangidae	18-38°	4,15,16,24,33,34,35
Schedophilus huttoni	Centrolophidae	18-56°	5
Seriolella caerulea	Centrolophidae	42-56°	33,34,35

Species	Family	Distribution range	Literature source
Seriolella porosa	Centrolophidae	18-56°	5,15,16
Seriolella violacea	Centrolophidae	18-56°	4,5,24,33,34,35
Seriolella punctata	Centrolophidae	42-56°	24,40
Champsocephalus esox	Channichthydae	38-56°	5,14,15,40
Cheilodactylus variegatus	Cheilodactylidae	18-40°	1,4,5,15,16,21,24,38
Myxodes cristatus	Clinidae	32-44°	4,29,36
Myxodes ornatus	Clinidae	32-34°	36
Myxodes viridis	Clinidae	18-44°	4,18,19,20,24,29,36,37
Clupea bentincki	Clupeidae	18-56°	20,29,33,34,35,40
Ethmidium maculatum	Clupeidae	18-56°	24,33,34,35
Sardinops sagax	Clupeidae	18-40°	15,24,29,33,34,35
Sprattus fuegensis	Clupeidae	26-56°	14,15,29,40
Congiopodus peruvianus	Congiopodidae	18-56°	4,5,14,15,20,29 20,29,40
Coryphaena hippurus	Coryphaenidae	18-44°	5,33,34,35
Sindoscopus australis	Dactyloscopidae	32-44°	29
Engraulis ringens	Engraulidae	18-38°	4,15,29,33,34,35
Epigonus crassicaudus	Epigonidae	18-44°	5,34,35
Micromesistius australis	Gadidae	46-56°	33,35,40
Thyrsites atun	Gempylidae	18-56°	4,15,24,34,35,40
Gobiesox marmoratus	Gobiesocidae	18-56°	1,4,15,18,19,20,40
Tomicodon chilensis	Gobiesocidae	18-44°	1,4,5
Sicyases hildenbrandi	Gobiesocidae	18-40°	5
Sicyases sanguineus	Gobiesocidae	18-56°	4,5,15,18,19,20,24,33,34,35
Heterogobius chiloensis	Gobiidae	42-56°	11,28
Ophiogobius jenynsi	Gobiidae	18-56°	19,20,29,40
Maurolicus muelleri	Gonostomatidae	18-44°	20
Anisotremus scapularis	Haemulidae	18-32°	1,4,15,24,33,34,35
Isacia conceptionis	Haemulidae	18-38°	4,15,16,24,33,34,35
Harpagifer bispinnis	Harpagiferidae	52-56°	14,15,17,29,40
Harpagifer georgianus	Harpagiferidae	54-56°	14,29
Girella laevifrons	Kyphosidae	18-40°	1,5,15,18,19,24,37,38
Graus nigra	Kyphosidae	18-40°	1,5,16,18,19,24,34,35,37,38
Kyphosus analogus	Kyphosidae	18-20°	5,34
Semicossyphus darwini	Labridae	18-40°	5
Semicossyphus maculatus	Labridae	18-40°	5,15,16,24,33,34,35
Auchenionchus microcirrhis	Labrisomidae	18-38°	1,4,18,19,24,37,38,39
Auchenionchus variolosus	Labrisomidae	32-36°	4,16,18,19,37,39
Calliclinus geniguttatus	Labrisomidae	32-56°	4,15,16,18,19,20,24,29,40
Calliclinus nudiventris	Labrisomidae	36-46°	3,12,29
Labrisomus philippii	Labrisomidae	18-42°	1,4,15,24,34,35
Careproctus crassus	Liparidae	54-56°	14,17
Careproctus pallidus	Liparidae	40-56°	14,40
Macruronus magellanicus	Macruronidae	40-54°	15,29,33,34,35,40
Merluccius australis	Merluccidae	36-56°	15,33,34,35,40
Merluccius gayi	Merluccidae	22-48°	4,15,31,33,34,35,40
Merluccius hubbsi	Merluccidae	54-56°	14,15,40
Salilota australis	Moridae	42-56°	14,15,17,20,40
Mugil cephalus	Mugilidae	18-42°	1,4,18,24
Gymnothorax modesta	Muraenidae	18-56°	5,15,23
Normanichthys crockeri	Normanichthyidae	18-56°	4,5,15,29,33,34,35
Dissostichus eleginoides	Nototheniidae	38-56°	5,14,15,33,34,35,40
Eliginops maclovinus	Nototheniidae	32-56°	14,15,16,17,20,29,33,34,35,40
Paranotothenia angustata	Nototheniidae	54-56°	14,29,40
Paranotothenia magellanica	Nototheniidae	54-56°	17,29,40
Patagonotothen wiltoni	Nototheniidae	40-56°	15,20,29,40
Patagonotothen brevicauda	Nototheniidae	38-56°	5,14,17,20,40
Patagonotothen canina	Nototheniidae	38-56°	5,15,29,40
Patagonotothen cornucola	Nototheniidae	38-56°	5,14,15,17,20,29,40
Patagonotothen longipes	Nototheniidae	38-56°	5,14,20,29,40
Patagonotothen sima	Nototheniidae	38-56°	5,14,17,20,29,40
Patagonotothen tessellata	Nototheniidae	38-56°	5,14,17,29,40

Species	Family	Distribution range	Literature source
Patagonotothen trigramma	Nototheniidae	54-56°	17,40
Ophichthus ater	Ophichthidae	18-40°	5
Ophichthus remiger	Ophichthidae	18-40°	5
Ophichthus dicellurus	Ophichthidae	18-40°	5
Ophichthus callaensis	Ophichthidae	18-40°	5
Ophichthus pacifici	Ophichthidae	18-40°	5
Genypterus blacodes	Ophidiidae	18-56°	5,14,16,20,29,33,34,35,40
Genypterus chilensis	Ophidiidae	18-56°	4,15,16,24,29,33,34,35
Genypterus maculatus	Ophidiidae	18-56°	4,15,29,33,34,35
Oplegnathus insignis	Oplegnathidae	18-26°	1,4,15
Hippoglossina montemaris	Paralichthyidae	18-40°	5
Hippoglossina mystacium	Paralichthyidae	38-56°	5,40
Hippoglossina macrops	Paralichthyidae	18-56°	4,5,15,16,24
Paralichthys adspersus	Paralichthyidae	18-40°	4,5,15,16,24
Paralichthys microps	Paralichthyidae	18-56°	5,15,16,20,33,34,35
Paralichthys patagonicus	Paralichthyidae	38-56°	5,40
Pinguipes chilensis	Pinguipedidae	18-56°	4,15,16,20,21,24,29,33,34,35
Caulolatilus princeps	Pinguipedidae	18-40°	5
Prolatilus jugularis	Pinguipedidae	18-56°	4,15,16,20,24,29,33,34,35
Chromis crusma	Pomacentridae	18-38°	1,4,15,16,21,24
Chromis intercrusma	Pomacentridae	18-40°	5
Nexilosus latifrons	Pomacentridae	18-24°	1,4,15,24
Salvelinus alpinus	Salmonidae	54-56°	14
Cilus gilberti	Sciaenidae	18-56°	16,24,28,33,34,35
Cynoscion analis	Sciaenidae	18-30°	4,15,33,34,35
Menticirrhus ophicephalus	Sciaenidae	18-34°	4,15,24
Micropogonias furnieri	Sciaenidae	44-46°	32,33,34,35,40
Sciaena deliciosa	Sciaenidae	18-34°	15,16
Sciaena fasciata	Sciaenidae	18-34°	4,15,24,33,34,35
Stellifer minor	Sciaenidae	18-34°	16,24
Sarda chilensis	Scombridae	18-40°	4,6,15,33,34,35
Scomber japonicus	Scombridae	18-34°	4,6,16,24,33,34,35,40
Thunnus alalunga	Scombridae	18-44°	6,15,33,40
Thunnus albacares	Scombridae	18-42°	6,33,34,35
Thunnus obesus	Scombridae	18-36°	6,25,33,34,35
Sebastes capensis	Scorpaenidae	18-56°	5,10,14,24,33,34,35
Sebastes oculatus	Scorpaenidae	18-56°	15,16,20,40
Acanthistius pictus	Serranidae	18-38°	4,24
Hemilutjanus macrophtalmos	Serranidae	18-40°	4,5,24,33,34,35
Paralabrax humeralis	Serranidae	18-56°	4,5,24,33,34,35
Stromateus brasiliensis	Stromateidae	54-56°	14,40
Stromateus stellatus	Stromateidae	18-56°	13,20
Leptonotus blainvillianus	Syngnathidae	18-56°	4,17,20,29,40
Tetragonurus cuvieri	Tetragonuridae	18-36°	13,31
Helcogramoides chilensis	Tripterygiidae	20-36°	1,18,19,24,37,38
Helcogramoides cunninghami	Tripterygiidae	32-42°	18,19,20,29,37,38,40
Xiphias gladius	Xiphiidae	18-40°	4,33,34,35,40
Austrolycus depressiceps	Zoarcidae	40-56°	14,17,20,29,40
Crossostomus sobrali	Zoarcidae	54-56°	14,29
Ilucoetes facali	Zoarcidae	54-56°	14,29
Phucocoetes latitans	Zoarcidae	54-56°	14,29

1: Berrios & Vargas in press; 2: Cáceres et al. 1993; 3: Cervigon et al. 1979; 4: Chirchigno 1974; 5: Chirchigno et al. 1982; 6: Collette & Nauen 1983; 7: Compagno 1984a; 8: Compagno 1984b; 9: Fariña & Ojeda 1993; 10: Fariña & Ojeda 1996; 11: Fowler 1951; 12: Inzunza & Pequeño 1988; 13: Kong et al. 1985; 14: Lloris & Rucabado 1991; 15: Mann 1954; 16: Miranda 1967; 17: Moreno & Jara 1984; 18: Muñoz & Ojeda 1997; 19: Muñoz & Ojeda 1998; 20: Navarro & Pequeño 1979; 21: Núñez & Vásquez 1987; 22: Ojeda 1983; 23: Ojeda 1989; 24: Ojeda, unpublished data; 25: Ojeda & Aviles 1987; 26: Oyarzún & Pequeño 1989; 27: Pequeño 1977; 28: Pequeño 1989; 29: Pequeño et al. 1995; 30: Quijada & Cáceres, submitted; 31: Hernández et al. 2000; 32: Sepúlveda 1987; 33: Sernapesca 1996; 34: Sernapesca 1997; 35: Sernapesca 1998; 36: Stephens & Springer 1974; 37: Stepien 1990; 38: Varas & Ojeda 1990; 39: Williams 1990; 40: Menni et al. 1984