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ORIGINAL ARTICLE

Diversity and distribution of cephalopod species off the coast of Chile

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Abstract

Cephalopods are increasingly acknowledged as an ecologically important group in Chilean ecosystems, but are also one of their less-known biogeographic components. Notably, this group is represented virtually exclusively by non-endemic species, although we hypothesized that their distribution over the coast should be constrained by similar physical determinants to those affecting endemic taxa. We thus present a first evaluation of the latitudinal patterns of diversity and distribution of cephalopod species in Chile, based on geographical data obtained from a review of the available literature. We constructed presence–absence binary matrices of coastal and oceanic species in 20 latitudinal units (2°), for then calculating the respective similarity matrices to obtain a distribution dendrogram using hierarchical cluster analysis (UPGM). The original binary matrices were resampled performing 1000 stochastic reassignments to calculating the 95th percentile as the criterion to identify significant clusters. Statistical comparisons between distributional groupings were performed using ANOSIM. We recorded 86 cephalopods in Chile, including oceanic (71) and coastal (15) species. Species richness showed two major breaks at 30° S and 42° S, and decreased toward higher latitudes. Cephalopod species showed well-defined endpoints of distribution within the Chilean coast, differentiating three main biogeographical units: northern (18–30° S), central (30–42° S) and southern (42–56° S) areas. Biogeographical patterns of cephalopod species in Chile showed no particular difference with those already described for most Chilean taxa. The marked distribution breaks of cephalopods at 30° and 42° S suggest that external forcing and physical factors other than temperature gradients may strongly constrain their dispersal.

Key words: *Biogeography, Cephalopoda, geographic range, southeastern Pacific, species richness*

Introduction

Present cephalopods are far from their Paleozoic splendor (Kröger 2005), but they continue to be a very diverse and abundant group inhabiting all marine environments of the world, from surface waters to more than 5000 m depth (Roper et al. 1984; Jereb & Roper 2005). Although some cephalopods are stenothermic, most species are considered stenohaline and eurithermic, and thus salinity would be a main determinant of their geographical distribution (Boyle & Rodhouse 2005; Jereb & Roper 2005).

More than 90 species of Cephalopoda have been recorded in Chilean waters (18–56° S), most of

them oceanic and of wide geographical distribution along the south Pacific, often exhibiting associations with particular water masses (Rocha 1997). The diversity of cephalopods along the coast would follow the classic pattern of increase towards lower latitudes (Valdovinos 1999), in apparent relationship with latitudinal gradients of salinity and temperature, similar to the observed in other molluscs such as prosobranch gastropods (Roy et al. 1998; Rex et al. 2005), but contrasting with the inverse patterns shown by bivalvian and placophoran molluscs (Valdovinos 1999; Valdovinos et al. 2003). The increasing diversity of prosobranch gastropods towards the tropics has been associated with variations in productivity, related in turn with

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the input of solar radiation and sea surface temperature (Roy et al. 1998; Rex et al. 2005). However, the contrasting trends among different mollusc groups suggest that the above hypothesis should not be readily extrapolated to cephalopods, especially due to the scarcity of basic information on their biology and ecology (Rocha 1997; Rocha & Vega 2003).

Even though cephalopods have not been subject to previous biogeographical analyses, their richness and distribution patterns should likely be sensitive to the high physical, chemical and geomorphological heterogeneity of the Chilean coast. Among the most important factors affecting the geographical distribution of the Chilean marine biota (e.g. see reviews by Brattström & Johanssen 1983; Santelices 1991; Rocha 1997; Fernández et al. 2000; Camus 2001; Thiel et al. 2007), we highlight: (a) the widespread influence of the cold Humboldt current system; (b) geographical variations of the frequency and intensity of upwelling, introducing spatial heterogeneity in local productivity and regimes of sea surface temperature; (c) a comparatively greater influence of physical interannual fluctuations (e.g. El Niño/La Niña events) in the north-central region; (d) a geomorphologic discontinuance due to the complete fragmentation of the coast from 41° 30'S southwards, where the high input of freshwater into coastal water masses promotes estuarine conditions; and (e) an extended oxygen minimum zone showing interannual and latitudinal variations in vertical extent and intensity, which attenuates from 41° S southwards. On mesoscales (tens to hundreds of kilometres), the above factors cause different taxa to show differential attenuation rates and latitudinal limits depending on their tolerance, dispersal ability, and susceptibility to external forcings. On geographical scales (thousands of kilometres), however, major discontinuances arise from the confluence of latitudinal breaks of different taxa (Brattström & Johanssen 1983; Lancellotti & Vásquez 1999, 2000; Fernández et al. 2000; Meneses & Santelices 2000; Santelices & Meneses 2000; Camus 2001; Thiel et al. 2007).

Overall, three main biogeographical units can be recognized along the coast: a warm-temperate area in northern Chile (18° S to ~30–32° S; southern part of the Peruvian Province), a cold-temperate area in austral Chile (~42–56° S; Pacific sector of the Magellanic Province), and a transitional area between both provinces. This classification accounts for the distribution of many mollusc and non-mollusc groups, most of them with high endemism levels. However, while several cephalopod species and genera were originally described from Chilean waters, it should be noted that all valid records off

the continental coast of Chile correspond to non-endemic, widely distributed species. Endemic cephalopods have been reported only on Eastern Island and the Juan Fernández Archipelago (Voss 1979; Vega et al. 2007), even though there may be more endemic taxa which are not yet discovered and/or published so far. In this context, we hypothesize that the diverse sources of variation found along the coast are strong enough as to induce a latitudinal differentiation of cephalopod distribution, as observed in some crustacean groups including widely distributed taxa (e.g. peracarids and pelagic barnacles; Thiel 2000; Hinojosa et al. 2006). Thus, this work presents an evaluation of the latitudinal patterns of diversity and distribution of cephalopod species in Chile, which is also the first assessment in this coast for a group formed by a majority of non-endemic components.

Materials and methods

The information analysed in this paper was obtained from a review of the available literature (see Table I legend) on geographical distribution of cephalopod species associated to the continental coast of Chile (latitudinal range: 18–56° S), excluding those from oceanic islands. Thus, we first compiled a preliminary list of species and their distributions incorporating proper nomenclatural corrections when required. This list was then corrected and updated by: (a) excluding misidentified species and uncertain records lacking confirmation (e.g. species reported either only once or from a single locality); and (b) including some new records and new species based on information obtained both from field samples and ongoing research (Ibáñez et al. 2006; Cardoso, personal communication; Ibáñez, unpublished data). We note that cephalopods have been less studied or sampled than other Chilean marine groups, and therefore some bias affecting our distribution records may be inevitable. None the less, recent works (e.g. Rocha 1997) and information derived from an increasing number of fishery studies over the whole coast (e.g. Castillo et al. 2007; Ibáñez & Cubillos 2007) have contributed to reinforce or improve the available knowledge on the distribution of cephalopod species. Thus, although biases related to sampling effort may exist, they may be similar or even smaller than those affecting the biogeographical knowledge of littoral species (e.g. see Camus 2001; Thiel et al. 2007), which are still largely undersampled in those areas little accessible or distant from marine research centres or institutions.

On this basis, we generated the database employed in subsequent analyses, consisting of a binary matrix

recording the presence–absence of cephalopod species every two degrees of latitude along the Chilean coast (Table I), from which we obtained the number of species present at each latitudinal segment. Table I also includes two types of complementary information: the first being a categorization of cephalopods into coastal or oceanic species (irrespective of their benthic or pelagic habits), which was coherent with the classification of coastal and oceanic zones proposed by Rocha (1997). Coastal species were defined as those inhabiting littoral or neritic zones associated to the continental shelf, which is extremely reduced (<10 km width in some points) and narrower than in the northern hemisphere (Valdovinos et al. 2003; Cione et al. 2007), causing these species to have a narrow longitudinal range. By contrast, oceanic species were defined as those occurring off the continental shelf, the majority of which can be found between the shelf margin and 80° W (e.g. as evidenced in the diet of the swordfish *Xiphias gladius* Linnaeus, 1758, captured between 74° and 80° W; Ibáñez et al. 2004; Castillo et al. 2007). In fact, more than 25% of oceanic species do not extend into the Pacific beyond 80° W, although a similar proportion can extend up to 170–180° W. Given that coastal and oceanic species both occur in extra Chilean areas, Table I includes an additional descriptor aiming to reflect the extent and predominant region of distribution of each species, considering four general categories (Pacific, Indo-Pacific, subantarctic, worldwide).

From the binary matrix of species by latitude (2° units), we generated two additional matrices separating coastal from oceanic species. For each of the three matrices, we calculated a similarity matrix (using Jaccard's index) to obtain a distribution dendrogram by means of hierarchical cluster analysis using the UPGM algorithm (PAST; Hammer et al. 2001). We then resampled the original binary matrix performing 1000 stochastic reassignments to generate a distribution of similarity pseudovalues, calculating the 95th percentile as the criterion to identify significant clusters in the original similarity matrix (Jaksic & Medel 1990). We followed a similar bootstrap procedure to obtain the percentage of replicates (1000 iterations) supporting each node of the dendrogram (only values $\geq 90\%$ are shown). In addition, we performed comparisons of selected dendrogram groups by means of ANOSIM (Clarke 1993; Hammer et al. 2001).

Results

Diversity

We recorded a total of 86 non-endemic cephalopod species in Chile (Table I, Figure 1), 11 of them

(12.8%) distributed over the whole coast, and 1 (1.2%) over 90% of the coast (56–22° S). Oceanic cephalopods were the most important group with 71 (82.6%) species, contrasting with coastal cephalopods represented by only 15 (17.4%) species. All species had wide distributions independently of their observed ranges in Chile: 20 (23.3%) in the Pacific Ocean, 21 (24.4%) in the subantarctic areas (South Pacific, South Atlantic and Antarctic Oceans), 9 (10.5%) in the Indo-Pacific Ocean and 36 (41.9%) in different areas worldwide (Table I). Figure 1 shows the latitudinal range and position of the 86 coastal and oceanic species along the Chilean coast, and Figure 2 shows the frequency distribution of the number of species across range size (km) classes. On the one hand, 87.2% of the species (75) exhibited at least one end point of distribution within the Chilean coast (see Figure 1): (a) 43.0% (37: 34 oceanic, 3 coastal) were northern species reaching a southern end point as they extend from warm-temperate areas; (b) 27.9% (24: 17 oceanic, 7 coastal) were southern species reaching a northern end point as they extend from cold-temperate areas; and (c) 16.3% (14: 10 oceanic, 4 coastal) were species with shorter, intra-Chilean latitudinal ranges, showing their south and north limits mostly in north-central or south-central positions. On the other hand, range sizes exhibited a nearly normal distribution with most species showing intermediate ranges (Figure 2), with the exception of those species occurring along the whole coast.

Overall, the number of cephalopod species (Figure 3) showed a significant decreasing trend toward higher latitudes (Spearman's $\rho = -0.721$, $n = 20$, $p = 0.0003$). However, such a trend was partly epiphenomenic, and Figure 2 shows that it may be decomposed into three different subpatterns. From north to south, the number of species between 18° and 30° S exhibited a monotonic increase from 48 to 55, with an average number of 51.9 ± 2.4 (sd) species, where the dominant component corresponds to species of warm-temperate distribution (Figure 1). The increasing trend was due to the southward incorporation of species of temperate and cold-temperate distributions. From 30° to 32° S, the number of species dropped to 45 due to the absence of a number of warm-temperate components, and gradually increased to a maximum of 57 at 42° S due to the incorporation of both short-range temperate components and cold-temperate components (Figure 1), with an average number for this area of 48.8 ± 4.5 (sd) species. Between 42° and 44° S, the confluence of many southern and northern endpoints of distribution marks an important faunal replacement (Figure 1), causing a strong decrease from 57 to 35 species. The area from 44° to 56° was

Table I. List of studied species and their geographical distribution in the Chilean coast. The information on distribution was obtained from Thore (1959), Nesis (1972, 1987, 1993), Retamal & Orellana (1977), Roper et al. (1984), Okutani & Clarke (1985), Andrade (1987), Voss (1988), Rocha et al. (1991), Alexeyev (1993, 1994a,b), Rocha (1997), Dunning (1998), Kubodera et al. (1998), Voss et al. (1998), Wormuth (1998), Valdovinos (1999), Villarroel et al. (2001), Ibáñez et al. (2004), Castillo et al. (2007), and Ibáñez (unpublished data). Records marked by asterisks correspond to taxa currently placed into a different genus (*) or in the process of being described as new species (**).

Species	Habitat	Distribution	Latitudinal distribution off Chile																							
			18°	20°	22°	24°	26°	28°	30°	32°	34°	36°	38°	40°	42°	44°	46°	48°	50°	52°	54°	56°				
<i>Stoloteuthis</i> sp. Verrill, 1881**	Coastal	Pacific	X	X	X	X	X	X	X																	
<i>Rossia glaucopsis</i> Loven, 1845	Coastal	Worldwide													X	X	X	X	X	X	X	X	X	X		
<i>Rossia mastigophora</i> Berry, 1911	Coastal	IndoPacific							X	X	X															
<i>Semirossia patagonica</i> (Smith, 1881)	Coastal	Pacific									X	X	X	X	X	X	X	X	X	X	X	X				
<i>Neorossia caroli</i> (Joubin, 1902)	Coastal	Worldwide						X	X																	
<i>Heteroteuthis</i> sp. Gray, 1849	Oceanic	Pacific	X	X	X	X	X	X	X																	
<i>Iridoteuthis</i> sp. Naef, 1912	Oceanic	Pacific	X	X	X	X	X	X	X																	
<i>Loligo gahi</i> Orbigny, 1835	Coastal	Subantarctic	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Lycoteuthis diadema</i> (Chun, 1900)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Enoploteuthis</i> sp. Orbigny, 1844	Oceanic	Pacific										X	X	X	X	X	X	X	X	X	X	X				
<i>Enoploteuthis semilineata</i> Alexeyev, 1994	Oceanic	Pacific									X	X	X	X	X	X	X	X	X	X	X					
<i>Abraaliopsis affinis</i> (Pfeffer, 1912)	Oceanic	Pacific	X	X	X																					
<i>Abraaliopsis gilchristi</i> (Robson, 1924)	Oceanic	Worldwide				X	X	X	X	X	X	X	X	X	X	X	X									
<i>Ancistrocheirus alessandrini</i> (Vérany, 1851)	Oceanic	Pacific										X	X	X	X	X										
<i>Pterygoteuthis gemmata</i> Chun, 1910	Oceanic	IndoPacific	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Pterygoteuthis giardi hoylei</i> (Pfeffer, 1912)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Pyroteuthis margaritifera</i> (Rüppel, 1844)	Oceanic	Worldwide				X	X	X	X	X	X	X	X	X	X	X										
<i>Octopoteuthis deletron</i> Young, 1972	Oceanic	Pacific							X	X																
<i>Octopoteuthis nielseni</i> (Robson, 1948)	Oceanic	Pacific	X	X	X	X	X	X	X	X	X	X	X	X	X											
<i>Onychoteuthis banksii</i> (Leach, 1817)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Moroteuthis ingens</i> (Smith, 1881)	Oceanic	Subantarctic													X	X	X	X	X	X	X	X	X	X		
<i>Moroteuthis knipovitchi</i> Filippova, 1972	Oceanic	Subantarctic													X	X	X	X	X	X	X	X	X	X		
<i>Moroteuthis robsoni</i> Adam, 1962	Oceanic	Worldwide									X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Kondakovia longimana</i> Filippova, 1971	Oceanic	Subantarctic																			X	X	X	X		
<i>Discoteuthis discus</i> Young & Roper, 1969	Oceanic	Worldwide	X	X	X	X	X	X	X																	
<i>Gonatus antarcticus</i> Lönnerberg, 1898	Oceanic	Subantarctic	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Pholidoteuthis boschmani</i> Adam, 1950	Oceanic	Worldwide										X	X	X	X	X	X	X								
<i>Architeuthis dux</i> Steenstrup, 1857	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Histioteuthis atlantica</i> (Hoyle, 1885)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Histioteuthis corona cerasina</i> Nesis, 1971	Oceanic	Pacific	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Histioteuthis dofleini</i> (Pfeffer, 1912)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Histioteuthis eltaninae</i> Voss, 1969	Oceanic	Subantarctic															X	X	X	X	X	X	X	X		
<i>Histioteuthis hoylei</i> (Goodrich, 1896)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Histioteuthis heteropsis</i> (Berry, 1918)	Oceanic	Pacific	X	X	X	X	X	X	X	X	X	X														
<i>Neoteuthis</i> sp. Naef, 1921	Oceanic	IndoPacific	X	X	X	X	X	X	X																	
<i>Nototeuthis dimegacotyle</i> Nesis & Nikitina, 1986*	Oceanic	Worldwide													X	X	X	X	X	X	X	X	X	X		
<i>Bathyteuthis abyssicola</i> Hoyle, 1885	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
<i>Brachyoteuthis picta</i> Chun, 1910	Oceanic	Subantarctic									X	X	X	X	X	X	X	X	X	X	X	X	X	X		

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Table I (Continued)

Species	Habitat	Distribution	Latitudinal distribution off Chile																			
			18°	20°	22°	24°	26°	28°	30°	32°	34°	36°	38°	40°	42°	44°	46°	48°	50°	52°	54°	56°
<i>Brachioteuthis riisei</i> (Steenstrup, 1882)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X							
<i>Batoteuthis skolops</i> Young & Roper, 1968	Oceanic	Subantarctic																	X	X	X	X
<i>Todarodes filippovae</i> Adam, 1975	Oceanic	Worldwide			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Martialia hyadesi</i> Rochebrune & Mabile, 1889	Oceanic	Subantarctic							X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Nototodarus hawaiiensis</i> (Berry, 1912)	Oceanic	Pacific	X	X	X	X	X	X	X													
<i>Ommastrephes bartramii</i> (Leseur, 1821)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Dosidicus gigas</i> (Orbigny, 1835)	Oceanic	Pacific	X	X	X	X	X	X	X	X	X	X	X	X	X	X						
<i>Sthenoteuthis oualaniensis</i> (Lesson, 1830)	Oceanic	IndoPacific	X	X	X	X	X															
<i>Eucleoteuthis luminosa</i> Sasaki, 1915	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Chiroteuthis veranyi</i> (Férussac, 1835)	Oceanic	Subantarctic	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Planctoteuthis</i> sp. Pfeffer, 1912*	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X							
<i>Planctoteuthis danae</i> (Joubin, 1931)*	Oceanic	Pacific	X	X	X	X	X	X	X	X	X	X	X	X								
<i>Mastigoteuthis agassizii</i> (Verrill, 1881)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Mastigoteuthis famelica</i> Berry, 1909	Oceanic	Worldwide												X	X	X	X	X	X	X	X	X
<i>Promachoteuthis</i> sp. Hoyle, 1885	Oceanic	Subantarctic							X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Taonius</i> sp. Steenstrup, 1861	Oceanic	Pacific												X	X	X	X	X	X	X	X	X
<i>Cranchia scabra</i> Leach, 1817	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X										
<i>Liocranchia reinhardtii</i> (Steenstrup, 1856)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X								
<i>Leachia cyclura</i> LeSueur, 1821	Oceanic	Worldwide	X	X	X	X	X	X	X													
<i>Leachia dislocata</i> Young, 1971	Oceanic	IndoPacific						X	X													
<i>Leachia pacifica</i> (Issel, 1908)	Oceanic	Subantarctic	X	X	X	X	X	X														
<i>Leachia rhynchophorus</i> (Rochebrune, 1884)	Oceanic	Subantarctic									X	X	X	X								
<i>Helicocranchia pfefferi</i> Massy, 1907	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X								
<i>Galiteuthis pacifica</i> (Robson, 1948)	Oceanic	IndoPacific	X	X	X	X	X	X	X													
<i>Galiteuthis suhmi</i> (Hoyle, 1885)	Oceanic	Worldwide										X	X	X	X	X	X	X	X	X	X	X
<i>Bathotauma lyromma</i> Chun, 1906	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X								
<i>Megalocranchia abyssicola</i> (Goodrich, 1896)	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X								
<i>Mesonychoteuthis hamiltoni</i> Robson, 1925	Oceanic	Subantarctic														X	X	X	X	X	X	X
<i>Teuthowenia pellucida</i> (Chun, 1910)	Oceanic	Subantarctic												X	X	X	X	X	X	X	X	X
<i>Vampyroteuthis infernalis</i> Chun, 1910	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X								
<i>Cirrothauma murrayi</i> Chun, 1911	Oceanic	Worldwide												X	X	X	X	X	X	X	X	X
<i>Opisthoteuthis</i> sp. Verrill, 1883**	Oceanic	Pacific		X	X	X	X	X	X													
<i>Japetella diaphana</i> Hoyle, 1885	Oceanic	Worldwide	X	X	X	X	X	X	X	X	X	X	X	X								
<i>Eledonella pygmaea</i> Verrill, 1884	Oceanic	Worldwide	X	X	X	X	X	X	X													
<i>Robsonella fontaniana</i> (Orbigny, 1834)	Coastal	Subantarctic	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Enteroctopus megalocyathus</i> (Gould, 1852)	Coastal	Subantarctic												X	X	X	X	X	X	X	X	X
<i>Octopus mimus</i> Gould, 1852	Coastal	Pacific	X	X	X	X	X	X	X	X	X											
<i>Scaevargus patagiatus</i> Berry, 1913*	Oceanic	IndoPacific	X	X	X	X	X	X	X													
<i>Pteroctopus hoylei</i> (Berry, 1909)*	Oceanic	IndoPacific	X	X	X	X	X	X	X													
<i>Thaumeledone brevis</i> (Hoyle, 1885)	Coastal	Subantarctic																			X	X
<i>Graneledone</i> sp. Joubin, 1918**	Coastal	Pacific								X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Pareledone charcotti</i> (Joubin, 1905)	Coastal	Subantarctic											X	X	X	X	X	X	X	X	X	X

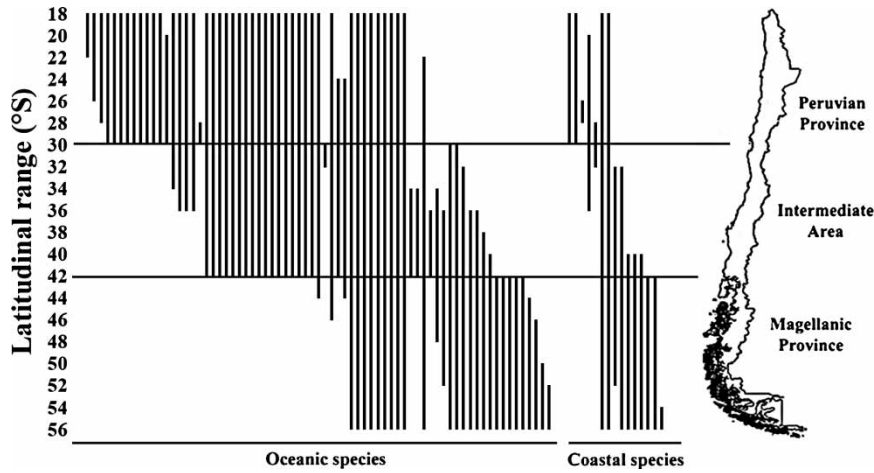


Figure 1. Latitudinal range (vertical bars) of coastal and oceanic cephalopod species off the Chilean coast. Horizontal lines mark the northern ($\sim 30^\circ$ S) and southern ($\sim 42^\circ$ S) boundaries of the transitional area between the warm- and cold-temperate biogeographic units over the coast.

of the Pacific South American coast. However, several northern species do not extend south of $30\text{--}32^\circ$ S, where the subtropical oceanic convergence occurs (Fariña et al. 2006) and the number of species drops from 55 to 45. Thus, it is likely that external forcings may prevent the dispersal of these cephalopods further south, such as the strong changes in eddy activity and wind stress occurring at 30° S (Hormazábal et al. 2004), and the contrasting productivity between coastal and offshore zones at the same latitude (see Thiel et al. 2007). A second and most important change occurs at 42° S, coincident with the West Wind Drift oceanic convergence (Fariña et al. 2006). At this latitude, most northern species end their distribution, and the number of species exhibits a sharp decrease being reduced by nearly 50%. The whole area between 42° and 56° S exhibits a similarly low diversity, being dominated by cold-water and subantarctic species. The main factors associated with this break in richness could be the decrease in salinity and temperature south of 42° S (see Camus 2001),

which could exceed the tolerance limits of many species. In addition, the austral region formed by fjords and channels exhibits some important off-shore-coast gradients in salinity and sea surface temperature (e.g. Dávila et al. 2002; Figueroa 2002; Silva & Guzmán 2006), which make coastal physical conditions very restrictive and may prevent oceanic species to reach nearshore habitats.

Overall, the number of cephalopod species decreases on average from northern to southern Chile, a similar trend to that observed for other Chilean taxa (e.g. Lancellotti & Vásquez 2000; Ojeda et al. 2000; Astorga et al. 2003), and also for taxa from the northern hemisphere (e.g. Roy et al. 1998; Rex et al. 2000). However, we remark that the decrease in diversity is far from monotonic and occurs at discrete steps, mainly as a by-product of the distributional breaks at 30° and 42° S, where the overlap between southern and northern cephalopods causes species number to peak. Thus, we should refer this trend as a between-region decrease in the mean number of species (north > central > southern

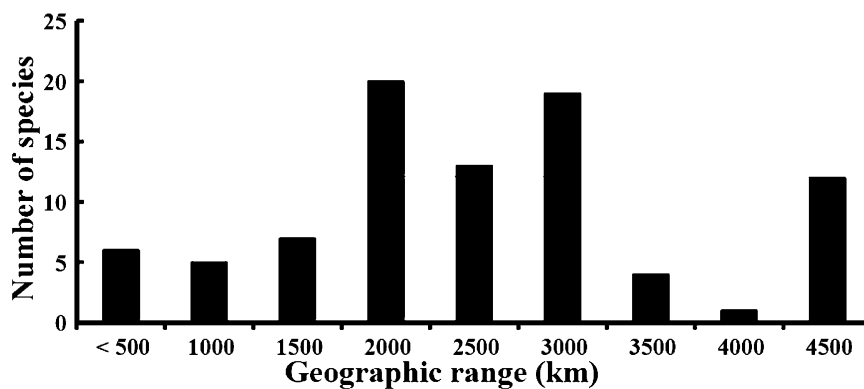


Figure 2. Frequency distribution of the number of cephalopod species by range size (km) classes.

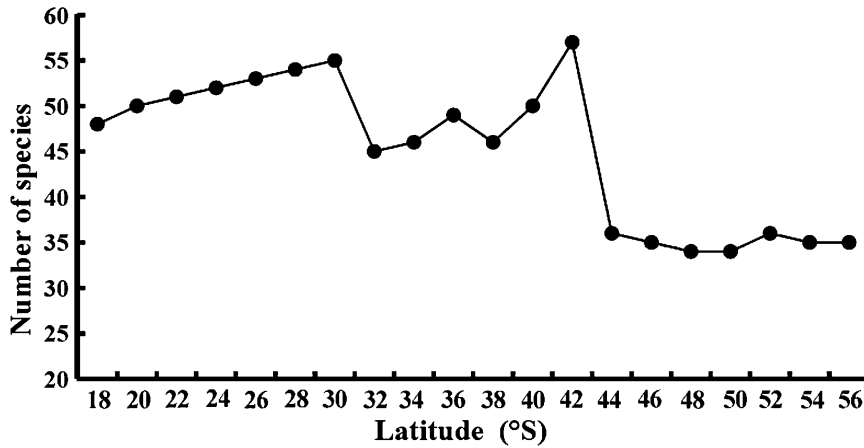


Figure 3. Number of cephalopod species recorded every two degrees of latitude over the Chilean coast.

Chile). Such abrupt transitions suggest that the diversity and geographical extent of non-endemic cephalopods in Chile are controlled by the presence or absence of major physical forcings. In turn, this may be the main noticeable difference between cephalopods and taxa with endemic components, as these latter tend to show slightly clearer gradients of diversity along the coast (see reviews by Lancelotti & Vásquez 2000; Camus 2001; Thiel et al. 2007).

Distribution

Cephalopods as a whole show well-defined biogeographic groupings, with two main species replacements at 30° and 42° S differentiating northern, central and southern areas. As expected, however, these three groups are not statistically significant at $p=0.05$ because nearly 30% of species are distributed either in the whole coast (18–56° S) or in the north-central zone (18–42° S), leading to a high level of similarity between any pair of latitudes. Nonetheless, the three areas are defined by nodes at least at 70% of similarity and well supported by bootstrap estimates, what we consider to be a consistent clustering for a coastal range of 4500 km where 57% of species have distribution ranges greater than 2000 km. Oceanic cephalopods represent ca. 83% of species, and therefore their clustering pattern is virtually the same as described above. The small group of coastal cephalopods shows a statistically weak patterning, but nonetheless most of them tend to have smaller distribution ranges which also exhibit a clear latitudinal segregation into northern, central and southern areas.

Our results show that the biogeographical patterns of non-endemic cephalopod species in Chile have no particular differences with those already described for most Chilean taxa (summarized by Fernández et al. 2000; Camus 2001; Thiel et al. 2007). The

distribution of cephalopods follows the traditional differentiation into three biogeographical units: a northern area (18–30° S) comprising the southern part of the warm-temperate Peruvian province, a southern area (42–56° S) comprising the cold-temperate Magellanic province, and an intermediate transitional area (30–42° S) characterized by the overlapping distribution of warm- and cold-water species. Outside the Chilean coast, cephalopod species occurring at the northern area have characteristic subtropical and temperate distributions (e.g. Roper et al. 1984), while all species occurring at the southern area have also a subantarctic distribution (e.g. Okutani & Clarke 1985; Boyle & Rodhouse 2005).

As mentioned above, the fact that such eurythermic, non-endemic species show well-defined distribution endpoints within the Chilean coast suggest that external forcings may be more important than previously thought, especially considering the high dispersal potential of many species through their planctonic paralarvae (Rocha et al. 1999; González et al. 2005; Jereb & Roper 2005). The similar latitudinal breaks shown by a number of endemic taxa are often interpreted as a response to physical gradients dependent on their tolerance ranges, particularly to water temperature. For instance, strong interannual thermal fluctuations such as El Niño events are known to affect cephalopod species, leading to abundance increases in coastal benthic octopuses (Castilla & Camus 1992) or abundance decreases and distribution variations in neritic and oceanic squids (Anderson & Rodhouse 2001; Villegas 2001; Rocha & Vega 2003). Similar variations can be observed in many algal and invertebrate taxa of diverse phyletic origin (e.g. Vásquez et al. 2006; Thiel et al. 2007; Camus 2008). However, several of these taxa are also known to have upper tolerance limits exceeding the highest temperatures recorded

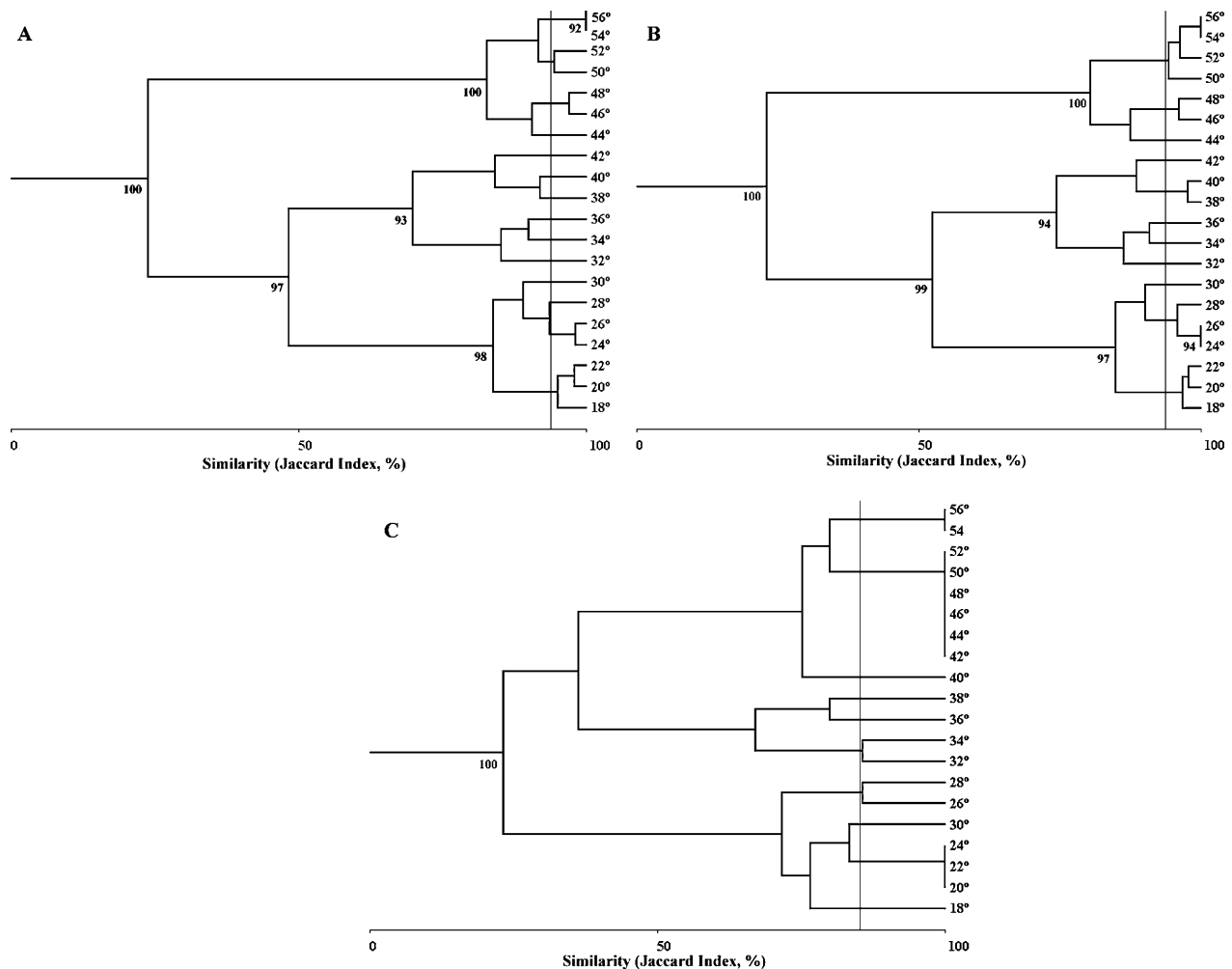


Figure 4. Hierarchical clustering of the presence–absence of cephalopod species in 2° latitudinal bands in the Chilean coast. A, all species; B, oceanic species; C, coastal species. The vertical line inside each dendrogram marks the 95th percentile of similarity obtained from stochastic reassignments of the original binary matrix. Nodes include values of bootstrap estimates (only values $\geq 90\%$ are shown).

during El Niño events (Wolff 1987; Urban 1994), and thus interannual variations cannot easily explain their biogeographical patterns. The same may occur with latitudinal variations of sea surface temperature, which cannot explain the variations of mollusc diversity along the coast, while continental shelf area appears as a key determinant (e.g. Valdovinos et al. 2003). Thus, we suggest that the marked distribution breaks of cephalopods may reflect the action of external forcings or factors other than temperature, which should also be important determinants for endemic species acting as constraints or barriers to dispersal.

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