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THE MAGELLAN-ANTARCTIC CONNECTION: LINKS AND FRONTIERS AT HIGH SOUTHERN LATITUDES.
W.E. ARNTZ, G.A. LOVRICH and S. THATJE (eds.)

Distribution patterns of Chilean shallow-water sea anemones (Cnidaria: Anthozoa: Actiniaria, Corallimorpharia), with a discussion of the taxonomic and zoogeographic relationships between the actinofauna of the South East Pacific, the South West Atlantic and the Antarctic*

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SUMMARY: The first complete zoogeographical analysis of Chilean shallow water sea anemones (Actiniaria and Corallimorpharia) and their taxonomic relations with neighbouring faunas is provided, based on extensive recent sampling in combination with a literature review. Between 1994 and 2004, we collected more than 1000 specimens of 32 distinct species of Actiniaria and Corallimorpharia at more than 100 sites along the Chilean coast between Arica (18°30'S; 70°19'W) and the Straits of Magellan (53°36'S 70°56'W). Sampling was done in the intertidal during low tides and in the subtidal by means of SCUBA diving down to depths of 40 m. The northern part of the Chilean fjord region showed the highest number of species (23). Our results contradict an abrupt general change in the marine faunal composition at 42°S, instead showing the continuation of species of the exposed coast and the joining of fjord species due to the availability of additional habitats in the richly structured fjord region south of 42°S, and also to eurybathy. The southern distribution limits of the species we found in northern and central Chile show only one significant concentration around the Peninsula Taitao (approx. 48°S). This either indicates a zoogeographic barrier for shallow water species at the Peninsula Taitao, or is a sampling artifact caused by poor data from the region between the Peninsula Taitao and the Straits of Magellan. According to the literature, 18 of the 63 described Chilean sea anemones (Pacific Ocean) can also be found in Argentina (Atlantic Ocean) and 13 in the Antarctic. However, many records and statuses of the common species of the South East Pacific and the South West Atlantic/Antarctic are uncertain or doubtful and need revision or confirmation.

Keywords: Actiniaria, Corallimorpharia, species list, zoogeography, distribution, benthos, Chile, Argentina.

RESUMEN: PATRONES DE DISTRIBUCIÓN DE ANÉMONAS DE MAR CHILENAS DE AGUAS SOMERAS (CNIDARIA: ANTHOZOA: ACTINIARIA, CORALLIMORPHARIA); CON UNA DISCUSIÓN DE LAS RELACIONES TAXONÓMICAS Y ZOOGEOGRÁFICAS DE LA ACTINOFAUNA DEL PACÍFICO SUDORIENTAL, EL ATLÁNTICO SUDOCCIDENTAL Y LA ANTÁRTIDA. – La presente publicación provee un primer análisis zoogeográfico completo de las anémonas de mar (Actiniaria y Corallimorpharia) de las aguas someras a lo largo de la costa chilena y de sus relaciones con faunas vecinas, basando en un extenso muestreo en los últimos años en combinación con revisiones de la literatura. Desde 1994 hasta 2004 obtuvimos mas de 1000 ejemplares pertenecientes a 32 especies de Actiniaria y Corallimorpharia. Se muestrearon mas de 100 lugares enclavados en el intermareal y el submareal hasta 40 metros de profundidad, a lo largo de la costa chilena entre Arica (18°30'S 70°19'W) y el Estrecho de Magallanes (53°36'S 70°56'W). La parte norte de la región de los fiordos chilenos presenta el máximo número de especies (23). Nuestros resultados muestran la continuación de especies características de costas expuestas y la agregación de especies típicas de los fior-

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dos, lo cual se contradice con el concepto arraigado del cambio brusco y general en la composición de la fauna marina a partir de 42ºS. Los límites de distribución sureña de especies que encontramos en la región del centro-norte de Chile muestran solamente una concentración significativa alrededor de la Península Taitao (aprox. 48ºS). Esto bien indica una barrera zoogeográfica para especies de aguas someras en la Península Taitao o también puede ser debido a un artefacto de muestreo causado por la falta de datos que existe de la región entre la Península Taitao y el Estrecho de Magallanes. Según la literatura, 18 de las 63 especies de anémonas de mar descritas para Chile (Pacifico Sudoriental) han sido también citadas en Argentina (Atlántico Sudoccidental) y 13 en la Antártida. Sin embargo muchos registros y estatus taxonómicos de las especies comunes del Pacifico Sudoriental y del Atlántico Sud-occidental/Antártida son dudosos y requieren revisión y confirmación.

Palabras clave: Actiniaria, Corallimorpharia, lista de especies, zoogeografía, distribución, bentos, Chile, Argentina.

INTRODUCTION

The coast of continental Chile extends over almost 4200 km and flanks a large part of the South East Pacific. While the coastline between Arica (18°20'S) and Chiloé Island (approx. 42°S) is poorly contoured, the region between Chiloé and Cape Horn (approx. 56°S) is highly structured and presents a large number of islands, channels and fjords. An increased number of species can be observed there (Fernández *et al*., 2000, own observation), probably due to the highly heterogeneous coast with a large variety of habitats (Ward *et al*., 1999), the occurrence of marked differences within short distances (Antezana, 1999) and the existence of refugia in the Chilean fjord region during glaciation (Valdovinos *et al*., 2003).

During the last three decades, a large number of papers have dealt with the biogeography of Chilean benthic invertebrates. While most studies have included only one taxonomic group (Sebens and Paine, 1979; Moyano G., 1991; Desqueyroux-Faúndez, 1994; Ojeda *et al*., 2000; Montiel *et al*., 2005), some have summarised available data on the biogeography of various taxa and oceanographic processes (Viviani, 1979; Brattström and Johanssen, 1983; Castilla *et al*., 1993; Lancellotti and Vásquez, 1999; Fernández *et al*., 2000; Camus, 2001). Most studies have proposed two main biogeographic regions within Chile: the Peruvian or warm-temperate Province between the Peninsula Illescas (or Bayovar) (approx. 6°S) and Chiloé Island (42°S) and the Magellan or cold-temperate Province between Chiloé Island and Cape Horn (56°S) (Fig. 1), which extends into Argentina to the Rio de la Plata (36-38°S) (Riemann-Zürneck, 1986; Zamponi *et al*., 1998a). Several authors have recognised a transitional area somewhere between 30 and 42°S where both faunas occur (e.g. Stuardo, 1964; Desqueyroux-Faúndez, 1994). Pickard (1973) subdivided the Magellan Province into three regions, the North Zone (42°S to approx. 46.5°S), the central zone (46.5°S to approx. 53°S) and the southern zone (S of approx. 53°S) due to different oceanographic conditions. Viviani (1979) and Stuardo and Valdovinos (1992) suggested the same sub-regions based on the distribution pattern of benthic invertebrates and called them Northern, Central and Southern Patagonia. A recent study including a wide set of invertebrates from the intertidal to 100 m depth. (Lancellotti and Vásquez, 1999) negates the widely assumed faunal break at 42°S and proposes a transitional temperate region between 35 and 48°S where a gradual but important change in the species composition occurs.

Many benthic organisms, especially those of shallow water, show population fluctuations in sea-

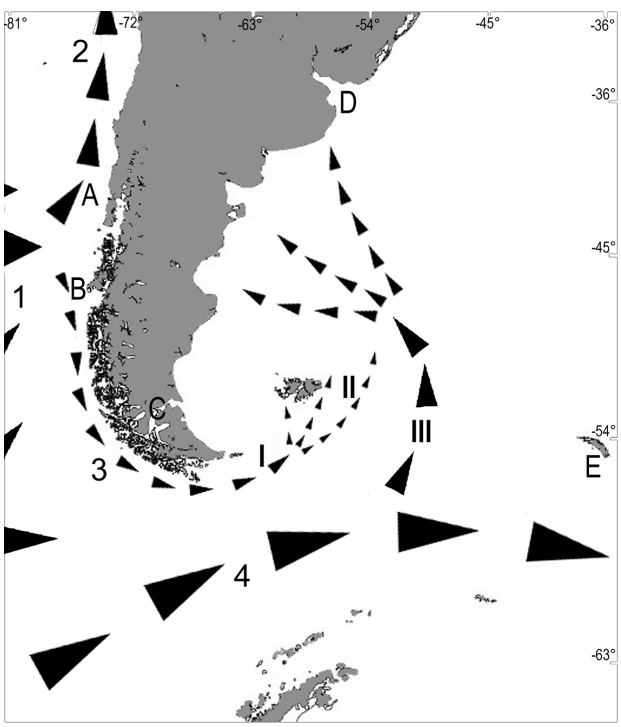

FIG. 1. – Southern South America with major currents (numbers): 1 Westwind Drift, 2 Humboldt Current, 3 Cape Horn Current, 4 Circumpolar Current; I Burdwood Bank, II Falkland Plateau, III Shag Rock Passage; zoogeographic barriers for benthic invertebrates: A Assumed limit between Peruvian and Magellan Province, B Peninsula Taitao and Golfo de Penas, C Straits of Magellan, D Rio de la Plata, E South Georgia.

sonal or several year cycles. Sea anemones with a—for invertebrates—comparably long life span are less susceptible to short term environmental changes and their populations show comparably few annual fluctuations. These conspicuous sessile marine invertebrates are present in almost all marine habitats; especially in higher latitudes they can be abundant or even dominating. These characteristics make them an excellent taxonomic group for long-term monitoring and detection of general zoogeographic patterns and trends (Riemann-Zürneck, 1986). Since the large vessel-based expeditions to the sea off Chile between 1850 and 1950 (Verrill, 1869; Hertwig, 1882; Carlgren, 1899 (for 1898); McMurrich, 1904; Carlgren, 1927; 1959), the Chilean actinofauna, although quite abundant, has received very little attention. While for many benthic invertebrates the data from the Lund University Chile Expedition created a good basis for subsequent taxonomic and zoogeographic work (e.g. Garth, 1957; Pawson, 1969), Oscar Carlgren died before he could finish his publication about the sea anemones of the Lund University Chile Expedition. As a consequence, the publication is incomplete and the existing descriptions are very short and preliminary (see Carlgren, 1959). Since the middle of the 20th century only a very small number of papers with restricted topics (Carter, 1965; Stotz, 1979; Brace, 1981; Riemann-Zürneck and Gallardo, 1990; Zamponi and Excoffon, 1995; Dayton *et al*., 1995; Häussermann and Försterra, 2001; Häussermann, 2003; Häussermann and Försterra, 2003; Häussermann, 2004b; 2004a; 2005) have been dedicated to the Chilean actinofauna. Sebens and Paine (1979) published the first biogeographic study of the Chilean Actiniaria and Corallimorpharia, mainly based on literature. Despite some recent expeditions to the Chilean fjord region (Joint Magellan "Victor Hensen" Campaign 1994; several Cimar Fiordos expeditions between 1995 and 2004), no papers have yet been published on the sea anemone fauna collected during these expeditions, nor have the specimens been identified.

Between 1997 and 2004, we sampled sea anemones in shallow water to 40 m depth along the Chilean coast between Arica and Punta Arenas. To date we have described one new species (Häussermann and Försterra, 2001), re-described four (Häussermann, 2003; 2004b; 2005) and reported a colonial one (Häussermann and Försterra, 2003). In this paper, we describe the distribution of the collected species and discuss the agreement of the distribution ranges with the traditionally assumed biogeographic provinces. We list all species described for Chile and discuss the taxonomic overlaps and the biogeographic connections with the actinofauna of the South East Pacific, the South West Atlantic and Antarctica.

MATERIAL AND METHODS

Between 1994 and 2004, we observed, collected, examined and preserved more than 1000 specimens of 32 clearly distinguishable shallow-water Actiniaria and Corallimorpharia at more than 100 sites along the Chilean coast from Arica (18°30'S 70°19'W) to Fuerte Bulnes, Straits of Magellan (53°36'S 70°56'W) [for a detailed list of sampling sites of northern and central Chile see the online Appendix of Häussermann and Försterra (2001) at http://www.senckenberg.uni-frankfurt.de/odes/ and for a list of sampling sites of southern Chile see the online appendix of Häussermann (in press) at http://dx.doi.org/10.1007/s00300-004-0637-x (restricted access); for a map of the sampling sites of north and central Chile see Häussermann (2003), for a map of sampling sites of southern Chile see Försterra and Häussermann (2003)]. We kept the distance between neighbouring study sites less than 200 km with the exception of the region between Puerto Chacabuco (45°27'S 72°48'W) and Puerto Natales (51°44'S 72°30'W), where we could not access the coast due to logistic constraints. We studied and photographed specimens in situ by means of SCUBA-diving to depths of 25 m in northern and central Chile and to 40 m in the fjords. We kept some specimens of each species for several days in aquaria for detailed examinations and documentation. *Oulactis coliumensis* was dredged off Dichato by the research vessel Kay-Kay from the Universidad de Concepción from approx. 20 m depth. *Dactylanthus antarcticus* was found at several sites in the Chilean fjord region by Carlos Viviani (in litt., 2003) and we took additional distribution data from Dayton *et al*. (1995). For preservation, we relaxed the specimens with menthol crystals for 45-180 min and fixed them in 10-15% seawater formalin. For the histological examinations, we embedded parts of specimens in paraffin, sectioned them at 8-9 μm, and stained them with Azocarmin triple staining (Humason, 1967). We examined fired and unfired cnidae from living and preserved specimens with a light microscope (1000x oil immersion), drew or photographed and measured them.

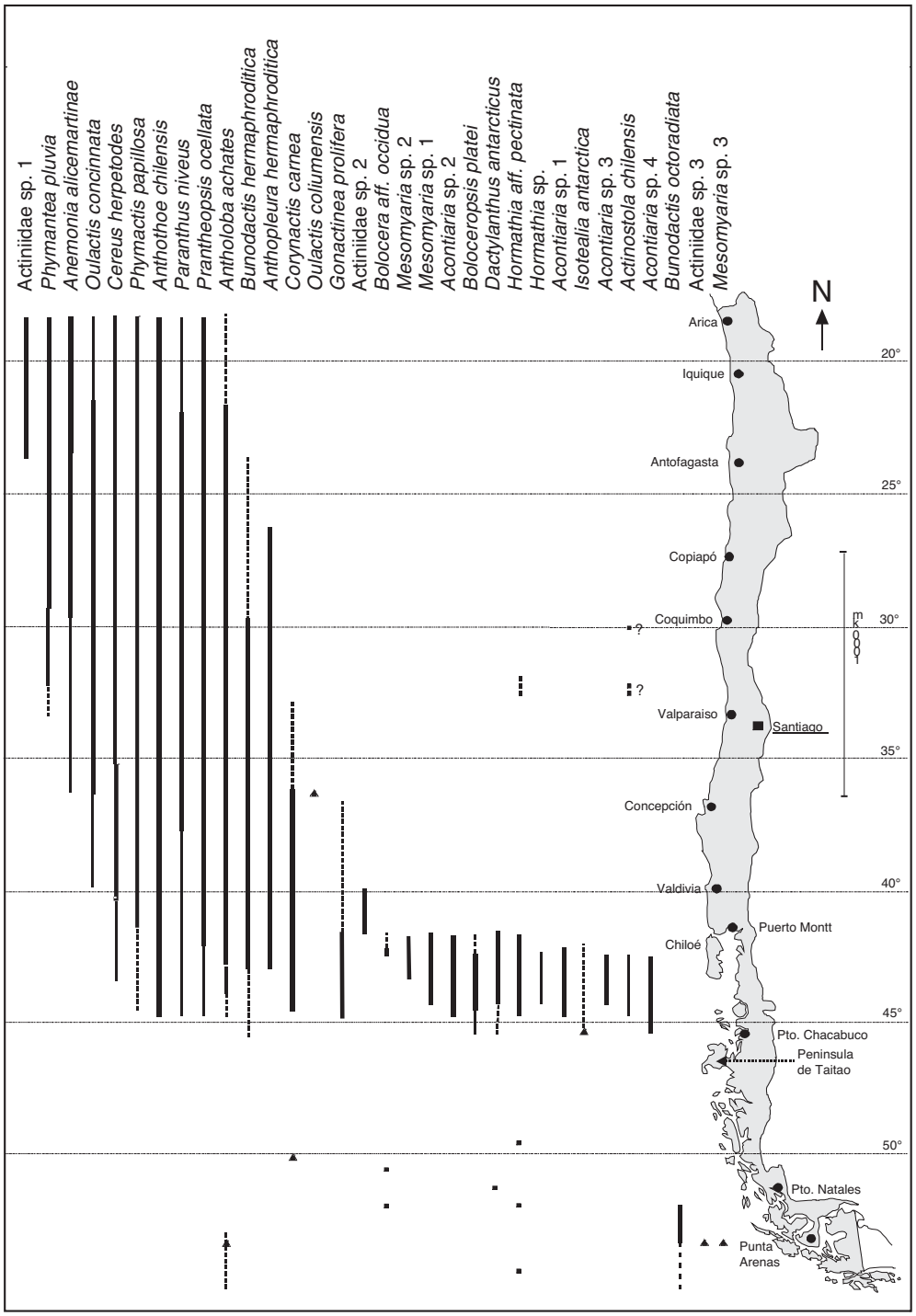

FIG. 2. – Distribution of sea anemones examined in the present study; complete lines and triangles: own findings, interrupted lines and squares: data from other authors.

RESULTS

From the 32 shallow-water sea anemone species collected along the Chilean coast, we identified 19 to the species level and three to the genus level; ten species have not yet been identified (Fig. 2). We found 16 species along the exposed coast of northern and central Chile between Arica (18°S) and Puerto Montt (42°S). From these 16 species, five species had their northern distribution limit and four species their southern distribution limit between Antofagasta (23°S) and Valdivia (40°S), and nine had their southern distribution limit south of Puerto Montt within the fjord region. *Antholoba achates* was found along the

TABLE 1. – List of sea anemones described from the coast of continental Chile.

Order Corallimorpharia
Family Corallimorphidae Hertwig, 1882
Corynactis carnea Studer 1878
Corynactis chilensis Carlgren, 1941 =? *C. carnea*
Corallimorphus profundus Moseley, 1877
Corallimorphus rigidus Moseley, 1877

Order Actiniaria
Suborder Endocoelantheae Carlgren, 1925
Family Halcuriidae Carlgren, 1819
Halcurias pilatus McMurrich, 1893

Suborder Nynantheae Carlgren, 1899
Tribe Athenaria Carlgren, 1899
Family Edwardsiidae Andres, 1881
Edwardsia intermedia McMurrich, 1893
Edwardsiella ignota (Carlgren, 1959)
Family Galatheanthemidae Carlgren, 1956
Galatheanthemum profundale Carlgren, 1956 (deep sea)
Family Halcampidae Andres, 1883
Cactosoma chilensis (McMurrich, 1904)
Halcampa abtaoensis Carlgren, 1959
Family Halcampoididae Appelöf, 1896
Scytophorus striatus Hertwig, 1882
Family Haloclavidae Verrill, 1899
Peachia chilensis Carlgren, 1934
Family Octineonidae Fowler, 1894
Octineon chilense Carlgren, 1959
Tribe Thenaria Carlgren, 1899
Subtribe Acontiaria Stephenson, 1935
Family Aiptasiidae Carlgren, 1924
?Aiptasia sp. McMurrich, 1904
(probably belongs to another species)
Family Aiptasiomorphidae Carlgren, 1949
Aiptasiomorpha elongata Carlgren, 1951
Family Hormathiidae Carlgren, 1932
Actinauge chilensis Carlgren, 1959
Amphianthus lacteus (McMurrich, 1893)
?*Chondrophellia nodosa var. coronata* (Verrill, 1883)
(a northern hemispheric species) = ?*Actinauge verrilli* McMurrich, 1893 = (probably another species *sensu* Carlgren, 1949) = *Actinauge fastigata* McMurrich, 1893
Hormathia pectinata (Hertwig, 1882)
= ?*Phellia spinifera* Hertwig, 1882
Phelliactis pelophila Riemann-Zürneck, 1973
?Stephanauge nexilis (Verrill, 1883) (a northern hemispheric species)
Family Sagartiidae Gosse, 1858
Anthothoe chilensis (Lesson, 1830) = ?*Sagartia* (*Actinia*) *nymphaea* (Drayton in Dana, 1846)
Cereus herpetodes (McMurrich, 1904)
Choriactis impatiens (Couthouy in Dana, 1846)
Choriactis laevis (Carlgren, 1899)
? Actinothoe lobata (Carlgren, 1899)
= ? *Metridium parvulum* McMurrich, 1904
= ? *M. senile* subsp. *lobatum*
Phellia exlex (McMurrich, 1904)

Subtribe Endomyaria Stephenson, 1921
Family Actiniidae Rafinesque, 1815
Anemonia alicemartinae Häussermann and Försterra, 2001 = *Actinia* sp. (*sensu* Sebens and Paine, 1979)
Anthopleura hermaphroditica (Carlgren, 1899)
Bolocera occidua McMurrich, 1893
*? *B. patens* (Hertwig, 1882) =? *B. kerguelensis*
Boloceropsis platei McMurrich, 1904
Bunodactis hermaphroditica (McMurrich, 1904)
Bunodactis octoradiata (Carlgren, 1899)
=? *Parantheopsis cruentata*
Condylanthus magellanicus Carlgren, 1899
?Bunodactis elongata (McMurrich, 1904)
(probably belongs to another species)
?*Bunodactis eydouxii* (Milne Edwards, 1857)
(probably belongs to another species)
Epiactis georgiana Carlgren, 1927
?*Gyrostoma incertum* McMurrich, 1904
Isosicyonis alba (Studer, 1879)
Isotealia antarctica Carlgren, 1899
=? *Leiotealia badia* McMurrich, 1893
Oulactis coliumensis (Riemann-Zürneck and Gallardo, 1990)
Oulactis concinnata (Drayton in Dana, 1846)
= *Isoulactis chilensis* Carlgren, 1959
Parantheopsis cruentata (Drayton in Dana, 1846)
Parantheopsis ocellata (Lesson, 1830)
= *Bunodes ocellata* (Lesson, 1830) = ?*Nemactis (Actinia) rubus* (Drayton in Dana, 1846) = ? *Sagartia* (*Actinia*) *nymphaea* (Drayton in Dana, 1846)
Phymactis papillosa (Lesson, 1830) = *P. clematis* (Drayton in Dana, 1846) =? *Phlyctenactis tuberculosa* sensu Zamponi and Excoffon, 1995
Phymanthea pluvia Carlgren, 1959
Family Liponematidae Hertwig, 1882
Liponema multipora Hertwig, 1882
Subtribe Mesomyaria Stephenson, 1921
Family Actinoscyphiidae Stephenson, 1920
Actinoscyphia plebeia (McMurrich, 1893)
Family Actinostolidae Carlgren, 1932
Actinostola chilensis McMurrich, 1904
= p.p. A. intermedia Carlgren, 1899
Actinostola crassicornis (Hertwig, 1882)
Anthosactis excavata (Hertwig, 1882)
Antiparactis lineolatus (Drayton in Dana, 1846)
Antholoba achates (Couthouy in Dana, 1846)
Ophiodiscus annulatus Hertwig, 1882
Ophiodiscus sulcatus Hertwig, 1882
Paranthus crassa (Carlgren, 1899)=? P. niveus
?Paranthus ignotus (McMurrich, 1904)
Paranthus niveus (Lesson, 1830)
Pseudoparactis tenuicollis (McMurrich, 1904)

Suborder Prothantheae Carlgren, 1891
Family Gonactiniidae Carlgren 1893
Gonactinia prolifera (Sars, 1835)

Suborder Ptychodacteae Stephenson, 1922
Family Preactiidae England in England and Robson, 1984
Dactylanthus antarcticus (Clubb, 1908)

Dubious species with uncertain classification: *?Polyopsis striata* Hertwig, 1882 and *?Aulorchis paradoxa* Hertwig, 1888.
Legend: "?": dubious species; "=?": uncertain/possible synonymy.

entire Chilean coast to Tierra del Fuego; *Corynactis carnea* was found between Valparaíso (32°S) and 50°S; and *Oulactis coliumensis* was only dredged at one location in this area (Häussermann, 1998 (unpublished); Häussermann and Försterra, 2001; Häussermann, 2003; Häussermann and Försterra, 2003; Häussermann, 2004b; 2005) (Fig. 2).

Thirteen species had their northern distribution limit near Puerto Montt (42°S) at the northern end of the fjord region; only three of them were found at one or a few sites south of the Peninsula Taitao by other authors. However, one or two of them (the taxonomic accordance of Doumenc's *Actinostola intermedia* with *A. chilensis* is uncertain) were dredged

TABLE 2. – Taxonomic relationships of the South East Pacific, the South West Atlantic and the Antarctic actinofauna.

Species in common South East Pacific/Antarctic:
- *Corallimorphus profundus* [1]
- *Actinoscyphia plebeia*
- *Actinostola crassicornis (in Chile* [2])
- *Bolocera occidua (= B. kerguelensis?)* [3, 4]
- *Choriactis laevis* [5] (in Chile [2])
- *Condylanthus magellanicus* [1] (in Chile [2])
- *Dactylanthus antarcticus*
- *Edwardsia intermedia* [6]
- *Epiactis georgiana* [3]
- *Galatheanthemum profundale* [1] (in Chile [2])
- *Isosicyonis alba* [3]
- *Isotealia antarctica* [3, 7]
- *Liponema multipora* [1]

Species in common South West Atlantic/Antarctic:
- *Actinostola crassicornis*
- *Bolocera tuediae* subsp. *occidua (=B. kerguelensis?)* [4]
- *Condylanthus magellanicus*[1] (in Chile [2])
- *Isosicyonis alba* [11]
- *Epiactis georgiana* [3, 11]

Species in common Magellan region/northern Scotia-Arc:
- *Corynactis carnea=Sphincteractis sanmatiensis* (*sensu* Riemann-Zürneck, 1979) [12]
- *Amphianthus* aff. *lacteus* [13]
- *Antholoba achates* [1]
- *Anthothoe chilensis* [14]
- *Bunodactis octoradiata* [2]
- *Choriactis laevis* [5]
- *Condylanthus magellanicus* (in Chile [2])
- *Parantheopsis cruentata* [1, 10]

Species in common South East Pacific/South West Atlantic:
- *Corynactis carnea* [12]
- *Actinostola crassicornis* (in Chile [2])
- *Amphianthus* aff *lacteus* [13]
- *Antholoba achates* [1]
- *Anthothoe chilensis* [14]
- *Bolocera occidua* (=?*B. tuediae* subsp. *occidua)*
- *Bunodactis octoradiata* [2]
- *Choriactis laevis* [5] (in Chile [2])
- *Condylanthus magellanicus*[1] (in Chile [2])
- *Epiactis georgiana* [3, 11]
- *Hormathia pectinata* [8 11]
- *Isosicyonis alba* [3, 11]
- *Isotealia antarctica* [3]
- *Metridium senile* subsp. *lobatum* [9]
- *Parantheopsis cruentata* [1, 10]
- *Paranthus crassa =?P. niveus*
- *Phellia exlex*
- *Phelliactis pelophila*
- **NON** *Phymactis papillosa* (probable *Choriactis impatiens* [2])

Species distributed around southern South America:
- *Antholoba achates* [1]
- **?***Isosicyonis alba* [3]
- **?***Metridium senile lobatum* [9]

[1] Wide distribution.
[2] Only reported for Magellan region.
[3] For Chile only mentioned once based on one (*B. occidua*) and two (*I. antarctica, E. georgiana, I. alba*) badly preserved specimens.
[4] The South American *Bolocera* species were synonymised with *B. kerguelensis* based on preserved material (Fautin, 1984). Since they are extremely variable and the preserved specimens present very few distinctive characteristics, the synonymisations should be reconsidered based on examination of *in vivo* material.
[5] Taxonomic status of species uncertain *sensu* Fautin (2003).
[6] Found at two non-Chilean sites: on Scotia Arc (1 spec.) and on Antarctic Peninsula (2 spec.) (Carlgren, 1927); identification of Carlgren's (1959) specimens uncertain.
[7] Identification of Antarctic specimens (McClintock and Baker, 1997; Bryan *et al*., 1998; Amsler *et al*., 1999) cannot be verified.
[8] Specimens found by Carlgren (1959) in Chilean fjords differ in size and cnidae from the type specimen described for the Magellan region and from the Argentinean specimens examined by Riemann-Zürneck (1973; 1986).
[9] Despite extensive sampling, we could not confirm the existence of this species along the Chilean coast.
[10] We still could not assign any Chilean specimens to this species.
[11] Disjunct distribution along the Argentinean coast (cold water areas).
[12] Taxa very poorly studied: since variability is very high, this species might represent a species complex.
[13] Identification of Argentinean species uncertain (Riemann-Zürneck, 1986).
[14] Not found south of the Peninsula Taitao in Chile. In the Atlantic, this species is cited for Mar del Plata to Rio de Janeiro, South Georgia and South Africa (Zamponi *et al*., 1998a; Zamponi *et al*., 1998b; Excoffon *et al*., 1997). However, the agreement of specimens from the Scotia Arc and from Argentina with specimens from Chile has to be confirmed since *A. chilensis* is very variable, even within Chile, and thus might represent a species complex.

in deep water off central Chile by Doumenc (1984). We found three species only in the Magellan region (Fig. 2). Along the Chilean coast, the greatest number of species in shallow water exists in the northern part of the Patagonian fjord region (23 species).

The literature review yielded the following results:

Including deep-water species, 63 species of sea anemones have been described for the Chilean coast (Table 1), 86 for the Antarctic (E. Rodriguez, in litt., 2004) and approximately 50 for the Argentinean coast. Based on the literature, 18 of the sea anemones (Actiniaria and Corallimorpharia) described for the South East Pacific are also reported from the South West Atlantic and 13 from the Antarctic; seven are described for all three regions. However, reports for 12 of the 18 species that Chile shares with Argentina and reports for eight of the 13 species that Chile shares with the Antarctic contain major taxonomic uncertainties or the localities are of minor zoogeographical value (see Table 2 and discussion). Fifteen of the 18 species (exceptions: *Anthothoe chilensis, Bunodactis octoradiata, Parantheopsis cruentata*) that Chile has in common with Argentina and all that it has in common with the Antarctic have their main vertical distribution in

deeper waters (>50 m). Only one, or possibly three species show a continuous distribution around the southern tip of South America (Riemann-Zürneck, 1986) (Table 2). Most species that inhabit the central Patagonian zone (sensu Pickard, 1973; Viviani, 1979; Stuardo and Valdovinos, 1992) were not found at the west coast of Tierra del Fuego, south of the Straits of Magellan (Riemann-Zürneck, 1986). Three of the Argentinean deep-water species show a conspicuous disjunct distribution with registrations east and north of the Falkland (Malvinas) Islands (47-52°S), and off Rio de la Plata at the Subtropical Convergence (approx. 38°S) (Riemann-Zürneck, 1991) (Table 2). Eight species that inhabit the southern Patagonian zone are also found along the northern part of the Scotia Arc to South Georgia (Table 2).

DISCUSSION

Distribution of sea anemones along the Chilean coast

Former studies

Sebens and Paine (1979) provided the first distribution map of 31 species of Chilean Actiniaria and Corallimorpharia. Sampling was carried out at 33 sites along the Chilean coast between Iquique (20°16'S 70°08'W) and Ushuaia, Argentina (54°50'S 68°12'W). Very little sampling was done in the northern fjords, and no study sites were situated in the Central and South Patagonian Zone between 43°14'S and 53°02'S. The high number of species appearing on their distribution map around Chiloe Island coincides with the high sampling effort of the Lund University Chile Expedition (Carlgren, 1959) in this area. In the collection deposited by Sebens and Paine at the Naturalis Museum in Leiden (Netherlands), only nine common species from northern and central Chile possess name tags while the other specimens of this collection do not seem to have been identified and thus cannot have contributed to the distribution map presented by Sebens and Paine (1979: 223).

The northern and central Chilean coast

The northern limit of the Peruvian Province is situated at Paita, Peru (approx. 5°S), where the Humboldt current turns westward towards the Galapagos Islands (Strub *et al*., 1998); its southern limit is situated somewhere between Valparaiso (33°S) and Puerto Montt (42°S), depending on the author (see Brattström and Johanssen, 1983; Camus, 2001). Only four of the northern Chilean shallow-water sea anemones found in this study have a distribution range within the limits of the Peruvian Province (Fig. 2); their southern distribution limits are spread over more than 1000 km. Most of the species found in north and central Chile extend clearly south of Puerto Montt into the fjord region (Fig. 2). Of the three species that have their northern distribution limit between Valparaiso (33°S) and Valdivia (40°S), two can also be found in the fjords (up to 45°S). The observed pattern suggests neither the existence of a sea anemone fauna that is characteristic of the Peruvian Province nor a transitional zone north of Puerto Montt. Instead, a gradual replacement of warm water species through cold water species can be observed along the coast.

One of the species of north and central Chile, *Anemonia alicemartinae*, either strongly increased in abundance or was introduced, and has continuously spread southward until it reached Concepción (37°S) (Häussermann and Försterra, 2001). Its distribution coincides precisely with the horizontal and bathymetrical extension of the southward *Chile Coastal Countercurrent* (Häussermann and Försterra, 2001).

The Patagonian fjord region

Eleven of the 23 species we observed in shallow water of the fjords have a clear northern distribution limit near Puerto Montt (42°S), where the fjord region ends. Two have also been reported from deep water off central Chile (Doumenc, 1984); however, the accordance of Doumenc's *Actinostola intermedia* with *A. chilensis* is uncertain. Ten species extend further north along the exposed coast. The species found in the fjords belong to three different faunal elements: a) shallow water species that are clearly restricted to fjord- and channel-specific habitats (e.g. *Acontiaria* sp. 1, *Mesomyaria* sp. 2); b) representatives of a deep water emergence (eurybathy) fauna (e.g. *Actinostola chilensis*, *Bolocera* aff. *occidua*) that is characteristic of shallow water of northern Chilean fjords, but can also be found in deeper water further north (e.g. *Hormathia* aff. *pectinata*); and c) the fauna of the exposed coast that is more present in the channels and islands than in the inner fjords and extends further north (e.g.

Antholoba achates, Cereus herpetodes, Parantheopsis ocellata). The observed pattern contradicts the classical hypothesis of a general faunal break at 42°S (Brattström and Johanssen, 1983; Camus, 2001). Only the faunal element that is restricted to fjord region specific habitats has a clear-cut northern distribution limit due to the abrupt lack of suitable niches further north. This confirms and completes the hypothesis of Riemann-Zürneck (1986) and Brattström and Johanssen (1983) that the South Chilean fauna possesses a high percentage of endemic species. The coexistence and merging of these three faunistic elements caused by an abrupt diversification of coast morphology south of 42°S due to the splitting up of the straight coastline into numerous channels and fjords results in an increased species number and thus characterises the fjord region as a biodiversity hotspot. The first studies in the northern Patagonian fjords revealed high species diversity on steep rocky substrata even in strongly fresh water influenced areas, especially right below the influence of the Low Salinity Layer (Försterra and Häussermann, 2003; Carvalho *et al*., 2005). While reaching farther north, the Patagonian cold-water fauna might be displaced to greater depths, where it can be found e.g. off Concepción (e.g. Schrödl, 2003; Cairns *et al*., 2005) or off Coquimbo (Doumenc, 1984), and is overlain by the northern warm water fauna.

South of the Taitao Peninsula (46-47°S), the South Patagonian Icefield is moulding the hydrographic conditions of the inner fjords (Pickard, 1973): the region is characterised by low salinities and high sedimentation (Pickard, 1973). A reported poverty of species along the South Patagonian Icefield south of Golfo de Penas (47-48°S) (Thatje and Mutschke, 1999) has been explained by the strong fresh water influence in this region (Pickard, 1971; Pickard, 1973; Strub *et al*., 1998). Due to technical restrictions, the expeditions to this area carried out with large vessels generally could only sample on soft bottoms and pebble ground, mainly at greater depth. Since most sea anemones settle on hard substrata, low anthozoan diversity along the South Patagonian Icefield might therefore be a sampling artifact due to general low sampling effort in this zone and especially due to soft bottom biased sampling (Thatje and Mutschke, 1999; Montiel *et al*., 2004). Due to logistic constraints, we could not sample between 46 and 52°S. There are only four species of sea anemones that are reported both from the northern fjords and from one or a few sites south of the Taitao Peninsula (Fig. 2); all of them have their main vertical distribution in deeper waters and only *Corynactis carnea* extends to water shallower than 30 m. The detected distribution pattern supports the hypothesis of a zoogeographic barrier at the Taitao Peninsula, as proposed by Lancellotti and Vásquez (1999): at 47°S, fjords and channels are interrupted by the Taitao Peninsula, which lies north of the Golfo de Penas and extends far into the Pacific Ocean (Fig. 1). This latitude also marks the southernmost oscillation (40-45°S) of the water masses of the *West Wind Drift,* which hit the continent and are split up into a northward and a southward component (Johnson *et al*., 1980; Castilla *et al*., 1993; Strub *et al*., 1998). It is plausible that the Peninsula, together with the Golfo de Penas, the changing oceanographic conditions and the parting of currents, form a biogeographic barrier, at least for shallow water species that are limited to protected habitats or the inner fjords. However, due to the poor data from the central and southern Patagonian zone, the southern distribution limits of most species found in the northern Patagonian fjord region still have to be traced.

Relations of the South-East Pacific actinofauna with neighbouring areas

Overlaps between the western Patagonian and the eastern Patagonian actinofauna

It can be inferred from the literature that 18 of the 63 species reported from Chile (29%) are also mentioned for the South West Atlantic. However, a detailed look at the reports reveals that of these 18 species, six are either of uncertain taxonomic status or the relevant records are doubtful; one species is restricted to the Magellan area, three more are described from the Argentinean shelf and extend into the (Chilean) Straits of Magellan, and two might represent species complexes (see Table 2). Since the Straits of Magellan are situated at the limit between the South East Pacific and the South West Atlantic, species with distribution limits in the Straits of Magellan cannot be interpreted as common species of eastern and western Patagonia.

Riemann-Zürneck synonymised the Chilean species *Metridium parvulum* McMurrich, 1904 and *Sagartia lobata* Carlgren, 1899 with *Metridium senile* and created the subspecies *M. senile lobatum*. She then cited it for the Argentinean coast (Riemann-Zürneck, 1975; 1986). This species inhabits

the shallow water around the Peninsula Valdes (own observation) and around Buenos Aires (D. Lauretta, in litt., 2004). Fautin *et al*. (1989) do not accept this synonymisation and leave the two species *Actinothoe lobata* (Carlgren, 1899) and *Metridium parvulum* McMurrich, 1904 separate and purely Chilean. Based on the literature, the species is found at depths between 8 and 35 m between Coquimbo, northern Chile, and Calbuco at the northern limit of the fjord region. However, despite intensive field work and extensive information from local divers, fishermen and scientists, we could not confirm the presence of a species of *Metridium* along the Chilean coast.

The hydrographic situation at the southern tip of South America (Fig. 1) leads one to expect a comparably low overlap of Pacific and Atlantic shallow water species. The southern part of the Patagonian fjord region, south of Taitao Peninsula, lies under the influence of southward flowing water masses (Cape Horn Current), which flow around the southern tip of South America through the Drake Passage (Pickard, 1973; Brattström and Johanssen, 1983; Riemann-Zürneck, 1986; 1991; Castilla *et al*., 1993; Strub *et al*., 1998). The relatively shallow layer of water rounding the South American continent turns north or north-east, partly sweeps over the Burdwood Bank and the Falkland Shelf (Riemann-Zürneck, 1991) and then crosses the Falkland Plateau (Fig. 1). Due to strong eastward currents around the southern tip of South America, sessile shallow water species can spread from Chile to Argentina, but vice-versa it is almost impossible (Riemann-Zürneck, 1986) because adults as well as larvae are supposed to be unable to move against these strong currents. However, even the eastward crossing of the Straits of Magellan is difficult due to the lower salinity of the surface water, the relatively high temperature differences between the Pacific and the Atlantic opening and the existence of deep-sea basins (Riemann-Zürneck, 1986). To enter the Atlantic Ocean rounding Cape Horn, larvae have to withstand temperatures around 6°C (Riemann-Zürneck, 1986). Although it has been regularly assumed in the literature (Semenov and Berman, 1977; Zamponi *et al*., 1998a), there is no evidence for a northward near-shore current on the Atlantic side south of 41°S (Piola and Georgi, 1982). The lack of such a current could explain the rarity of South East Pacific shallow-water sea anemones along the coast of Argentina.

Overlaps between the South East Pacific and the Antarctic actinofauna

The faunal overlap of Chilean and Antarctic sea anemone species that can be inferred from the literature should also be interpreted cautiously. From the 13 species mentioned in the literature for Chile and the Antarctic (21% of the Chilean species), five are based on uncertain records or doubtful identifications, one is a deep-sea species, and three are—for Chile—only reported from the Magellan area (one of these is also of uncertain status) (see Table 2). Eight Magellanic species are reported along the northern part of the Scotia Arc to South Georgia, but not for the Antarctic. Plausible reasons for a relatively low overlap of the South Chilean fauna with the Antarctic can be found in the hydrographic situation: the Scotia Arc connects South America with the Antarctic and presents Magellanic aspects in its northern part and Antarctic aspects in its southern part (Arntz and Brey, 2003). The Antarctic Convergence lies approximately at the latitude of South Georgia, oscillating in a way that leaves this island either north or south of it (Arntz and Brey, 2003). The eastward direction of the strong *Circumpolar Current* facilitates the dispersion of larvae from the southern tip of South America and from the Antarctic towards South Georgia, but hinders a westward spread from South Georgia.

Unusual distribution pattern of some Argentinean sea anemones

The unusual, disjunct distribution pattern of three Argentinean sea anemone species (see Table 2) (Riemann-Zürneck, 1973; 1986) is already known from other benthic coelenterates that inhabit the Argentinean continental shelf, e.g. the siphonophore *Rhodalia miranda* (Riemann-Zürneck, 1991). These species are found south and east of the Falkland (Malvinas) Islands, at the Malvinas Canyon and off Rio de la Plata, south of the Subtropical Convergence (Riemann-Zürneck, 1991). These distribution patterns can be explained by the special hydrographic situation of the South West Atlantic. A stable and constant flow of cold circumpolar water swashes over the Shag Rock Passage at 48°W, crosses the South Atlantic Basin and rises along some of the large canyons on the Argentinean shelf. The conditions around the Falkland Islands, which are under permanent influence of Subantarctic water masses, seem to be more similar to those in southern Chile

than to those in southern Argentina (Riemann-Zürneck, 1986; Moyano, 1991; Desqueyroux-Faúndez, 1994). The described current patterns limit Subantarctic benthic species to regions that constantly offer stable cold conditions.

Zoogeographic patterns found in other invertebrate taxa

The zoogeographical limit between the Peruvian and the Magellan Province at 40 to 42°S has been described for sponges (Desqueyroux-Faúndez, 1994), crustaceans (Garth, 1957), asteroids (Bernasconi, 1964), fish (Mann, 1954; Ojeda *et al*., 2000), foraminiferans (Balech, 1954) and bryozoans (Moyano, 1991). Some of the mentioned papers additionally subdivide the Peruvian Province into a North Chilean and a Central Chilean Sub-Province (e.g. Balech, 1954; Bernasconi, 1964; Desqueyroux and Moyano, 1987). In contrast, the Chilean polychaete fauna is characterised by a gradual replacement of warm-water species by cold-water species along the Chilean coast and no abrupt change at 42°S can be observed (Montiel *et al*., 2004, 2005). For polychaetes, Montiel *et al*. (2005) suggest a sub-division into a Pacific and an Atlantic part of the Magellan Province since the species overlap is only 10%. Thus, the distribution pattern of polychaetes coincides quite well with that of sea anemones. Several authors also reported a longitudinal zoogeographic barrier for benthic taxa of the South East Pacific at the eastern mouth of the Straits of Magellan (Stuardo and Valdovinos, 1992; Strub *et al*., 1998), while others consider the Straits of Magellan to be a latitudinal zoogeographical barrier for Chilean species (Balech, 1954; Stuardo, 1964; Riemann-Zürneck, 1986). However, the latter may also be a sampling artifact (Riemann-Zürneck, 1986), since the known distribution patterns often reflect the range of sampling activities. Among nudibranchs, on the other hand, most species that are described for southern Argentina can also be found in southern Chile (Schrödl, 2003). Schrödl (2003) reports that cold-water species from the Straits of Magellan have been observed up to Concepción (37°S); while warm-water species from the central Chilean coast have generally not been described for the region south of Chiloé Island (42°S). However, most invertebrate sampling has been quite scarce along the exposed islands even of the northern fjord region (Guaitecas and Chonos Archipelago and west coast of Chiloé Island), so this might also be a sampling artifact. The number of Magellanic shelled gastropods and nudipleurans shared with areas south of the Antarctic Convergence is very low (Linse, 2000; Schrödl, 2003); remarkably, the percentage of Magellanic bivalves in these southern waters is much higher (Linse, 2000).

CONCLUSIONS

Abrupt diversification of the coast morphology south of 42°S increases the number of habitats and allows the overlap of three different shallow water faunal elements in the northern Patagonian zone: a) shallow water species that depend on fjord habitats; b) emerged deep water species; and c) shallow water species from the exposed coast of north and central Chile. This strongly increases overall species number and diversity in the fjords.

A southern limit of the Peruvian Province close to Puerto Montt cannot be confirmed from the available distribution data of sea anemones.

There is a distribution limit from south to north at 42°S for shallow water species that are restricted to fjord- and channel-specific habitats.

We hypothesise that, due to splitting of currents and different oceanographic conditions, the Taitao Peninsula together with the Golfo de Penas (47-48°S) form a zoogeographic barrier, at least for shallow-water species of the inner fjords.

The percentage of western Patagonian sea anemone species that also occur in eastern Patagonia lies between 10 and 22%.

The percentage of South East Pacific sea anemones that also occur in the Antarctic lies between 8 and 14%.

Conspicuousness, life style, reproduction, abundance, longevity and population dynamics make sea anemones a potentially perfect taxonomic group for general zoogeographic surveys. However, the poor effort that has been dedicated to sea anemones in the southern oceans, their generally difficult taxonomic situation, the problems in identification of living animals (Häussermann, 2004a), and the general lack of voucher material for uncertain distribution data still leave many gaps and doubts. More refined zoogeographic conclusions will be possible after more sampling on hard substrata, especially in the central and southern Patagonian zones in depths right below the low salinity layer.

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