

Free-living benthic marine invertebrates in Chile

Invertebrados bentónicos marinos de vida libre en Chile

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ABSTRACT

A comprehensive literature review was conducted to determine the species richness of all the possible taxa of free-living benthic marine invertebrates in Chile. In addition, the extent of endemism to the Pacific Islands and deep-sea, the number of non-indigenous species, and the contribution that the Chilean benthic marine invertebrate fauna makes to the world benthic marine invertebrate fauna was examined. A total of 4,553 species were found. The most speciose taxa were the Crustacea, Mollusca and Polychaeta. Species richness data was not available for a number of taxa, despite evidence that these taxa are present in the Chilean benthos. The Chilean marine invertebrate benthic fauna constitutes 2.47 % of the world marine invertebrate benthic fauna. There are 599 species endemic to the Pacific Islands and 205 in the deep-sea. There are 25 invasive or non-indigenous species so far identified in Chile. Though the Chilean fauna is speciose there is still a considerable amount of diversity yet to be described, particularly amongst the small bodied invertebrates and from the less well explored habitats, such as the deep-sea.

Key words: Chile, species richness, benthos, free-living invertebrates.

RESUMEN

Se realizó una revisión exhaustiva de la literatura para determinar la riqueza de especies de todos los taxa de invertebrados bentónicos de vida libre en Chile. Además, se analizó el endemismo de invertebrados marinos bentónicos para las islas chilenas del Pacífico y el mar profundo y el número de especies no indígenas; del mismo modo que la contribución de estos invertebrados a la riqueza mundial de invertebrados bentónicos marinos. Para Chile se acumuló un total de 4.553 especies de invertebrados bentónicos. Los taxa con más especies fueron Crustacea, Mollusca y Polychaeta. En algunos taxa de invertebrados no se encontró información sobre la diversidad de especies presentes en Chile, a pesar de existir evidencia de que éstos están presentes en el bentos marino chileno. Los invertebrados bentónicos marinos chilenos contribuyen con el 2,47 % de la riqueza mundial de dichos invertebrados. Se encontraron 599 especies endémicas de las islas chilenas del Pacífico y 205 especies endémicas para el mar profundo. Hasta ahora en Chile se han identificado sólo 25 especies invasoras de invertebrados bentónicos marinos. Los invertebrados bentónicos marinos chilenos son diversos, pero aún hay especies no descritas, especialmente dentro de los invertebrados bentónicos de pequeño tamaño corporal que se encuentran en hábitat poco explorados, como por ejemplo el mar profundo.

Palabras clave: Chile, riqueza de especies, bentos, invertebrados de vida libre.

INTRODUCTION

Biodiversity is defined as the total diversity and variability of living things and the systems of which they are a part (Heywood et al. 1995). According to Bowman (1993) a narrow

interpretation of biodiversity is the “extant global variety of life forms”. It is this narrow interpretation the “extant variety of Chilean free-living benthic marine organisms” that is addressed in this paper in the form of an assessment of the diversity associated with high

level taxonomic groupings and general comments about their status. The other ways in which biodiversity can be measured within the benthic marine environment and the ways in which this information can be used to address the threats to species diversity will be discussed elsewhere.

Continental Chile has an extensive coastline of about 4,300 km in length (Camus 2001), running predominantly north-south from 18°22' to 56°00' S. The coastline of Chile represents approximately 0.65 % of the world's total coastline. If the entire coastal topography is taken into account the total length of the continental Chilean coastline is 83,850 km (Servicio Hidrográfico y Oceanográfico de la Armada de Chile (SHOA). The oceanic islands, San Félix (26°17' S, 80°05' W) and San Ambrosio (26°20' S, 70°58' W) which together make up the Desventuradas Islands, the Juan Fernández Archipelago (33°40' S, 79°00' W), Easter island (27°09' S, 109°23' W), and Sala y Gómez island (26°27' S, 105°28' W), add a further 700 km. The Chilean continental shelf has an average width of 6.5 km and covers an area of approximately 27,470 km², the rest of the Chilean exclusive economic zone (EEZ) (3,393,770 km²) is deep-sea, a mix of abyssal, bathyal and hadal depths, deep ocean trenches (8,000 m off the Mejillones Peninsula), sub-oceanic ridges and seamounts (Castilla & Oliva 1987).

The continental coast of Chile is generally divided into three biogeographic zones, the Peruvian/Chilean province extending from Peru to around 40° S and the Magellanic province extending from around 43° S south, with an intermediate non-transitional zone in between (Camus 2001). The exact latitudinal range for each of these provinces varies depending on the set of taxa used for the analyses (Viviani 1979, Brattström & Johannsen 1983, Lancellotti & Vásquez 1999, Ojeda et al. 2000, Camus 2001, Hernández et al. 2005).

The major large-scale oceanographic process affecting the Chilean coast is the South Pacific anti-cyclonic gyre which reaches the coast between ca. 40 and 45° S where it branches into two current systems, the northward Humboldt system and the southward Cape Horn system (Castilla et al. 1993, Strub et al. 1998). Between ca. 18 and 40° S the Humboldt current induces upwelling which has a major influence on the coastal ecosystem,

making it one of the richest in the world (Arntz et al. 1991, Thiel et al. 2007). In areas of strong upwelling the deeper (bottom) water is often characterized by an oxygen minimum zone (OMZ) (Levin et al. 2002, Ulloa & Pol 2004). In northern Chile this occurs between depths of 50 and 400 m. In central Chile the OMZ is more seasonal but in winter it typically extends from depths of 100 to 300 m (Palma et al. 2005). The northern and central Chilean coast is also subject to periodic El Niño-Southern Oscillation (ENSO) events where warm, oxygen poor water masses move into the coastal regions disrupting the 'normal' coastal upwelling system (Arntz et al. 2006).

The objective of this paper is to review the species richness of all the taxa of benthic invertebrates that could potentially be found in Chilean marine territorial waters, something that no other review has accomplished. In addition, an assessment is made of the endemic diversity of the Pacific islands and the deep-sea, of the invasive or non-indigenous species (NIS), and the contribution that the Chilean benthic marine invertebrate fauna makes to the world benthic marine invertebrate fauna. Finally we comment on the state of knowledge, taxa by taxa, of the Chilean benthic marine invertebrate fauna.

MATERIAL AND METHODS

In this paper we have included any free-living species, described in the literature, which spends a significant proportion of its life-cycle in or on the benthic environment. We have not included any species endemic to Antarctica or whose life-cycle is exclusively pelagic. Species were added to the list on the following basis. All organisms identified to species level were included on the list. Where an organism was only identified to genus level (i.e., *Genus* sp.), then the decision as to whether it should be included on the list was made as follows. If the "*Genus* sp." had not been recorded elsewhere in the literature as being present in Chile then it was included. If the "*Genus* sp." was part of a list by the same authors that identified other species of the same genus then it was included. Finally, if a paper identified a "*Genus* sp." of a genus that had been recorded elsewhere in the literature then it was not included, unless the authors specifically

noted that their “*Genus* sp.” was distinct from other species of the same genus recorded elsewhere in the literature. Every effort was made to check for possible synonymies. Where a group is mentioned in the literature as being present in Chile but no species are identified we have made appropriate comments to that affect. An extensive and comprehensive review of literature was conducted and any species listed as present within Chilean territorial waters (see Introduction) was added to the list. We reviewed over 435 published articles for Chilean marine free-living invertebrates, the principal references used for each high level Linnean taxa are listed in Table 1. Web-based world databases were

consulted on occasion, particularly to clarify synonymy. However, significant information was obtained from online world databases only in the cases of Porifera (van Soest et al. 2005) and Isopoda (Schotte et al. 1995). Brusca & Brusca (2003) was used as a guide to the world total species numbers for the major taxa covered in this study. The exceptions were Nematoda and Turbellaria for which world totals were obtained from Warwick et al. (1998) and Artois & Schockaert (2005) respectively. From this information we calculated the contribution of the Chilean benthic marine invertebrate fauna to the world biodiversity of benthic marine invertebrates.

TABLE 1

The principal references used for each taxa

Referencias principales usadas para cada taxa

Group	Reference
Cnidaria	Moyano (1995), Cairns et al. (2005), Häussermann & Forsterra (2005), Glynn et al. (2007)
Porifera	Desqueyroux & Moyano (1987), Desqueyroux-Faúndez (1990), Desqueyroux-Faúndez & van Soest (1996), van Soest et al. (2005)
Turbellaria	Marcus (1954)
Polychaeta	Rozbaczylo (1985, 2000), Rozbaczylo & Carrasco (1995), Rozbaczylo & Simonetti (2000), Rozbaczylo & Moreno (2006)
Oligochaeta	Gluzman (1990)
Echiura	Saiz-Salinas et al. (2000)
Bryozoa	Moyano (1991, 1999, 2005)
Sipuncula	Tarifeño & Rojas (1978)
Mollusca	Valdovinos (1999)
Nemertea	Friedrichs (1970)
Entoprocta	Viviani (1969)
Brachiopoda	Foster (1989)
Insecta	Camus & Barahona (2002)
Crustacea	General (Báez 1994), Decapoda (Retamal 1981, Guzmán 2003, Poupin 2003), Stomatopoda (Guzmán, 2002), Isopoda (Menzies 1962, Schotte et al. 1995), Amphipoda (González, 1991, De Broyer & Rauschert 1999), Tanaidacea (Schmidt & Brant 2001), Cumacea (Gerken & Watling 1998, Muhlenhardt-Seigel 1999), Mysidacea (Holmquist 1957, Müller 1993), Mystococarida (Dahl 1952), Harpacticoida (George 1996, George 2005), Ostracoda (Hartmann-Schröder & Hartmann 1962, Kornicker 1975), Cirripedia (Parin et al. 1997, Pitombo & Ross 2002)
Chelicerata	Pycnogonida (Hedgpeth 1961, Child 1992), Halacarida (Newell 1984, Bartsch 2004)
Nematoda	Wieser (1953, 1954, 1956), Gambi et al. (2003)
Kinorhyncha	Lang (1953), Higgins (1977)
Priapulida	Sielfeld (2002a)
Echinodermata	Pawson (1967), Castillo (1968), Codoceo & Andrade (1978), Larraín (1995), O’Loughlin (2002), Mutschke & Ríos (2006)
Pterobranchia	Sielfeld (2002b)
Enteropneusta	Sielfeld (2002b)
Ascidae	Van Name (1954), Clarke & Castilla (2000)
Cephalochordata	Fowler (1945)

Where possible, the location or range for each species was recorded and from this information we were able to determine the number of species within each taxa endemic to the 'Pacific islands' (Easter Island, the Juan-Fernández archipelago, Sala y Gómez island and the Desventuradas Islands) and the 'deep-sea' (a mix of abyssal, bathyal and hadal depths, deep ocean trenches, sub-oceanic ridges and seamounts). The remaining species were considered 'continental', defined as species found on the coast of continental Chile, including species collected on the continental shelf, it also contains species that are found on the Pacific islands but which are not endemic to them.

Non-indigenous species present in Chile have been included in the list based on the criteria defined by Castilla & Neill (in press): species imported for aquaculture, and those NIS whose presence in Chile is either well documented in the literature or were reasonable candidates for NIS status.

RESULTS

The total number of free-living Chilean benthic marine invertebrate species identified in this review was 4,553. Table 2 presents the full list of species diversity in each taxa, a mix of phyla, sub-phyla and classes. The full list of species has been placed online at the following web address (This list of species is provided as supplementary material at the following links, www.ecim.cl/online_list/index.html and www.bio.puc.cl/cffpsr/publicaciones/online_list/index.html). The three most diverse taxa were the Crustacea, Mollusca and Polychaeta. The most diverse taxa within the Crustacea were the Decapoda, Amphipoda, Harpacticoida, Isopoda and Ostracoda (Table 3). Within the Mollusca, the most diverse taxa were the Gastropoda and Bivalvia (Table 3). A number of other taxa had more than 100 species, these were Bryozoa, Nematoda, Cnidaria, Porifera, Chelicerata and Echinodermata. The least diverse taxa, those with less than 100 species, were the Nemertea, Ascidiacea, Turbellaria, Brachiopoda, Entoprocta, Sipuncula, Insecta, Kinorhyncha, Priapulida, Enteropneusta, Pterobranchia, Cephalochordata, Phoronida and Rotifera. For a

number of taxa we were unable to find any species recorded as being present in Chilean territorial waters. They were Placozoa, Gastrotricha, Gnathostomulida, Cycliophora, Collembola, Tardigrada and Loricifera, though the groups Gastrotricha, Collembola, and Tardigrada have all been recorded as present in Chile.

The Chilean benthic marine invertebrate fauna as a proportion of the world benthic marine invertebrate fauna, in the case of the well studied taxa, ranges between less than 1 and 8 % (Table 4). The highest proportions were for the Nematoda followed by Bryozoa, Nemertea and Polychaeta. The lowest proportions were for the Turbellaria and Mollusca. As stated in the introduction, Chile's coastline represents ca. 0.65 % of the world total coastline, in comparison the diversity of the marine benthic fauna represents 2.47 % of the world biodiversity, for those taxa covered.

The preliminary number of species endemic to the Pacific islands is presented in Table 5. The taxa with the most endemic species were the Mollusca, Crustacea and Polychaeta, other taxa with large numbers of species endemic to the Pacific Islands were Bryozoa, Cnidaria, Porifera and Chelicerata. The most diverse taxa in the deep-sea were Crustacea, Nematoda and Bryozoa. However for most taxa there was little information available on their diversity in the deep-sea within Chilean territorial waters.

There are currently 25 NIS listed as present in the marine benthic environment of Chile and the taxa containing NIS are identified in Tables 2 and 3. The most NIS are found in the Polychaetes followed by the Mollusca. Ascidiacea, Porifera, Bryozoa and Crustacea also contain NIS. For all the other taxa in this study there is no information on the presence of NIS within Chilean territorial waters.

DISCUSSION

We report a total of 4,553 species of free-living benthic marine invertebrates listed in the literature for Chilean territorial waters. This is a much higher number of species than any of the previous reviews; for example, over 1,500 more species than Simonetti et al. (1995). This is because our review was comprehensive and set out to find information on all the possible

TABLE 2

Comparison of our assessment of the diversity of the Chilean benthic environment with those of Molina (1788), Gay (1848, 1854), Simonetti et al. (1995), and Lancellotti & Vásquez (2000). The numbers in parentheses are the number of non-indigenous species (NIS) in each group. NI indicates that there was no information available in the literature identifying species of this taxon

Comparación de nuestra evaluación de la diversidad del ambiente bentónico chileno con las publicadas por Molina (1788), Gay (1848, 1854), Simonetti et al. (1995) y Lancellotti & Vásquez (2000). Los números entre paréntesis corresponden al número de especies no indígenas (NIS) de cada taxa. NI indica que no se encontró información disponible en la literatura identificando especies de este taxa

Group	Molina (1788)	Gay (1848, 1854)	Simonetti et al. (1995)	Lancellotti & Vásquez (2000)	This study
Placozoa	0	0	0	0	NI
Cnidaria	0	22	196	39	273
Porifera	0	0	227	76	206(3)
Gastrotricha	0	0	0	0	NI
Rotifera	0	0	0	0	1
Gnathostomulida	0	0	0	0	NI
Cycliophora	0	0	0	0	NI
Turbellaria	0	0	0	0	42
Polychaeta	0	12	588	295	600(8)
Oligochaeta	0	0	0	0	11
Echiura	0	1	2	0	3
Bryozoa	0	0	331	0	387(2)
Sipuncula	0	2	15	0	17
Mollusca	8	227	1,187	611	973(6)
Nemertea	0	2	0	0	57
Entoprocta	0	0	0	0	17
Phoronida	0	0	1	0	1
Brachiopoda	0	7	18	0	20
Collembola	0	0	0	0	NI
Insecta	0	0	0	0	11
Crustacea	8	117	606	336	1,219(1)
Chelicerata	0	3	0	0	178
Tardigrada	0	0	0	0	NI
Nematoda	0	0	0	0	326
Kinorhyncha	0	0	0	0	5
Loricifera	0	0	0	0	NI
Priapulida	0	0	2	0	4
Echinodermata	2	12	0	67	142
Pterobranchia	0	0	2	0	2
Enteropneusta	0	0	1	0	2
Ascidacea	1	3	0	40	55(5)
Cephalocordata	0	0	0	0	1
Total	19	408	3,166	1,464	4,553(25)

marine invertebrate taxa that could be present in the benthos, none of the previous reviews had attempted to do so. We also included a wider geographic area than the other studies, with the exception of Simonetti et al. (1995) where terrestrial, freshwater, pelagic marine, and in some cases Antarctic fauna were included. In the case of some groups, for example 'helminths' covered in Simonetti et al. (1995), no attempt was made to discuss the free-living species and the discussion concentrated on the parasitic forms that are important in agriculture. In the case of Mollusca in particular, Simonetti et al. (1995) identified *ca.* 200 species more than we have recorded for this work. This difference, in large part, represents the terrestrial, freshwater and pelagic marine species of molluscs present in Chile. With reference to the papers by Brattstrom & Johanssen (1983) and Lancellotti & Vásquez (2000) we found more species. However, these papers are concerned with the zoogeography of the continental Chilean marine benthic invertebrate fauna, and therefore the authors only used a subset of the total marine benthic diversity selecting species for which there was sufficient information with which to conduct an analysis of that type. In all reviews, including the historic ones by Molina (1788) and Gay (1849, 1854) the two most abundant taxa were Crustacea and Mollusca. Leaving aside issue of whether these two taxa are in fact the most speciose, this result is to be expected as both taxa are: (a) predominantly macrofaunal and easily observed, (b) contain the majority of economically important marine invertebrates. For some taxa we were unable to find any information in the literature about their presence, or absence, in the Chilean benthic fauna. In most, if not all, cases this is a result of a lack of 'sampling effort' rather than the taxa being absent from Chilean waters. For example, Gastrotricha are common and abundant members of the meiofauna of sandy beaches (Rodríguez et al. 2001, Lee & Correa 2005), however to date no paper has been published identifying the species present in Chile.

Historically there have been more than 42 major expeditions to Chilean waters which have added a considerable amount of information about the diversity of benthic invertebrates. In addition to Molina (1788)

and Gay (1849, 1854) another naturalist of historical significance, D'Orbigny, traveled through South America between 1826 and 1833. The resulting eleven volumes of the "Voyage dans l'Amérique Meridionale" describe a number of Chilean species from material collected on that trip (Taylor & Gordon 2002, Vénéce-Peyré 2004). A number of important expeditionary cruises have passed through Chilean waters, including the HMS Beagle (1831-1836) with Charles Darwin on board. Later the famous H.M.S. Challenger expedition passed through Chile between 1872 and 1876. One of the most important expeditions to Chile during the last century was the Swedish Lund expedition (1948-1949) which produced a whole series of important monographs on a wide diversity of taxa (Brattström & Dahl 1951). More recent expeditions include the B/I Victor Hensen which visited the Magallenic region in 1994, the CIMAR (Crucero de Investigación Científico-Marina en Áreas Remotas) series of 12 cruises which is an initiative of the Comité Oceanográfico Nacional (CONA, Chile) designed to further research in the more remote regions and less well studied areas of Chilean territorial waters (1995-2006), and the German PUCK Expedition on board of the R/V Sonne (2001). These expeditions have generated a considerable amount of type material which is deposited in major museums around the world (British Museum of Natural History (London, United Kingdom); Muséum National d'Histoire Naturelle (Paris, France); National Museum of Natural History (Washington, District of Columbia, USA); Naturhistoriska Riksmuseet (Stockholm, Sweden); Zoologisches Institut und Zoologisches Museum der Universität Hamburg (Germany); as well as in national collections (Museo Nacional de Historia Natural, Santiago); "Colección Flora y Fauna Profesor Patricio Sánchez Reyes", Facultad de Ciencias Biológicas de la Pontificia Universidad Católica de Chile, Santiago (SSUC); Museo de Zoología de la Universidad de Concepción; Museo del Instituto de Oceanología de la Universidad de Valparaíso). There have also been a number of more recent attempts to review the biodiversity of flora and fauna in Chile (Simonetti et al. 1995, CONAMA 2006a).

TABLE 3

The number of species in each of the taxa of Crustacea and Mollusca. The numbers in parentheses are the number of NIS in each taxa

Números de especies para los taxa Crustacea y Mollusca. Los números entre paréntesis corresponden al número de especies invasoras de cada taxa

Crustacea		Mollusca	
Order	Specie	Order	Specie
Decapoda	367(1)	Aplacophora	8
Stomatopoda	8	Bivalvia	219(2)
Leptostraca	3	Cephalopoda	20
Isopoda	174	Gastropoda	649(4)
Amphipoda	266	Monoplacophora	1
Tanaidacea	29	Polyplacophora	63
Cumacea	19	Scaphopoda	13
Mysidacea	29		
Tantulocardia	NI		
Mystacocarida	1		
Harpacticoida	185		
Ostracoda	110		
Cirripedia	28		
Total	1,219(1)		973(6)

TABLE 4

The Chilean marine benthic invertebrate fauna as a proportion of the world marine benthic invertebrate fauna. Brusca & Brusca (2003) was used as a guide to the world total species numbers for the major taxa covered in this study. The exceptions were Nematoda and Turbellaria for which world totals were obtained from Warwick et al. (1998) and Artois & Schockaert (2005) respectively

La fauna chilena de invertebrados marinos bentónicos como una proporción de la fauna mundial de dichos invertebrados. El trabajo de Brusca & Brusca (2003) fue usado como guía para determinar el número total de especies para los taxa principales usados en este estudio.

En el caso de Nematoda y Turbellaria, los totales mundiales fueron obtenidos desde Warwick et al. (1998) y Artois & Schockaert (2005), respectivamente

Group	World	Chile	%
Porifera	5,500	206	3.75
Cnidaria	10,000	273	2.73
Turbellaria	6,200	42	0.68
Polychaeta	10,000	600	5.98
Bryozoa	4,500	387	8.6
Mollusca	93,195	973	1.04
Nemertea	900	57	6.33
Crustacea	30,000	1219	4.06
Nematoda	4,000	326	8.15
Echinodermata	7,000	142	2.03
Total	171,295	4,225	2.47

TABLE 5

The number of species endemic to the Chilean Pacific islands: Easter Island, the Juan Fernández Archipelago, Sala y Gómez island, and the Desventuradas Islands. "Continental" refers to species found on the coast of continental Chile, including species on the continental shelf, it also includes some species that are found on the Pacific islands but which are not endemic to them. The "deep-sea" includes species found on sea-mounts, oceanic ridges, deep-sea plains off the continental shelf and trenches. NI indicates that there was no information available in the literature identifying species of this taxa

Números de especies endémicas en Isla de Pascua, Archipiélago Juan Fernández, isla Sala y Gómez e Islas Desventuradas. El concepto de "Continental" se refiere a especies encontradas en la costa de Chile continental, incluida la plataforma continental, además se incluyen algunas especies no endémicas de las islas oceánicas chilenas. El concepto de "mar profundo" se refiere a especies encontradas en montes submarinos, cordilleras oceánicas, llanuras profundas fuera de la plataforma continental y fosas. NI indica que no se encontró información en la literatura identificando especies de este taxa

Group	Pacific islands	Continental	Deep-sea
Placozoa	NI	NI	NI
Cnidaria	39	226	8
Porifera	31	167	8
Gastrotricha	NI	NI	NI
Rotifera	0	1	0
Gnathostomulida	NI	NI	NI
Cycliophora	NI	NI	NI
Turbellaria	5	37	0
Polychaeta	102	498	0
Oligochaeta	0	11	0
Echiura	0	3	0
Bryozoa	62	315	10
Sipuncula	2	10	5
Mollusca	184	789	0
Nemertea	3	54	0
Entoprocta	0	17	0
Phoronida	0	1	0
Brachiopoda	1	15	4
Collembola	NI	NI	NI
Insecta	0	11	0
Crustacea	126	947	146
Chelicerata	25	147	6
Tardigrada	NI	NI	NI
Nematoda	0	310	16
Kinorhyncha	0	5	0
Loricifera	NI	NI	NI
Priapulida	0	4	0
Echinodermata	16	124	2
Pterobranchia	0	2	0
Enteropneusta	0	2	0
Ascidacea	3	52	0
Cephalocordata	0	1	0
Total	599	3,749	205

The most abundant taxon in the Chilean marine benthos is the Crustacea, the most recent revision of which was by Báez (1994). Within the Crustacea the most abundant taxon is the Decapoda, which contain the majority of the commercially important crustaceans, and are predominantly macrofaunal. As a result, and as discussed previously, this taxon has received a considerable amount of attention from marine biologists over the years, starting back in the 18th century (Molina 1788). Recent reviews include those by Retamal (1981) and Boschi & Gavio (2005). Amphipoda, the second most abundant taxon of crustaceans, are found in a wide variety of niches within the benthic environment, from the intertidal to the deep-sea trenches. The other Peracarida taxa, Isopoda, Tanaidacea and Cumacea, are also relatively abundant. All the peracardid taxa are actively studied by researchers based here in Chile, and new species are being added on a regular basis (González & Thiel 2004). The Harpacticoida, the third most abundant taxon of crustaceans are an important component of the meiobenthos and often the most abundant and diverse taxon within meiofaunal samples. Our current knowledge of this taxon is based primarily on the work of two authors, George (1996, 1998, 2005) and Mielke (1985, 1986, 1989, 1992), neither of whom is currently based in Chile. It is likely, therefore, that the number of species within this taxon will grow with more research. Another abundant taxon of meiofaunal crustaceans are the Ostracoda which are present in all the benthic habitats. This taxon was the subject of a monograph by Hartmann-Schröder & Hartmann (1962), and this work was then extensively reviewed and revised by Kornicker (1975) and further species were added. Again, there are no researchers actively working on this taxon in Chile currently, but there is undoubtedly more species to be discovered. The Cirripedia are well studied, in the intertidal and subtidal at least, it is unlikely that there remain many new species to be added. The exception, however, may be in the deep-sea where a number of new species have been added in recent years (Parin et al. 1997). None of the remaining taxa of crustaceans (Mysidacea, Stomatopoda, Leptostraca and Mystacocarida) are particularly speciose on a global scale and that pattern holds within the Chilean marine benthos. The

only taxon within the Crustacea for which we could find no information was the Tantulocardia which are a small, typically deep-sea, meiofaunal taxon. However, this group has been found in deep-water sediments of the Drake passage, south of Cape Horn (Gutzmann et al. 2004) and it is probable that will be found within Chilean waters eventually.

The Mollusca is also a well studied taxon, the majority of species are macrofaunal and a number are economically important. The most recent major review was that by Valdovinos (1999). There is a sharp increase in the diversity of the Mollusca south of 42° S which Valdovinos et al. (2003) attributed to various factors including the greater shelf area, geographic isolation produced by ocean currents and the presence of refuges during past periods of glaciation. The taxonomy of the Mollusca is under constant revision and 50 (5.1 %) of the species listed in our review are currently being checked and revised. It is not expected that number of macrofaunal species will increase much, however the micro-mollusca are little studied and there may well be additional species to be added from this category (Valdovinos 1999).

The Annelida, particularly the Polychaeta have been well studied in Chile over the years. The most recent reviews of the polychaetes are by Rozbaczylo (1985), Rozbaczylo & Moreno (2006) and Rozbaczylo & Moreno (in press) and there are a number of researchers within Chile actively working on this taxon. The polychaetes are the most abundant of the annelids by far, new species are added regularly, and there are almost certainly many more species to be added to the list of polychaetes. There are four additional families of polychaetes: Ctenodrillidae, Nerillidae, Polygordidae and Protodrillidae, to be added from the interstitial fauna to the Chilean records (M.R. Lee, personal observation, S. Cifuentes, personal communication). The relative positions of the Echiura and Clitellata (which includes oligochaetes) within the Annelida is subject to much discussion in the literature (see Purschke et al. 2000). Westheide (1997) goes as far as to place the Clitellata as a clade within the Polychaeta. In this paper we have treated each as a separate taxon. The Oligochaeta are abundant if not especially speciose members of the meiofauna on both

sandy and rocky-shores (M.R. Lee, personal observation). However, despite their ecological importance, particularly in the breakdown and recycling of organic matter, they are a poorly studied taxon, not just in Chile, but globally (Giere 2000). Echiura are a species-poor taxon rarely encountered in the intertidal. As many are found in deep water it is likely that new species will be added only with increased sampling effort of the deep-sea habitats.

The other diverse taxa, those with more than 100 species, were the Nematoda, Cnidaria, Chelicerata, Echinodermata, Bryozoa and Porifera. The Nematoda are found in all the habitats available in the benthic environment and are one of the most important groups within the meiofauna. There is certainly a great deal still to be ascertained regarding their biodiversity, particularly in the deep-sea habitats. The current list of 326 species is based on the work of only a few authors, primarily the Lund expedition reports of Weiser (1953, 1954, 1956). The Epsilonematidae in Chile were studied by Clasing (1980, 1983, 1986). The most recent contribution concerned the nematodes of the deep-sea Atacama trench off the Chilean coast (Gambi et al. 2003), the information in this paper only listed nematode genera, but they state that they found 119 species in their samples, so once this information is published the list will increase. In this paper the number of Cnidaria has increased 29 % relative to the last major revision by Moyano (in Simonetti et al. 1995) as a result of recent work by Häussermann and others who have revised, and in some cases redescribed, the diversity of corals and anemones of the Chilean coast (Häussermann 2003, 2004, 2006, Cairns et al. 2005, Försterra et al. 2005, Häussermann & Försterra 2005). The taxon of cnidarians currently undergoing the most revision are the hydrozoans which are found on nearly all the substrates available in the benthic marine environment. The importance of hydrozoans and other "passive suspension feeders" has been underestimated for many years, but new evidence has determined they can play an important role in ecosystems food chains (Gili et al. 1998, Orejas et al. 2000a, 2000b, Genzano 2005). There have been recent efforts in the south of Chile to revise this taxon (Peña & Cantero 1999, Orejas et al. 2000b), to describe some new species

(Galea 2006a) and redescribe others (*Hybocodon chilensis* (Hartlub, 1905) (Galea 2006b). The Chelicerata include the Halacaridae mites and the Pycnogonida. The Pycnogonida seem to be relatively well known (Hedgpeth 1961, Child 1992) as do the halacarid mites (Newell 1984, Bartsch 2004), however, there are important gaps in the information. There are several other taxa of Acari which are, or could be, found within the benthos, for example, Hyadesidae mites are common in intertidal samples, particularly in phytal material (M.R. Lee, personal observation), but we were unable to find any species specific information in the literature for this taxa.

The Bryozoa is a diverse and well studied taxon in Chile with a lot of information being derived from a number of the expeditions and cruises in Chilean waters. Recently Bryozoa have begun to attract a significant amount of attention as a source of useful pharmaceutical compounds, for example bryostatin (e.g., Sun & Alkon 2006). These investigations may well drive further research into their diversity and the identification of new species. Within Chile the Porifera is a diverse taxon, however there is no Chile based taxonomist actively working on the taxon. There is considerable diversity within the Echinodermata and the ecologically important taxa Asterozoa and Echinozoa have received some attention (e.g., Espoz & Castilla 2000, Fuentes & Barros 2000, Ortiz et al. 2003), though other taxa within the Echinodermata; Crinozoa, Ophiurozoa and Holothurozoa have received less. Important work on echinoderms was carried out by Larraín (Larraín 1995), working at the Universidad de Concepción where an important collection of echinoderms is held.

Taxa with lower diversities, less than 100 species, were the Nemertea, Turbellaria, Brachiopoda, Entoprocta, Sipuncula, Insecta, Kinorhyncha, Priapulida, Ascidiacea, Pterobranchia, Enteropneusta, Cephalochordata, Phoronida and Rotifera. The majority of the Nemertea species in Chile were described by Friedrich (1970) based on material collected by the Lund expedition. Less than 20 % of the described species have been added since then, mainly by Sánchez (Sánchez 1973). There are probably a few species still to be added to the Chilean fauna, but mainly from the interstitial

environment. For example, samples from Chile are currently being used in the revision of the family Ototyphlonemertes (S. Andrade, personal communication). Turbellaria are not well studied in Chile despite their abundance and potential diversity and there are no recent reviews of the group. They are to be found in all the benthic environments and in some habitats (e.g., the swash zone of high-energy beaches) they can be the dominant organisms (Lee & Correa 2005). Over 50 % of the turbellarian species recorded in the literature for Chile belong to the relatively large body sized polyclads and triclads. Approximately two thirds of turbellarian biodiversity consists of species of less than two millimeters in length (Cannon 1986). Therefore, it is highly likely that the list of Chilean species will expand considerably with further research. After the first work on Sipuncula collected by the Lund Expedition, Tarifeño (in Simonetti et al. 1995) revised and brought up to date the list of species. The number of species of Sipuncula has increased recently with surveys of the fauna of the Magallanic region (Saiz-Salinas & Pagola-Carte 1999). The Entoprocta in Chile were studied by Viviani (1969) though further information beyond the number of species in Chile, such as their ranges, biology and ecology, is unavailable. The Insecta form an interesting and under studied component of the benthos (Camus & Barahona 2002). They are often regarded as terrestrial organisms, temporally visiting the intertidal during low tide. This is however, a misconception, as the larval stages of many species spend their entire time in the intertidal and this stage in the life-cycle is often the longest. They could therefore be considered marine organisms with a short airborne reproductive stage. They are typically restricted to the intertidal zone where they may be very abundant, for example chironomid larvae in phytal samples (M.R. Lee, personal observation).

Kinorhyncha are confined to the meiofauna and globally are not particularly species rich, a few species may remain to be described from Chilean waters. Priapulida is likewise a low diversity taxon, more species may be discovered with increased sampling of the deep-sea habitats. Brachiopoda are typically found in cold and or deep-water and the recorded biodiversity for this taxon is unlikely rise without an increase in sampling effort in

these types of environments, particularly the deep-sea. Ascidiaceans play an important role in the structuring of intertidal communities in Chile and *Pyura chilensis* (Molina, 1872) and *P. praeputialis* are also an exploited resource along much of the coast. The most recent review of this taxon was by Clarke & Castilla (2000). Hemicordata is a small taxon with a global diversity of only 105 species, divided between three clades, only two of which are benthic, the Enteropneusta and Pterobranchia, (Cameron 2005). Within Chile there are two species from each, with the Pterobranchia being restricted to cold southern waters. There may well be more species to be identified from Chile, but judging by their poor global diversity, not many. Rotifera, Phoronida, and Cephalochordata, each have a single species recorded from Chilean territorial waters. However, as none of these taxa is diverse globally within the marine environment, it is unlikely that there are many species still to be described from within the Chilean fauna.

There is no published information about the presence or absence of species of seven taxa in Chilean marine territorial waters to be found in the literature. Gastrotricha, Collembola and Tardigrada are present in the marine benthos of Chile (Rodríguez et al. 2001, Sellanes et al. 2003, Lee & Correa 2005). Gastrotricha are common members of the meiofaunal assemblage of sandy beaches and also appear in trapped sand microhabitats on the rocky shore. Collembola live in the intertidal and on some sandy beaches can be present in extremely high densities. Tardigrades inhabit most sedimentary and phytal habitats including the trapped sand microhabitats and exposed sandy beaches. Recent sampling of *Perumytilis purpuratus* (Lamarck, 1819) beds in central Chile has revealed at least two species (*Echiniscooides* sp. and *Batilipes* sp., M.R. Lee, unpublished data). Placozoa is a taxon with two species *Trichoplax adhaerens* (Schulze, 1883), and *T. reptans* (Monticelli, 1893). Nothing is known of its ecology as it has only been found in marine aquaria worldwide, though the original observations were made on specimens that came from Red Sea algal detritus (Miller & Ball 2005). This taxon may well be present in Chile but has yet to be observed. Gnathostomulida are typical of low energy, slightly anoxic, marine environments (Sterrer

& Farris 1988). Again there is no observation of this taxon in Chile, however, it is likely that they are present. Cycliophora is a single species (*Symbion pandora*) taxon (Funch & Kristensen 1995) that lives commensally on the mouth parts of the crustacean *Nephrops norvegicus* (Linnaeus, 1758) (Winnepenninckx 1998). It is possible that this taxon will be found in Chile, however, they may be easily confused with the Rotifera, to which they are closely related, and which also often live commensally on crustaceans. Loricifera (Higgins & Kristensen 1988) are very small meiofaunal organisms and are normally found in deep water sediments, it is probably only a matter of time before they turn up in samples from off the Chilean coast as they have been observed in samples in the Drake Passage region directly south of Cape Horn (Gutzmann et al. 2004).

The level of understanding of the diversity in benthic marine environment is not evenly distributed across the range of taxa. Species with large body size in shallow water are well studied, but species with small body size or from the deep-sea are less well known. Even in the intertidal there are still a considerable number of species of small body size yet to be identified and described. Understandably, from the earliest work through to the present day the majority of work has concerned itself with those species that are directly or indirectly of commercial or applied value. However, small body-sized organisms, largely ignored in most studies, could contribute 50 % or more of the diversity in some habitats (M.R. Lee, unpublished data). There are several taxa, the Tardigrada, Kinorhyncha, Loricifera, Gastrotricha and Gnathostomulida, which are exclusively meiofaunal and many others where the majority of species are meiofaunal in size, e.g., Harpacticoida and Nematoda. Clearly, the less accessible habitats are the least well studied, these include the deep-sea habitats (trenches, ridges and seamounts), the bases of cliffs, and off-shore reefs. However, even in the well studied habitats there is still much to learn.

Estimates of the contribution of Chilean benthic marine invertebrate species to the world fauna benthic marine invertebrates are of necessity rough guides, for each major group estimates vary considerably from one source to another. The diversity of the Chilean free-

living marine benthic invertebrate fauna represents 2.47 % of the world invertebrate diversity, for this environment. It is very difficult to judge whether these figures represent the true situation or, more likely, reflect the amount of effort spent on describing the Chilean benthic marine invertebrate fauna relative to other areas of the planet. For example, the highest contribution (8.90 %) was for the Bryozoa, this is a result of the extensive work of Moyano (1991, 1999, 2005). Similarly the Nematoda with 8.15 % of the world fauna reflects the extensive work of Weiser (1953, 1954, 1956) on material from the Lund Expedition, which is recognised as a classic work in the free-living nematode taxonomic literature. Nemertea with 6.33 % fauna again represents the benefit of the extensive sampling of the Lund expedition. Another significant contribution to the world fauna is made by the Polychaeta (5.98 %) which reflects the extensive and long-term research of Rozbaczylo and collaborators (Rozbaczylo 2000).

Our analysis of the endemism associated with the Pacific Islands indicates that 13.23 % of the species present in Chilean marine benthic environment are found exclusively on the islands. While many of the large predominantly macrofaunal taxa have been studied on the Pacific Islands (see Castilla 1987, for a general account), the smaller body-size and small, in terms of diversity, taxa are less well studied. For example there is no information on the Nematoda on the Pacific Islands despite them being the fifth most diverse taxon in the overall analysis. With respect to the deep-sea we have even less information, for most groups none at all. The deep-sea fauna recorded in this analysis represents 4.53 % of the total biodiversity of the benthic marine environment of Chile. There is therefore clearly a considerable amount of information still to be gained from sampling the deep-sea habitats.

The World Conservation Union (IUCN) does not list any Chilean marine invertebrates as either, critically endangered, endangered or vulnerable (IUCN 2006). There is a process currently under way at the Comisión Nacional del Medio Ambiente (CONAMA, Chile) to consider the conservation status of Chilean species, however, currently no marine

invertebrate species have been considered (CONAMA 2006b). The paucity of information on the conservation status of species is due in large part to our lack of knowledge of the biology and ecology of the vast majority of benthic marine invertebrates. For many species we know little more than that it is present in Chilean territorial waters and where it was found. This lack of knowledge needs to be addressed if we are ever to successfully protect the marine ecosystems as a whole in Chile.

A similar comment can be made about invasive or non-indigenous species in Chile. There are currently only 25 NIS of benthic marine invertebrates listed (Castilla et al. 2005, Moreno et al. 2006, Castilla & Neill in press). This number appears surprisingly low in the global context and readers are referred to Castilla et al. (2005) and Castilla & Neill (in press) for discussions on this situation.

Future research should be directed at those taxa with predominantly small body size individuals and those inhabiting the deep-sea. Currently so little is known about these species that we can not say how important they are to the general ecology of a given habitat. For example, if the population of harpacticoid copepods at a given site is killed off as a result of their sensitivity to elevated metal concentrations how will that affect the algal cover in the rocky intertidal at that site? In order to facilitate this research funding agencies need to take a longer term, broader, view of the advancement of scientific knowledge in Chile and fund not only applied research, but the basic "blue skies" research that underpins that applied work. The ability to identify organisms to species level is fundamental to all other work in the marine environment, be it conservation, ecology or aquaculture. You can not protect a species if you do not know it exists, nor biodiversity in general if you can not quantify it accurately. Ecology conducted at the family level is much weaker than that conducted at the species level, methods using taxonomic surrogacy suffer from fundamental flaws due to a lack of understanding of the true meaning of the Linnaean system of ranks (Bertrand et al. 2006). However, researchers with the knowledge required to make these identifications, taxonomists, are dying breed,

thanks in large part to the lack of available funding (Kim & Byrne 2006). Training courses, like the "Third International Course on Ecology and Taxonomy of Peracarida" held in Coquimbo in July 2006, should also be actively encouraged and supported by the major funding bodies as a way of enhancing expert taxonomic knowledge within the Chilean scientific community. Also required are further expeditions, preferably, organized at a national level, with the objective of filling in the holes in our knowledge of the biodiversity of the benthic environment identified in this paper.

This review of the information available in the literature has revealed that the free-living invertebrate fauna of the benthic environment of Chile is speciose. We have illustrated, taxa by taxa, where the gaps in our knowledge lie. It is important to remember that this review is a snapshot of the state of knowledge in 2007 and that in 12 months time the picture may well be different. New species will be added to the list, and some species will disappear when they are discovered to be junior synonyms or incorrectly identified. Note also, that the taxonomy is not stable, most groups are continually under review. Fortunately the increased availability of online databases will allow us to keep better track of these changes (e.g., Turbellaria (Artois & Schockaert 2005), Isopoda (Schotte et al. 1995), Porifera (van Soest et al. 2005)). A comprehensive view of biodiversity is vital to a better understanding of how the marine benthic environment functions, and how best to protect it from our activities.

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