

**Biodiversity, zoogeography and ecology of polychaetes
from the Magellan region and adjacent areas**

**Diversität, Zoogeographie und Ökologie von
Polychaeten der Magellanregion und angrenzender
Gebiete**

Américo Montiel San Martín

**Ber. Polarforsch. Meeresforsch. 505 (2005)
ISSN 1618 - 3193**

A mis queridos padres

Américo Montiel San Martín

Universidad de Magallanes
Av. Bulnes 01890
Casilla 113 - D
Punta Arenas
Chile

Die vorliegende Arbeit ist die inhaltlich unveränderte Fassung einer kumulativen Dissertation, die in der Sektion Vergleich Ökosystemforschung bei Prof. Dr. W. Arntz angefertigt und 2004 in dem Fachbereich 2 (Biologie/Chemie) der Universität Bremen vorgelegt wurde.

Contents

Summary	III
Zusammenfassung	V
Resumen	VII
1 Introduction	1
1.1 Current status of polychaete research	1
1.2 Polychaetes: a blank spot in South American marine zoogeography	2
1.3 Aims of the study	7
2 Materials & Methods	8
2.1 Expedition data	8
2.2 Literature data	8
2.3 Multivariate analysis	8
2.4 Biodiversity, life-history and species distribution categorization	10
3 Results	12
3.1 Multivariate analysis	12
3.2 Biodiversity patterns	13
3.3 Feeding and reproductive patterns	16
3.4 Polychaete distribution patterns	19
4 Discussion	21
4.1 General consideration about the thesis	21
4.2 What is a zoogeographical region in the marine realm?	21
4.3 The Magellan region: a zoogeographic region?	21
4.4 Zoogeographic patterns and endemism	23

5 Biodiversity & Ecology	25
5.1 Publication 1: Polychaete assemblages on the Magellan and Weddell Sea shelves: a comparative ecological evaluation. Mar. Ecol. Prog. Ser.	26
5.2 Publication 2: Impact of iceberg scouring on macrobenthic communities in the high – Antarctic Weddell Sea. Polar Biol.	51
6 Zoogeography	58
6.1 Publication 3: Distributional patterns of shallow-water polychaetes in the Magellan region: a zoogeographical and ecological synopsis. Sci. Mar.	59
7 Taxonomy	74
7.1 Publication 4: <i>Aricidea pisanoi</i> (Annelida: Polychaeta), a new species of Paraonidae from the southernmost waters of South America (Chile). J. Mar. Biol. Ass. U.K.	75
7.2 Publication 5: New records to Chile of the family Paraonidae (Annelida: Polychaeta). Helgoland Mar. Res.	78
8 Acknowledgements, appendix & references	84
8.1 Acknowledgements	85
8.2 List of stations from expeditions with the RV's "Victor Hensen" 1994, "Polarstern" and "Vidal Gormaz" 1996	86
8.3 List of species determined from the quantitative samples	88
8.4 Results of the SIMPER analysis of presence/absence data of polychaete species from the CAHO, FKLD and HUMB quadrants	100
8.5 References	103

SUMMARY

Summary

The polychaetes are one of the most diverse and abundant invertebrate groups in soft bottom habitats worldwide. Despite their importance they were ignored for many decades in the zoogeographical analysis at the southern tip of South America.

Ecological and zoogeographical patterns of the polychaete fauna inhabiting this area were analysed based on own samples obtained during three expeditions and a compilation of literature data referring to another 13 expeditions.

Three zoogeographical entities were distinguished by multivariate analysis of species composition:

- Cape Horn entity (CAHO) on the western continental shelf of the Magellan region (42°S-55°S; 76°-69° W).
- Humboldt entity (HUMB) on the continental shelf of the Chilean Pacific coast (22°-42°S; 74°-70° W) north of the Magellan region.
- Falkland entity (FKLD) on the southeastern continental shelf (42°S-55°S; 69°-55° W) in the Atlantic.

The subsequent comparison of these three zoogeographic entities resulted in distinct differences in species richness, trophic guild distribution, ontogenetic development modes and the distribution range of species.

Total number of species was highest in CAHO (269), intermediate in HUMB (135) and lowest in FKLD (102). Mean species number per quadrant was highest in HUMB (24.3 ± 11.2), intermediate in CAHO (23.4 ± 25.1) and lowest in FKLD (10.1 ± 8.3).

Regarding trophic guild composition, the share of suspension feeders, detritus feeders and predators/omnivores was 4%-43%-53% in CAHO, 2%-63%-35% in HUMB, and 22%-22%-56% in FKLD, respectively. The predominance of detritus feeders over suspension feeders in CAHO and HUMB, and a higher percentage of suspension feeders in FKLD is most likely linked to differences in sedimentation rates and bottom water particle loads. In CAHO, the sedimentation rates are high induced by the glacial and fresh water run-off carrying fine inorganic sediments, whereas in HUMB the high sedimentation rates are induced by upwelling processes, an oxygen minimum zone, and disturbances produced by El Niño conditions. In contrast high productivity, strong current patterns and low fine inorganic discharges favoured the occurrence of a higher percentage of suspension feeders in FKLD.

Regarding the ontogenetic development, the share of planktonic development and direct development was 75%-25% in CAHO, 78%-22% in HUMB and 76%-24% in FKLD, respectively. The planktonic development in the two Pacific entities (CAHO and HUMB) differed significantly as compared to the FKLD. The direct development differed significantly only between CAHO and FKLD. The higher proportion of species with planktonic development in the two Pacific entities may be explained by greater habitat heterogeneity than the more uniform bottom sediments in FKLD. Additionally, species with planktonic development have better long distance distribution capabilities, which is an advantage for fast recolonization of disturbed areas as found in CAHO.

Regarding the range of distribution, the percentage of endemism in the three entities is rather low (< 15%). Species overlap between CAHO, HUMB and

SUMMARY

Antarctica areas is relatively high (> 30%), most likely owing to northward transport of larvae by Antarctic Intermediate Waters and the West Wind Drift. Accordingly, we see a continuous replacement of Antarctic species by temperate species towards lower latitudes along the Pacific coast of South America. On other hand, the percentage of species overlapping between HUMB, CAHO and FKLD is relatively high (23%), due to the exchange of species through the Straits of Magellan.

The ecological and zoogeographical findings of this study indicate that the Magellan region cannot be considered as one single zoogeographic entity. The environmental settings with water currents from different origins, differences in continental shelf topography as well as the complex channel and fjord system lead to three distinctly different environments which resemble the zoogeographical entities described in this study.

ZUSAMMENFASSUNG

Zusammenfassung

Die Polychaeten sind weltweit eine der vielfältigsten und häufigsten marinen Evertebratengruppen auf Weichbodenhabitaten. Trotz ihrer grossen Bedeutung wurden sie jahrzehntelang bei zoogeographischen Untersuchungen an der Südspitze Südamerikas vernachlässigt.

In der vorliegenden Arbeit werden ökologische und zoogeographische Charakteristika der Polychaetenfauna dieser Region untersucht und beschrieben. Dabei wird auf eigene Proben zurückgegriffen, die während dreier Expeditionen gewonnen wurden, sowie auf eine Zusammenstellung von Literaturdaten von weiteren 13 Expeditionen.

Durch multivariate Analyse der Artenzusammensetzung konnten drei zoogeographische Gebiete unterschieden werden:

- das Kap Hoorn-Gebiet (CAHO) auf dem westlichen Kontinentalschelf der Magellanregion (42°S-55°S; 76°-69° W).
- das Humboldt-Gebiet (HUMB) auf dem Kontinentalschelf der chilenischen Pazifikküste (22°-42°S; 74°-70° W) nördlich der Magellanregion.
- das Falkland-Gebiet (FKLD) auf dem südöstlichen Kontinentalschelf (42°S-55°S; 69°-55° W) im Atlantik.

Der sich anschliessende Vergleich dieser drei zoogeographischen Gebiete ergab deutliche Unterschiede in den Artenzahlen, der Verteilung von Ernährungstypen sowie unterschiedlichen Fortpflanzungstypen und auch der Grenzen der Verbreitungsgebiete vieler Arten.

Höchste Artenzahlen wurden in CAHO (269) gefunden, die entsprechenden Werte für HUMB (135) und FKLD (102) waren deutlich kleiner. Die durchschnittliche Artenzahl pro Quadrant, ein Maß für die Biodiversität, war am höchsten in HUMB (24.3 ± 11.2), am zweithöchsten in CAHO (23.4 ± 25.1) und am niedrigsten in FKLD (10.1 ± 8.3).

Das Verhältnis von Suspensionsfiltrierern zu Detritivoren und Predatoren / Omnivoren war jeweils 4%-43%-53% in CAHO, 2%-63%-35% in HUMB und 22%-22%-56% in FKLD.

Die Dominanz von Detritivoren über Suspensionsfiltrierer in CAHO und HUMB, sowie das größere prozentuale Vorkommen letzterer in FKLD ist auf unterschiedliche Sedimentationsraten und Partikeldichten in den bodennahen Wasserkörpern der Gebiete zurückzuführen.

In CAHO sind die Sedimentationsraten hoch, bedingt besonders durch den Zufluss von Gletscher- und Süßwasser mit einem hohen Anteil an feinen, anorganischen Partikeln, wohingegen die hohen Sedimentationsraten in HUMB zurückzuführen sind auf „Upwelling“, eine Sauerstoffminimumzone, sowie auf durch El Niño verursachte Störungen.

Im Gegensatz dazu begünstigen hohe Produktivität, starke Strömungen und eine nur geringe Ablagerung von feinen anorganischen Partikeln in FKLD die Existenz eines relativ hohen Prozentsatzes von Suspensionsfiltrierern.

Betrachtet man die Fortpflanzungsmodi, ist das Verhältnis zwischen planktischer und direkter Entwicklung 75%-25% in CAHO, 78%-22% in HUMB und 76%-24% in FKLD.

Die Anzahl von Arten mit planktischer Entwicklung unterschieden sich signifikant nur zwischen CAHO und HUMB auf der Pazifikseite und FKLD in Atlantik. Signifikante Unterschiede bei der direkten Entwicklung konnten nur zwischen CAHO und FKLD gefunden werden. Der höher Anteil von Arten mit

ZUSAMMENFASSUNG

planktischer Entwicklung in den beiden pazifischen Gebieten kann durch die größere Heterogenität der Habitate erklärt werden, verglichen mit dem eher gleichförmigen Sedimentmuster in FKLD. Arten mit planktischer Entwicklungsweise haben bessere Möglichkeiten, sich schnell über weite Entfernungen zu verbreiten, was insbesondere vorteilhaft ist bei der Besiedlung gestörter Lebensräume, wie sie in CAHO häufig sind.

Endemismen sind den drei Gebieten eher selten (< 15%). Relativ viele Arten kommen sowohl in CAHO und HUMB und der Antarktis vor (> 30%). Hierbei spielt wahrscheinlich der Transport von Larven nach Norden durch „Antarctic Intermediate Waters“ und die „West Wind Drift“ eine wichtige Rolle. Dementsprechend werden entlang der Pazifikküste Südamerikas in Richtung niedrigerer Breiten die antarktischen Arten kontinuierlich durch solche der gemässigten Zonen ersetzt. Andererseits überlappen 23% der Arten zwischen HUMB, CAHO und FKLD, was relativ hoch erscheint und möglicherweise auf einen Austausch von Arten durch die Magellanstrasse erklärt werden könnte.

Die ökologischen und zoogeographischen Ergebnisse dieser Untersuchung lassen vermuten, dass die Magellanregion nicht als ein einheitliches, zoogeographisches Gebiet angesehen werden kann. Umweltbedingungen sowie Strömungen unterschiedlicher Herkunft, Unterschiede in der Topographie der Kontinentalschelf wie auch das komplexe Kanal- und Fjordsystem der Magellanregion führen zur Unterscheidung dreier deutlich verschiedener Lebensräume, die den drei in dieser Untersuchung beschriebenen zoogeographischen Gebieten entsprechen.

RESUMEN

Resumen

Los poliquetos son uno de los grupos más diversos y abundantes en los hábitats marinos de fondos blandos de todos los océanos. A pesar de su relevancia, este grupo ha sido ignorado durante décadas en los análisis zoogeográficos del cono sur de Sudamérica (región de Magallanes).

En el presente estudio, se analizan los patrones ecológicos y zoogeográficos de la poliquetofauna que habita el área de Magallanes. Las investigaciones que aquí se presentan están basadas en datos recogidos durante tres expediciones y en la recopilación bibliográfica de otras trece campañas científicas.

Como resultado del análisis multivariado realizado sobre la composición específica de poliquetos, tres entidades zoogeográficas fueron distinguidas:

- Entidad del Cabo de Hornos (CAHO), que se extiende sobre la plataforma occidental de la región de Magallanes (42°S-55°S; 76°-69° W).
- Entidad de Humboldt (HUMB), se extiende sobre la plataforma occidental frente a la costa de Chile, al norte de la región de Magallanes (22°-42°S; 74°-70° W).
- Entidad de Falkland (FKLD) se extiende sobre la plataforma atlántica suroriental de la región de Magallanes (42°S-55°S; 69°-55° W).

Comparaciones subsecuentes mostraron marcadas diferencias en los valores de biodiversidad, modo reproductivo, gremios tróficos y rangos de distribución característicos de estas comunidades.

El número total de especies mayor se encontró en CAHO (269) seguido de HUMB (135) siendo FKLD la entidad zoogeográfica que presentó el número más bajo (102). El promedio de especies por cuadrante, el cual es interpretado como medida de biodiversidad, resultó ser mayor en HUMB ($24,3 \pm 11,2$) intermedio en CAHO ($23,4 \pm 25,1$) y bajo en FKLD ($10,1 \pm 8,3$).

En lo que respecta a la composición de gremios tróficos, la proporción de suspensívoros, detritívoros y predadores/omnívoros fue respectivamente de 4%-43%-53% en CAHO, de 2%-63%-35% en HUMB y 22%-22%-56% en FKLD. La predominancia de detritívoros sobre suspensívoros en CAHO y HUMB, y el mayor porcentaje de suspensívoros en FKLD se relaciona con las diferencias de tasas de sedimentación y precipitación de material particulado sobre el fondo. En CAHO, las elevadas tasas de sedimentación son inducidas por la descarga de sedimento inorgánico fino transportado por el agua dulce de los glaciares y ríos, mientras que en HUMB, los altos valores de sedimentación son inducidos por las condiciones de surgencia, zona mínima de oxígeno y los disturbios producidos por las eventos de El Niño. En contraste, en FKLD, la alta productividad primaria y las fuertes corrientes, combinadas con la baja descarga de sedimento inorgánico fino favorecen el alto porcentaje de suspensívoros.

En los aspectos referidos al modo reproductivo, la proporción de fases de desarrollo planctónico y directo fueron de 75%-25% en CAHO, 78%-22% en HUMB y 76%-24% en FKLD, respectivamente. El porcentaje de desarrollo planctónico en la dos entidades pacíficas (CAHO y FKLD) diferió significativamente del encontrado en FKLD. En el caso del desarrollo directo se diferenció significativamente sólo entre CAHO y FKLD. La alta proporción de

RESUMEN

especies con desarrollo planctónico en las entidades pacíficas pueden ser explicada por la mayor heterogeneidad de composición de los en comparación con la casi uniforme composición del sedimento presente en FKLD.

Los rangos de distribución y porcentajes de endemismo, presentaron valores bajos (> 15%) en las tres entidades. El porcentaje de especies que mostraron solapamiento en su distribución en CAHO, HUMB y áreas antárticas presentó un porcentaje elevado (> 30%), mayormente causado por el transporte de larvas por la "Agua Antártica Intermedia" ("Antarctic Intermedian Water") y la "Corriente de deriva del oeste" ("West Wind Drift"). De acuerdo con estos hechos, se observa un continuo sustitución de especies antárticas por especies de carácter templado hacia bajas latitudes a lo largo de la costa suroccidental de Sudamérica. Por otro lado, el porcentaje de especies con distribución solapada entre HUMB, CAHO y FKLD fue también relativamente alto, debido principalmente al elevado intercambio de especies a través del estrecho de Magallanes.

Los resultados ecológicos y zoogeográficos de este estudio indican que la región de Magallanes no puede ser considerada una sola entidad biogeográfica. Las condiciones oceanográficas, con corrientes marinas de diferente origen, la variada topografía de la plataforma continental, así como la complejidad del sistema de canales y fiordos de la región de Magallanes, da lugar a marcadas diferencias ambientales, las cuales se reflejan en las entidades zoogeográficas descritas en este estudio.

INTRODUCTION

1 Introduction

1.1 Current status of polychaete research

Marine biodiversity research overlaps with several other fields of marine science, especially with the quantitative ecology of soft bottom communities (Snelgrove et al. 1997, Gray 2000, Ellingsen 2001) and with biogeography (Briggs 1985, Brown & Lomolino 1999, Hubbell 2001). Traditionally, these three topics are treated independently despite their strong interrelationships. During the last decade, the scientific attention shifted to a certain extent from marine ecology and zoogeography to marine biodiversity (Fig. 1). My thesis represents a unified approach using biogeography, biodiversity and quantitative ecological data to study the polychaete fauna of the Magellan region.

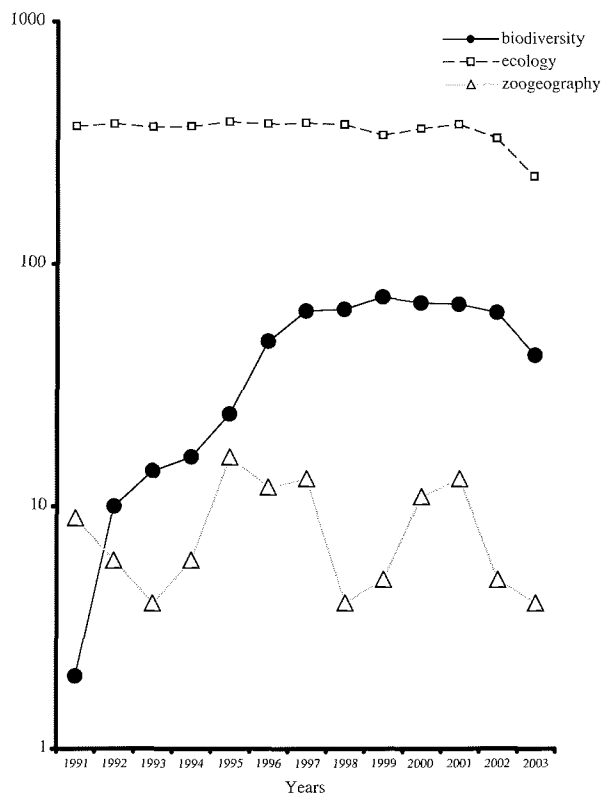


Fig 1. Number of papers dealing with biodiversity, ecology and zoogeography found in Aquatic Science and Fisheries Abstract (ASFA) services. The information was assembled from the following search strings "biodiversity not ecology or zoogeography; ecology not biodiversity or zoogeography; zoogeography not biodiversity or ecology".

INTRODUCTION

Polychaetes play a significant role in marine ecology not only because of their high biodiversity (see below) but also because of their high plasticity in reproductive and trophic strategies. Polychaetes show many different reproductive modes (Wilson 1991, Giangrande 1997) and they belong to 20 different trophic categories (Jumars & Fauchald 1979). Polychaetes worldwide make up a large proportion of the total macrofauna in soft bottoms (Hutchison 1998) and with more than 16,000 species known so far, they are placed fourth in ranking marine invertebrate species richness (Blake 1995, Bouchet 2000).

On the other hand, the polychaetes appear to be midway forms in the evolution of the Metazoa. Their coelomate metameric body plan is more complex than that of pseudocoelomates, yet providing a prototype for the more elaborated structures found in the diverse arthropods and perhaps in the molluscs (Giese & Pearse 1975, Giribet 2003). After a long stability period, the systematic of polychaetes is undergoing a major reassessment owing to new quantitative cladistic techniques. The new classification bases on 124 characters of 80 accepted families and does not follow the Linnaean categories. This classification clusters the polychaetes into two clades: Scolecida and Palpata. Scolecida are not subdivided, whereas to the Palpata belong the Aciculata and Canipalpata. The Aciculata contain the Phyllodocida and Eunicida. The Canipalpata are divided into the Sabellida, Spionida, and the Terebellida (Rouse & Fauchald 1997, Rouse & Pleijel 2001).

1.2 Polychaetes: a white spot in South American marine zoogeography

Polychaetes have been used in South American zoogeographical studies in the last decade only (Lancelotti & Vásquez 1999, Fernandez et al. 1998, Glasby & Alvarez 1999, Camus 2001). Despite the polychaetes' characteristics mentioned above, polychaetes were thought to be no proper zoogeographical indicators because of their wide geographical distribution range on all taxonomic levels and especially because of their long-distance dispersal capabilities. Most polychaete families, except a few poor-known, occur in all oceans and at all depths. Published studies on the species level, which would be required for zoogeographic analysis, are scarce, and the Magellan Region is by no way an exception in this (e.g. Hartmann-Schröder & Hartmann 1974, Knox & Lowry 1977). The zoogeography of this region has been reviewed several times, but nevertheless knowledge has remained comparatively poor. The Magellan region is famous because of the Straits of Magellan, which plays an important economical and political role in Chile. The history of the Magellan region as a biogeographic entity, however, is rather unclear. Oldest descriptions of this South American region date back to Forbes (1854), who mentioned "Araucanian", "Fuegian", and "East Patagonian" entities (Fig. 2).

Some decades later Von Ihering (1897, p. 316) modified this view and established a 'Magellan district' on the basis of molluscs. Ekman (1935) described "antiboreales Südamerika" based on a wider spectrum of information. Balech (1954) was the first to propose a zoogeographic scheme for the Magellan region, subdividing it into 5 districts: two on the Atlantic side (Santacrucense and Chubutiano), two on the Pacific side (Valdiviano and

INTRODUCTION

Chiloense) and the Fuegino district, which connects both sides at the tip of South America.



Fig 2. Zoogeographic division of South American waters sensu Forbes (1854).

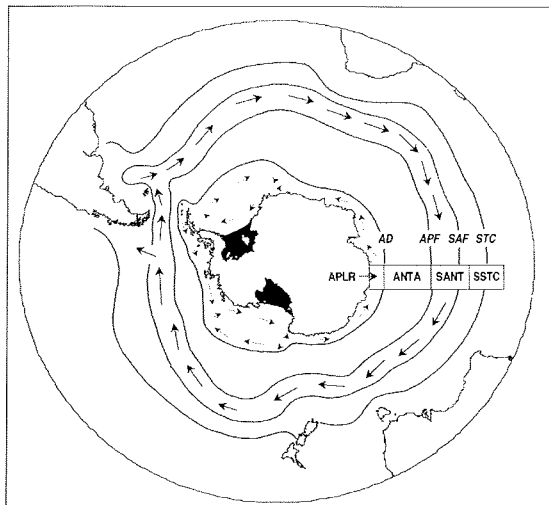


Fig 3. Zoogeographic division of South American and Antarctic waters sensu Longhurst (1998).

INTRODUCTION

Fifty-six years later and after several reviews (Hedgpeth 1970, Viviani 1979, Brattström & Johanssen 1983, Stuardo & Valdovinos 1992, Lancelloti & Vásquez 1998), Camus (2001) questioned, whether the Magellan region as a zoogeographic entity should be extended into the Atlantic area of the South American coast as done before by various authors.

Recently, Montiel et al. (submitted), based on polychaete distribution patterns, followed the scheme of Longhurst (1998, Fig. 3) based on oceanographic and phytoplankton data: the Falkland Coastal Province (FKLD) on the Atlantic side is separated from the Humboldt Current Coastal Province (HUMB), stretching over the entire Chilean Pacific coast. However, in contrast to Longhurst (1998), the fjord and channel areas on the southeastern Pacific coast of Chile were considered as a zoogeographic Cape Horn entity (CAHO) on its own, although the differences between the CAHO and HUMB entities appeared only weak.

Among the first indications for an independent CAHO entity was the particularly high zoogeographic affinity of its polychaete fauna to the Antarctic fauna (cf. Fig. 4), and, in a latitudinal view, the continuous replacement of faunal elements by Antarctic species towards higher latitudes along the Chilean coastline (cf. Fig. 5). The late final separation of Antarctica and South America some 20 million years ago and the different oceanographic conditions at the tip of South America are common explanations for these seemingly close relationships. From an oceanographic view, the Magellan region is under the regime of the West Wind Drift, which deflects northward and contributes to the formation of the Humboldt Current system.

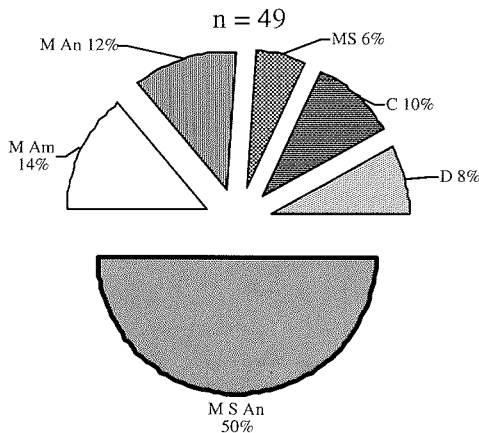


Fig 4. Zoogeographic affinities of Magellanic polychaete species (after Gambi & Mariani 1999). MS: Magellan Subantarctic C: Cosmopolitan; D: Discontinuous distribution; MS An: Magellan Sub-antarctic Antarctic; M Am: Magellan American, MAn: Magellan Antarctic.

INTRODUCTION

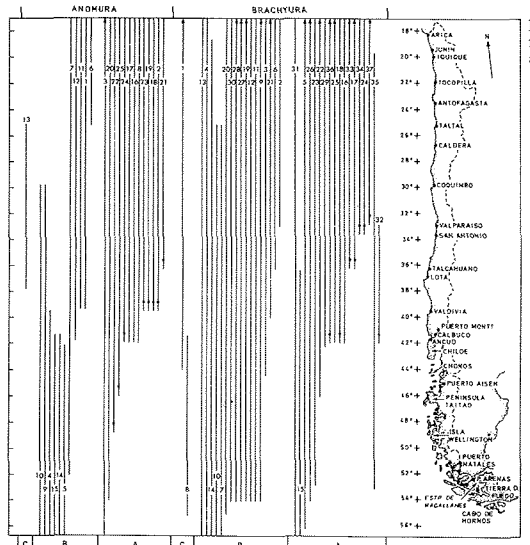


Fig 5. Distribution of the decapods (after Brattström & Johanssen 1983).

Beside the oceanographic conditions, ice is another important and structuring factor. The Last Glacial Maximum (LGM, Markgraf et al. 1992) is likely to be a major cause for today's zoogeographic patterns in the Magellan region. Recent studies on the effects of ice disturbance on benthic communities give evidence of the important role of ice as a shaping element for benthic communities (Santos & Simon 1980; Colan et al. 1998; Gutt & Starmann 2001; Teixido et al. 2003; Gerdes et al. 2003).

Glaciological and paleoceanographic information show that the LGM affected the CAHO area in two ways:

- During the LGM all fjords and channels in the CAHO were totally covered by an ice sheet (Fig. 6) that extended from 55° S to 35° S (Clapperton et al. 1995; Benn & Clapperton 2000). Sea level was lower during the Quaternary than nowadays, which led to the incursion of seawater after the retreat of the glacial ice from the fjords and channels. According to McCulloch & Davies (2001), the earliest marine incursion into the Strait of Magellan, based on pollen, diatom and lithostratigraphic analysis, occurred around 8265 (¹⁴C) yr BP.

INTRODUCTION

The climate of the CAHO region is governed by the westerly atmospheric circulation which is strongly affected by the extent of Antarctic sea ice, the position of the Antarctic Circumpolar Current (ACC) and the strength of the tropical anticyclonic cell over the Pacific and Atlantic Oceans. Fluctuations of the LGM cause oscillations in the position of the Polar Front, thus changing the current regime in a way that different water masses might have influenced the Magellan region in former times as compared to nowadays (for details see Gersonde et al. 2004).

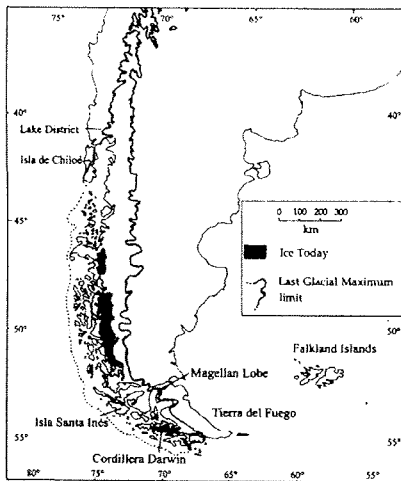


Fig. 6. Map of South America showing the extension of glacier ice at present and during the last glacial maximum (after Hulton et al, 1994).

Taking into account these ice disturbance effects in the past, it is obvious that after the LGM new habitats became available for colonization by the neighbouring benthic fauna. An early colonization phase must have happened after the LGM but the mechanisms and the resulting early patterns are unknown. Sousa (2001) distinguished four mechanisms by which marine communities become re-established: (1) vegetative growth of survivors within the area; (2) recruitment from propagules that survive the disturbance; (3) lateral inward stage encroachment by juveniles or adults from the surrounding undisturbed assemblages and, (4) recruitment from dispersed propagules including spores, larvae, or fragments capable to attach the substrate and grow vegetatively. Only the two latter mechanisms are considered for explanation of polychaete zoogeographical patterns, especially for the existence of the CAHO entity.

INTRODUCTION

1.3 Aims of the study

Based on the above mentioned recent and historical environmental settings the aims of the present thesis are:

1. to describe polychaete assemblages in the Magellan region by means of species richness per defined area.
2. to describe composition of life forms regarding (i) trophic guilds and (ii) reproduction modes.
3. to analyse zoogeographical patterns and compare recent patterns with older ones described in literature.
4. to analyse the colonization process of the CAHO entity, which presumably was realized by larval dispersal from neighbouring communities, especially via the Falkland Current from the Atlantic, via WWD from Antarctic areas, and to a less degree from adjacent Pacific areas.

MATERIAL & METHODS

Expedition data

Samples in CAHO (Cape Horn) area were collected during three expeditions: the Joint Chilean-German-Italian Magellan Campaign with RV "Victor Hensen" in 1994 (Arntz & Gorny, 1996), the Cimar-Fiordo II Expedition with RV "Vidal Gormaz" in 1996 (Mutschke et al. 1996), and the expedition ANT XIII/4 with RV "Polarstern" in 1996 (Fahrbach & Gerdes, 1997). A total of 171 cores from 41 stations were collected with a multibox corer (Gerdes 1990) and a Reineck box corer (Reineck 1958). The macrofauna was sieved through 0.5 mm mesh size, sorted and fixed in 4% buffered formaldehyde seawater solution prior to counting and identification of all polychaetes to species level (Appendix 1 and 2).

Literature data

To obtain a more complete inventory of the polychaete fauna in the continental shelf areas (<1000 m) in and around the CAHO area, an extensive literature search was carried out. This search resulted in information on species from 444 sampling locations (georeferences) from 13 expeditions, with the purpose to recognize with more accuracy differences between the HUMB and CAHO entities along the Chilean continental shelf. I include into the frame of this thesis additional data obtained during the PUCK expedition (Palma et al. in press) and the Mar Chile I expedition (Hartmann – Schröder, 1965), thus increasing with these additional data the total station number to 485 (Table 1 and App. 1).

Multivariate analysis

Station based information was organized in a grid of 106 quadrants, each 1° latitude x 1° longitude (Fig. 7). Quadrants without polychaete findings were not considered and quadrants with only one station were combined with the neighbouring quadrant.

The 106 quadrants were ordered with ANOSIM (Analysis of Similarities) and MDS (multidimensional scaling) into zoogeographic entities. The Similarity Percentage Analysis (SIMPER; Clarke 1993) described the contribution of each species to the dissimilarity between the obtained groups of quadrants. All analyses were carried out using the software PRIMER version 5.2.1. (Clarke & Warwick, 1994) with the Bray-Curtis Similarity Index, based on standardized polychaete presence/absence data.

MATERIAL & METHODS

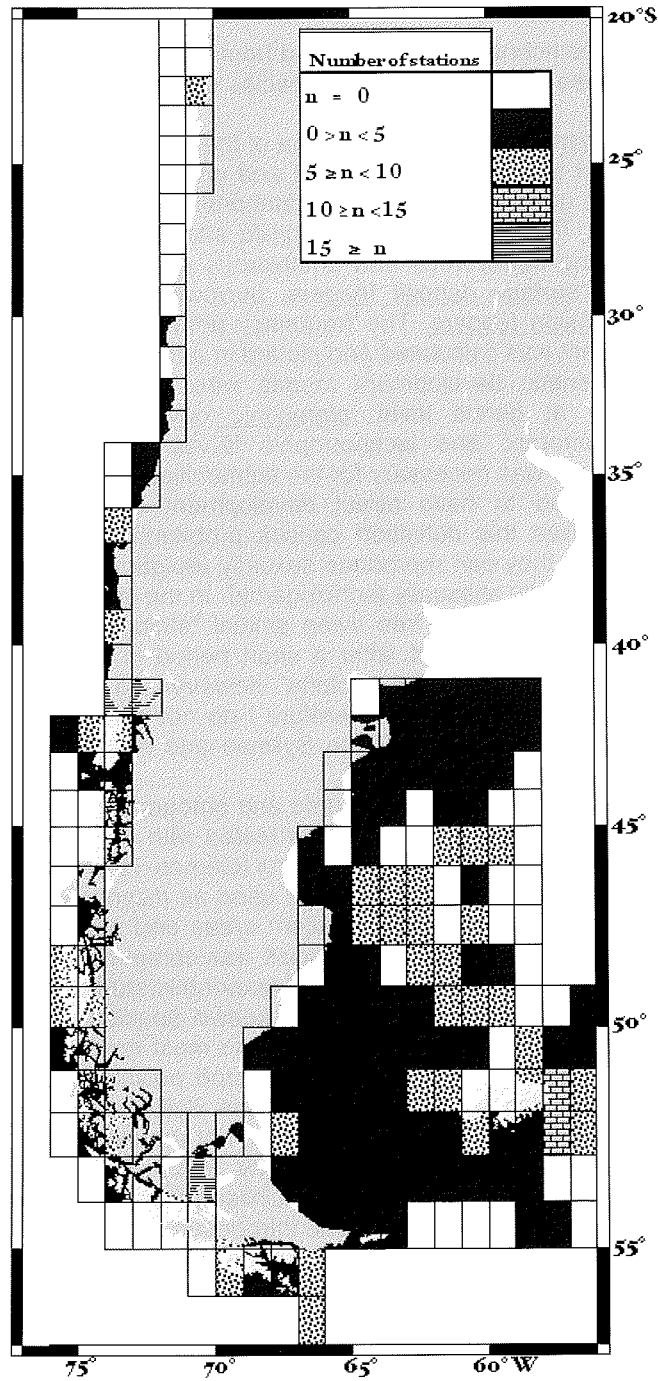


Fig. 7. Grid of the marine realm around of the tip of South America with indications of sampling locations per quadrant.

MATERIAL & METHODS

Species richness, life history, and species distribution categorization

Species richness was calculated from the species number per quadrant. Based on these data, a cumulative species curve for each zoogeographic entity was drawn.

I compared the polychaete fauna of the three zoogeographical entities also with respect to the trophic structure and ontogenetic development modes. For the trophic guild analysis feeding categories recommended by Fauchald & Jumars (1979), Gaston (1983) and modified after Crame (1992) were used: predators, including carnivorous and omnivorous species; detritus feeders, including all (sub-) surface deposit feeders, burrowing motile and sessile species, and suspension feeders. The frequency percentage of each trophic category per quadrant was calculated and plotted in a triangular chart.

Ontogenetic development modes were classified according to Giangrande (1997) at genus level: planktonic development, including free-spawning planktotrophic and lecithotrophic larvae and direct development. Special treatment was necessary for the subfamilies Syllinae and Autolytinae which are considered to have direct development by Giangrande (1997). In these subfamilies this definition causes problems; they have a dual reproductive strategy: they can reproduce sexually (epigamy) with planktonic larvae as well as seemingly asexually (schizogamy). In the latter case, a number of segments are detached as a free living sexual "stolon", which transports the male or female gametes, and, after a short period in the water column, releases the gametes and dies. The "stolons", however, do not own a gut and thus are not able to feed and grow. Therefore I do not consider these forms as functional individuals and consider the Syllinae and Autolytinae as having a planktonic development mode.

Differences in trophic structures and ontogenetic development modes between the zoogeographic entities were tested with ANOVA and subsequent post-hoc test on differences between means (Games-Howell test, Gagnon et al, 1989).

Many of the polychaete species used as discriminators for the zoogeographic entities also occurred in adjacent areas and other parts of the world oceans. Because of this fact, each species was categorized according to its distribution range based on the fundamental taxonomic studies of Hartman (1959 a, b) and Rozbaczylo (1985), in which all known species and their distribution ranges world wide were listed. In addition the most recent taxonomical reviews for the species distribution of the eunicemorph polychaetes by Orenzans (1990), the Spionidae families (Blake, 1983), the Syllidae (Licher, 2000) and Glyceridae (Böggemann, 2002) were consulted. For the categories, the following acronyms were used: CAHO: Cape Horn entity, FKLD: Falkland entity, HUMB: temperate areas north of the CAHO on the Chilean Pacific shelf between app 20° and 41° S. Additional acronyms were introduced according to Longhurst (1998) for species with a wider distribution in the adjacent Subantarctic and other Antarctic areas surrounding this continent (SANT and ANTA, respectively).

MATERIAL & METHODS

Table 1. Chronological and synoptic list of expeditions carried out in Magellan waters.

Campaign	Research Vessel	N° stations per expedition	Source
HMS Challenger	“Challenger”	6	McIntosh 1885
Swedish Antarctic Expedition	“Antarctic”	28	Hartman 1953
Discovery Expedition	“Discovery”	1	Monro 1930-36
Discovery Expedition	“William Scoresby”	112	Monro 1930-36
Lund Univ. Chile Expedition	“Arauco II” & Galvarino”	95	Wesenberg-Lund 1962
Mission du Cap Horn	“Romanche”	23*	Fauvel 1941
Mar Chile I	“Chipana”	32	Hartmann-Schröder 1965
USNS Eltanin	“Eltanin”	26	Hartman 1967
Akademic Knipovich	“Akademic Knipovich”	20	Averince 1972
Akademic Knipovich	“OB”	4*	Averince 1972
Walther Herwig 15 th , 36 th & 76 th	“Walther Herwig”	71	Hartmann-Schröder 1983
Allan Hancock Pacific Expedition	“Vema”	25*	Maurer & William 1988
Italian Oceanographic expedition	“Cariboo”	16	Gambi et al. 1999
Shinkai Maru 4 th , 5 th , 10 th & 11 th	“Shinkai Maru”	22*	Bremec et al. 2000
CIMAR Fiordos	“Vidal Gormaz”	19	Montiel et al. 2004
UMAG, data base.	“Lenga”	3**	Ríos et al. 2003
PUCK	“Sonne”	18	Palma et al. submitted

* Information on species per station or station georeference not available.

RESULTS

3 Results

124 years of polychaete research in this part of the world resulted in the record of 481 polychaete species from 108 genera and 44 families.

Of these 481 species, 130 species were found only once and 95 species were reported without exact sampling position. The latter were not considered for the analysis, thus leaving 386 species for numerical and statistical analyses.

3.1 Multivariate analysis

ANOSIM (Analysis of Similarities) revealed significant differences in polychaete inventories between all three zoogeographical entities CAHO, FKLD and HUMB (cf. Table 2). The MDS plot confirmed these observations by arranging the stations in three distinct quadrant groups, two referring to the Pacific and one to the Atlantic shelf at the tip of South America (Fig. 8).

Table 2. ANOSIM pairwise test of presence/absence data of polychaete species from 106 quadrants in the **CAHO**: Cape Horn entity, **FKLD**: Falkland entity, **HUMB**: Humboldt entity. In bold significant difference.

Pairwise test			
Zoogeographic entities	R	P (%)	Number \geq observed
CAHO-FKLD	0.477	0.1	0
CAHO-HUMB	0.376	0.1	0
FKLD-HUMB	0.704	0.1	0

Sample statistic (Global R): 0.526

Significance level of sample statistic: 0.1%

SIMPER analysis (Appendix 3) identified the most important species contributing to the average dissimilarities between the three zoogeographic entities (average = 94.32). Regarding CAHO versus FKLD (average dissimilarity = 94.32), the main species in CAHO were *Glycera capitata*, *Onuphis pseudoiridescens*, *Polyeunoa leavis* and *Leanira quatrefagesi*, whereas in FKLD *Idanthyrsus macropaleus*, *Serpula narconensis*, *Perkensiana antarctica* and *Chaetopterus variopedatus* were the most important discriminators between both entities. Average dissimilarity (95.97) between CAHO against HUMB was caused mainly by *Paraprionospio pinnata*, *Ninoe chilensis*, and *Lumbrineris chilensis* in the HUMB. Highest average dissimilarity (99.21) was found between FKLD and HUMB, the most important contributors have already been mentioned above (cf. Appendix 3).

RESULTS

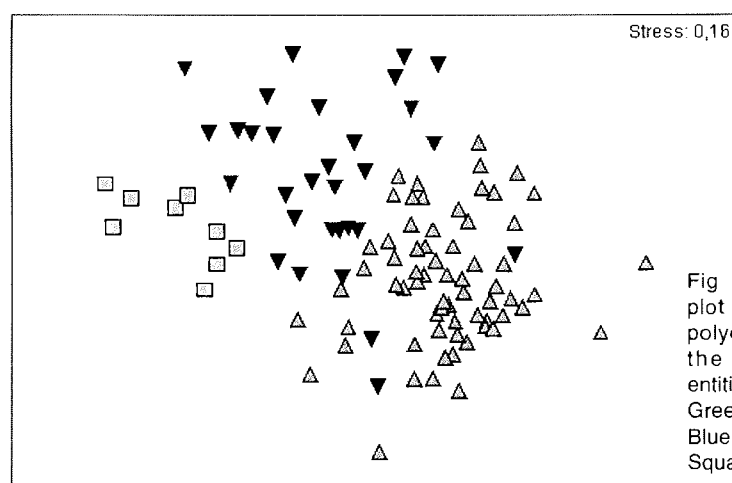


Fig 8. nMDS ordination plot on binary data of polychaete species for the zoogeographic entities.
Green triangle: CAHO;
Blue triangle: FKLD;
Square: HUMB.

3.2 Biodiversity patterns

The mean species richness (species numbers per quadrant) in the zoogeographic entities was highest in HUMB (24.3 ± 11.2), intermediate in CAHO (23.4 ± 25.1), and lowest in FKLD (10.1 ± 8.3 ; see Fig. 9; Table 3). Total number of species was 269 in CAHO, 135 in FKLD and 102 in HUMB, respectively (Fig 10 a, b & c).

Table 3. Multiple comparison test for unequal sample groups of species richness (species numbers per quadrant). Games – Howell test of mean values per zoogeographic entity (SD = Standard deviation; SQ = number of quadrants). Significance level at 5% (**) and no significant differences (++).

	CAHO	FKLD	HUMB
Mean \pm SD (SQ)	23.4 \pm 25.1 (31)	10.1 \pm 8.3 (66)	24.3 \pm 11.2 (9)
CAHO		**	++
FKLD			**
HUMB			

RESULTS

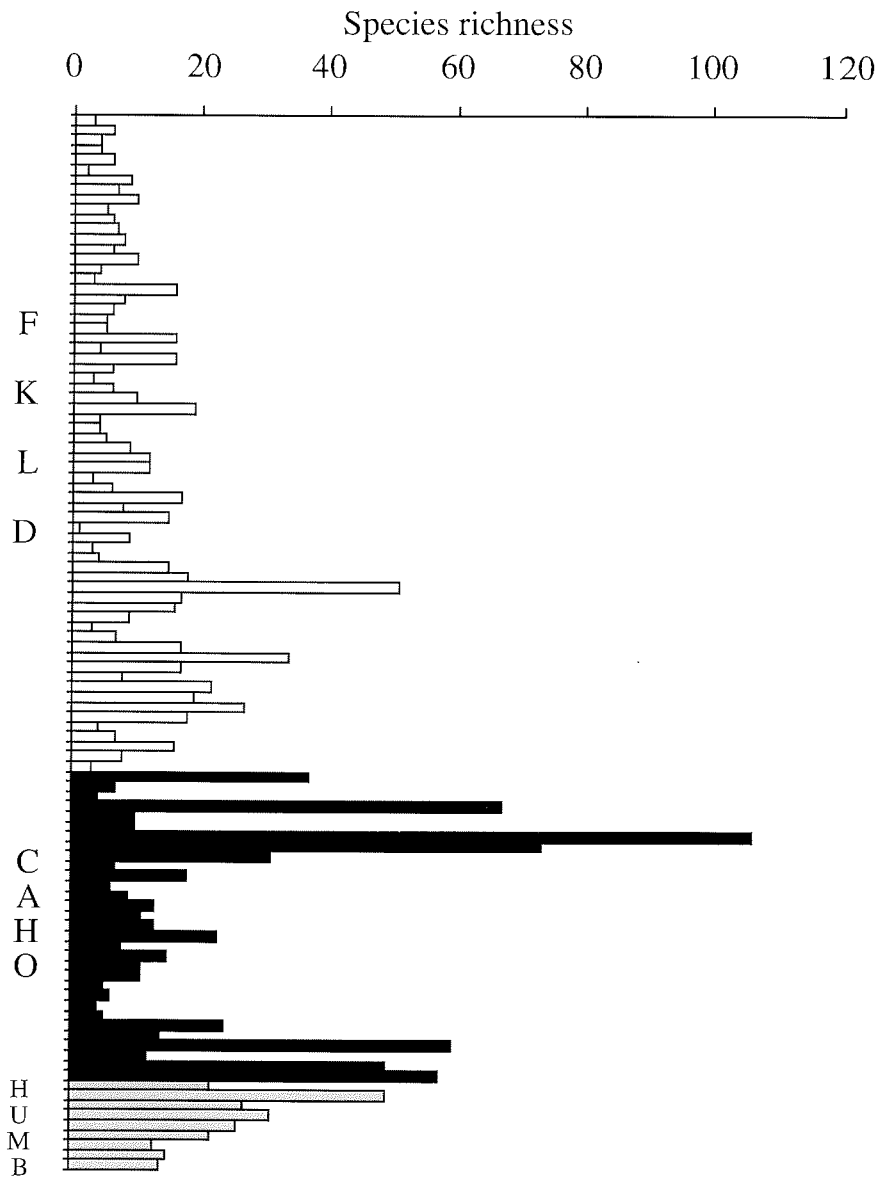
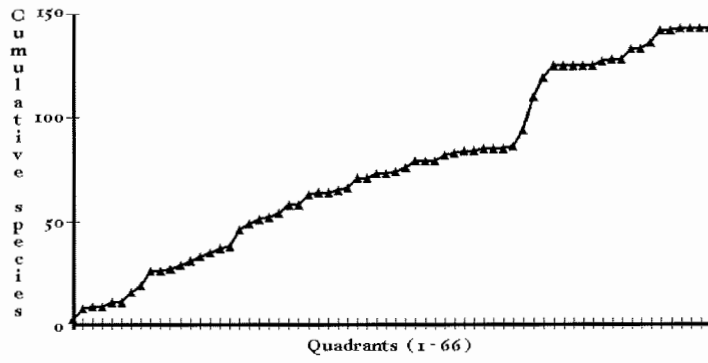


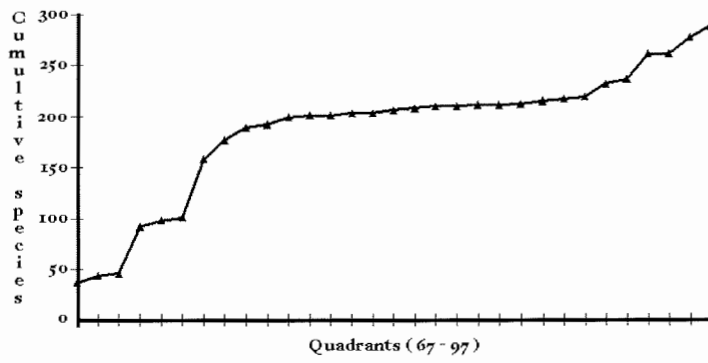
Fig 9. Species richness (species numbers per quadrant) in FKLD (white), CAHO (black) and HUMB entities (grey).

RESULTS

A



B



C

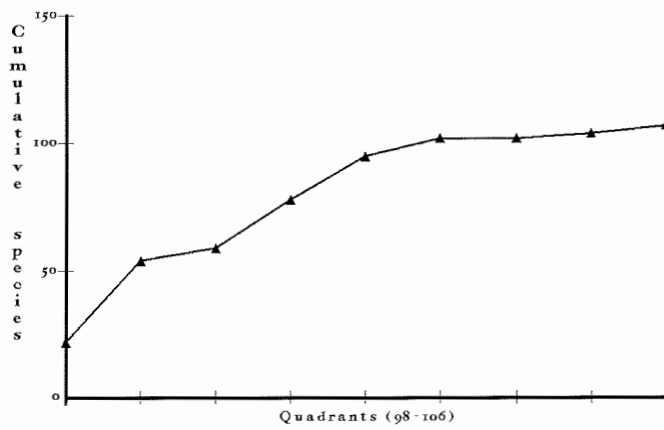


Fig 10. Cumulative species curves per quadrant (A) FKLD (B) CAHO (C) HUMB entities.

RESULTS

3.3 Feeding and reproductive patterns

Suspension feeders occurred in the CAHO and HUMB entities in significantly lower percentages (4% and 2%, respectively) as compared to the FKLD entity (22%). The share of detritus feeders was highest in HUMB (63%), intermediate in CAHO (43%), and lowest in FKLD (22%; Fig. 11a, b & c; Table 4).

Table 4. Multiple comparison test for unequal sample groups of trophic guilds (percentages in entities; Games–Howell test). Significance level at 5% (**) no significant differences (++).

	CAHO	FKLD	HUMB
Suspension feeders			
CAHO	4%	22%	2%
FKLD	22%	22%	2%
HUMB	4%	22%	2%
Detritus feeders			
CAHO	43%	22%	63%
FKLD	43%	22%	63%
HUMB	43%	22%	63%
Predators/omnivores			
CAHO	4%	22%	2%
FKLD	4%	22%	2%
HUMB	4%	22%	2%

In CAHO, *Maldane sarsi* and *Paramphinome australis* were the most frequent detritus feeders, the predator/omnivor guild was represented mainly by *Leanira quatrefagesi* and *Glycera capitata* while *Idanthyrsus macropaleus* and *Serpula narconensis* were the most frequent suspension feeders.

In FKLD, *Thelepus plagiostoma* was the most frequent detritus feeder. The predator/omnivor guild was represented by *Harmothoe spinosa* while *Idanthyrsus macropaleus*, *Serpula narconensis* and *Perkinsiana antarctica* were most frequent suspension feeders.

In HUMB, *Paraprionospio pinnata*, *Cossura chilensis* and *Spiophanes chilensis* were the most frequent detritus feeders. The predator/omnivor guild was represented by *Nephtys ferruginea* and *Glycera americana*, and *Chone striata* was the most frequent suspension feeder.

RESULTS

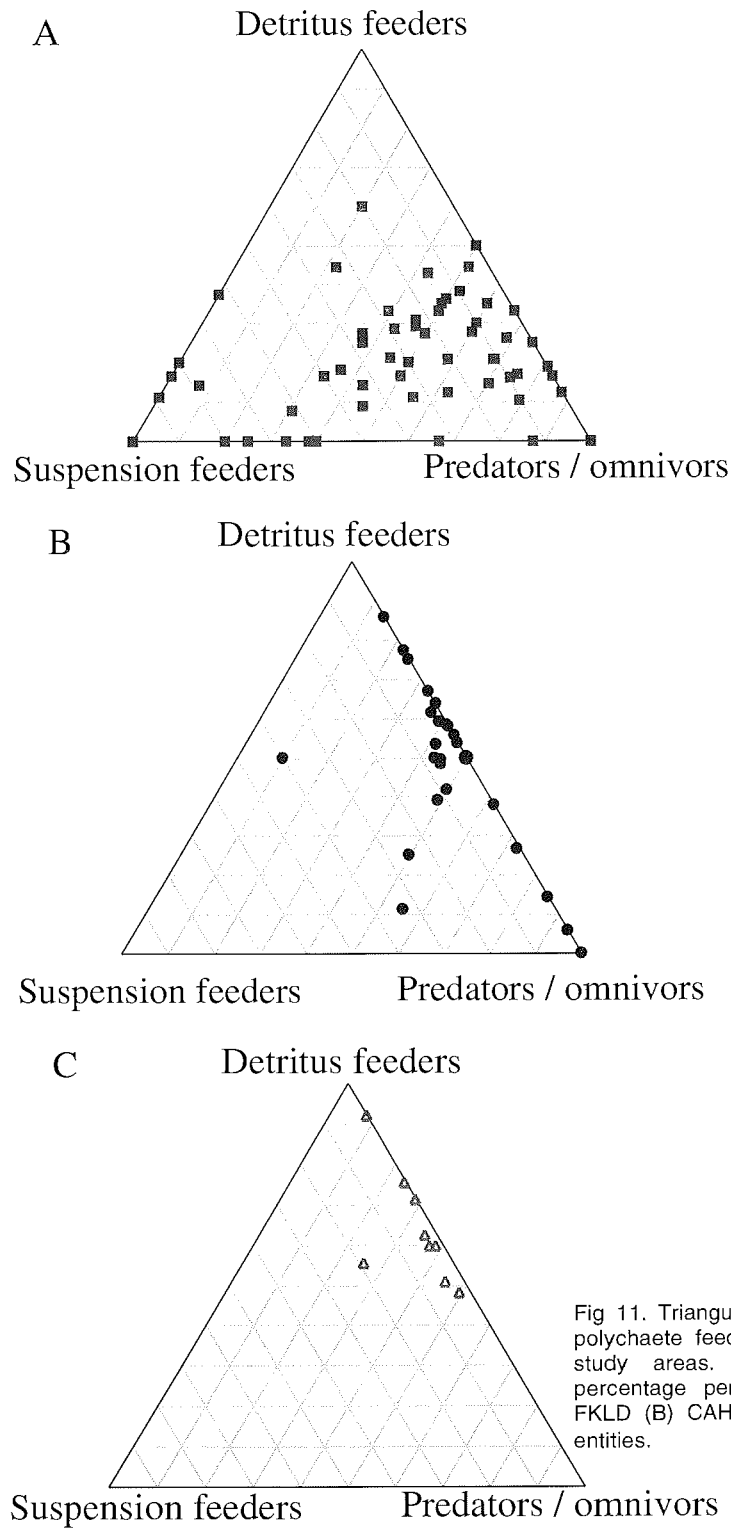


Fig 11. Triangular charts showing polychaete feeding modes in the study areas. Values refer to percentage per quadrant in (A) FKLD (B) CAHO and (C) HUMB entities.

RESULTS

In all entities polychaetes showed a high percentage of planktonic development: 78% in HUMB, 75% in CAHO, and 76% in FKLD, respectively. Correspondingly, direct development was found to be lower in the three entities with 22%, 25% and 24%, respectively. The planktonic development in FKLD was found significantly different from the HUMB and CAHO entities. Direct development differed significantly only in the CAHO and FKLD entities (Table 5; Fig. 12).

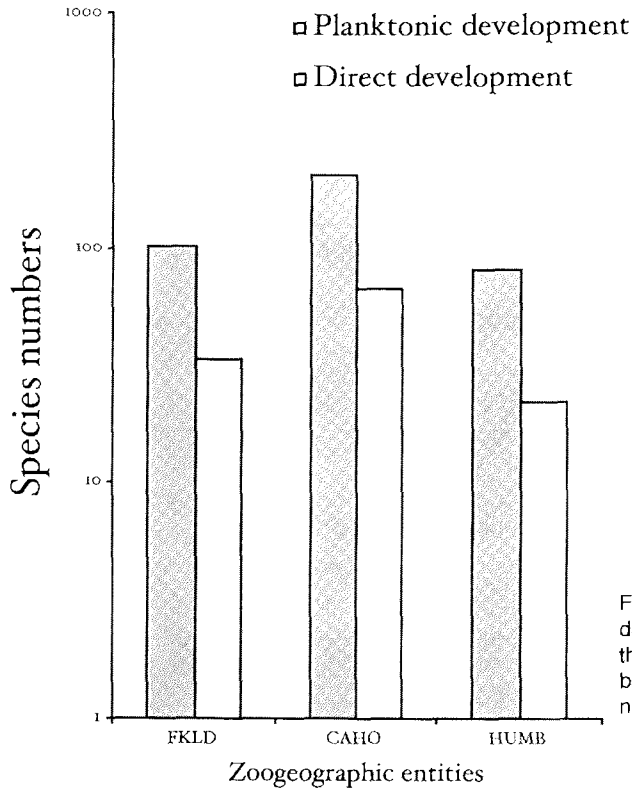


Fig 12. Polychaete development modes in the three entities under study, based on species numbers.

Table 5. Multiple comparison test for unequal sample groups of development modes in polychaete species in the entities (Games–Howell test). Significance level at 5% (**), not significant different (++)

	CAHO	FKLD	HUMB
Planktonic development			
CAHO		**	++
FKLD			**
HUMB			
Direct development			
CAHO		**	++
FKLD			++
HUMB			

RESULTS

3.4 Polychaete distribution patterns

The distribution patterns of the polychaete fauna are shown in Fig. 13. Thirty-nine species (10 %) appeared with disjunctive findings worldwide. Forty-three (11 %) of the 386 species showed a cosmopolitan distribution, and comparatively few species were restricted to just one of the three distinguished entities: 3% to FKLD, 5% to CAHO, and 13% to HUMB. The majority of the remaining species (58 %) were widely distributed in the Magellan region and (Sub) Antarctic areas. These species were separated into 3 complex species groups, whose (i) species with distributions restricted mainly to CAHO and areas along the Chilean Pacific shelf down to the Antarctic (CAHO complex), (ii) species being mainly distributed in the Atlantic sector down to the Antarctic (FKLD complex), and (iii) species with distribution patterns being restricted to South American waters only (Fig. 13b).

The biggest of these groups was that with affinities to the CAHO complex (29%; 111 species). The smallest group showed closest affinities to FKLD (6%; 22 species) on the Atlantic side and areas south of the Antarctic Convergence. A third group of species was restricted exclusively to the Atlantic and Pacific coasts of South America (23%; 87 species).

RESULTS

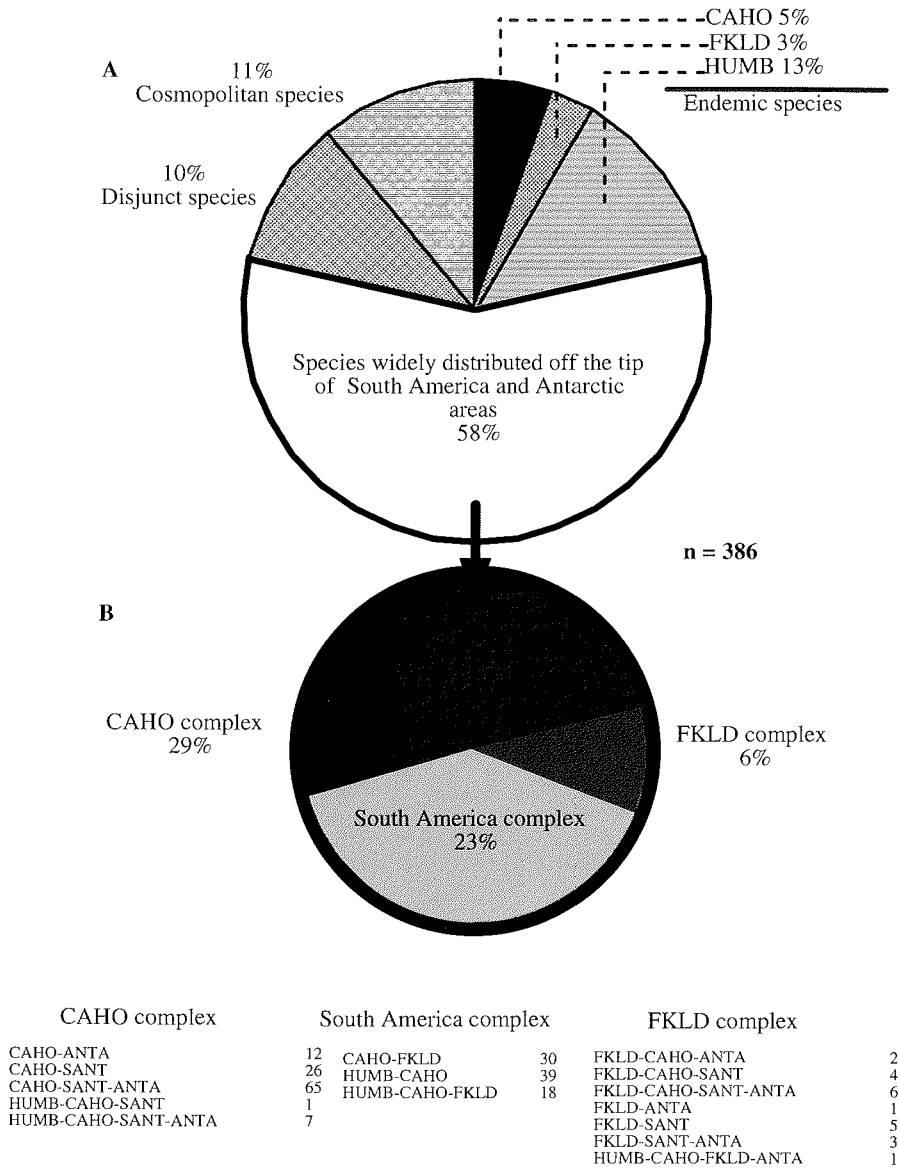


Fig 13. (A) Percentage of polychaete species numbers in different entities of the Magellan region and the percentage of arbitrary species widely distributed in waters around South America and in Antarctica. (B) Subdivision of the arbitrary species group into group complexes containing species with different affinities to South American entities and/or Antarctic waters.

DISCUSSION

4 Discussion

4.1 General consideration about this thesis

In the Magellan region polychaetes are not only important in terms of density (Maurer & William, 1988, Gerdes & Montiel. 1999), biodiversity (Cañete et al. 1999; Gambi & Mariani 1999, Montiel et al, submitted) and secondary production (Gerdes & Brey 1999), they also can be considered as discriminators in zoogeographical discussions, because they are rather constantly distributed along the South American coast lines.

In order to answer the questions of this thesis a comprehensive revision of the polychaete fauna was necessary with respect to biodiversity, taxonomy, ecology, and trophic as well as reproductive characteristics. My thesis therefore bases on 5 publications covering three major themes:

- biodiversity and ecology are tackled by the manuscripts 1 and 2.
- manuscript 3 deals with zoogeographical questions of the polychaete fauna of the MR and adjacent areas
- manuscripts 4 and 5 deal with taxonomy and present new species records from the study area.

4.2 What is a zoogeographic region in the marine realm?

The classification of a geographic region based on the biota is a permanent aim in marine and terrestrial biogeography (Forbes, 1854; Brown & Lomolino, 1998). The concept of zoogeography was first applied in terrestrial ecology. Marine biogeographical classifications normally base on attributes such as discontinuity in species composition and number (Longhurst, 1998) or percentage of endemism (Cox & Moore, 1993; Myers & Giller 1988). However, it is well known that endemism and the above mentioned discontinuities are strongly affected by sampling effort. For example, Arntz (1999) noted that one of the main problems in comparing the Antarctic and the Magellan regions is the difference in sampling efforts in these regions. Especially in poorly studied regions – and the Magellan region still has to be considered as such - I suggest that the use of additional criteria such as trophic guilds or reproduction modes allows to describe a zoogeographic pattern with much more accuracy.

My approach like several others (Gorny 1999; Brandt, 1999, Thatje, 2003) before considered one group of marine invertebrates, but additionally more ecological characteristics such as trophic guilds and reproductive modes are used.

4.3 The Magellan region: a zoogeographic region?

Analysing zoogeographic patterns on the basis of the polychaete species inventory and reproductive modes and trophic guilds of species around the tip of South America, three entities could be distinguished:

- CAHO on the continental shelf of the southeastern Pacific coast (42°S to 55°S; 76°- 69° W).

DISCUSSION

- FKLD on the southwester Atlantic continental shelf (42°S to 55°S; 69° - 55° W).
- HUMB on the continental shelf of the Chilean Pacific coast (22° - 42°S; 74°-70° W) north of the Magellan region.

Concerning the mean number of species per quadrant, CAHO (23 species) and HUMB (24 species) did not show any significant differences, but both differed significantly from FKLD (10 species; Tab. 4). The latter result may be a product of the high correlation between the species number and the different sampling efforts in the three entities. However, SIMPER and ANOSIM, which allow the comparison of areas with different sampling efforts (Chapman & Underwood 1999), showed significant differences in the polychaete inventories in and between the three entities.

The total number of species was higher in CAHO (269 species) than in HUMB and in FKLD (102 and 135 species, respectively). The high species number in the CAHO entity might be explained by the fact that this entity meets the demands of many species by presenting a very heterogeneous spectrum of different habitats such as fjords and channels, deep and shallow sites, muddy areas and biogenic hard substrates such as *Chaetopterus* tubes (Gutt, 1999) and *Macrocystis* fields with their holdfasts as specific microhabitats therein (Santelices & Ojeda 1984).

What are the reasons for the differences in dominance of detritus feeders versus suspension feeders between CAHO and HUMB on the one side, and FKLD on the other side? In CAHO extremely high fluxes of fine inorganic material are coming from melting ice and being transported by fresh water runoff, (mean of 3098 m³ s⁻¹; Dávila, 2002). This fine material might clog the sensitive filter apparatus of suspension feeders and seems to favour the existence of deposit feeders (Kowalke, 1998). The high percentage of deposit feeders in the HUMB is difficult to explain, but most probably this has to be considered as a result of the complex processes in this area with upwelling, an oxygen minimum zone, and disturbance produced by El Niño oscillations (Arntz, 1991).

Contrasting suspension feeders dominate in FKLD. This entity under the influence of the Falkland Current is a highly productive area with complex current patterns. The topography of the shelf in depths between 100 to 500m is rather irregular with canyons, steps, terraces, and embayments (Piccolo, 1998). Sediments are mostly medium grained sands, and some places show high percentages of gravel, formed either by small pebbles or bioclasts from various invertebrate groups (Bastida et al. 1992). River runoff on this South American shelf and thus the flux of fine inorganic material is much lower. Piccolo (1998) reports values from Chubut (56 m³ s⁻¹) and Santa Cruz River (700 m³ s⁻¹). All these regional environmental conditions favour the existence of suspension feeders and might explain their higher dominance as compared with both other entities on the Pacific side of the continent. In general the trophic guild determines not only an attribute of a species but it also reveals to some extent the environmental conditions in which the species lives (Erwin, 1997).

DISCUSSION

Concerning reproductive modes, planktonic development in FKLD was significantly lower as compared to the other two entities. Direct development differed significantly only between CAHO and FKLD.

Descendants of species with planktonic development are dispersed faster over longer distances than in the direct development mode. This is an advantage for quick recolonization of disturbed areas by active movement and passive transport by currents (Levin 1984; Peck et al. 1999). The larger proportion of species with planktonic development in CAHO might be explained by this property, because this entity is most affected by disturbance. Gallardo and Penchaszadeh (2001) found similar results in gastropods: species with planktonic development were more frequent on the Pacific side as compared to the Atlantic coast of South America. The authors argue that the scarcity of species with planktonic development on the Atlantic side reflects the “near continuous soft-bottom habitat there” and a greater habitat heterogeneity along the Pacific coast.

According to these authors differences in the geological history, i.e. geomorphology and bottom substrates, of the coasts and consequently in the composition of benthic communities influence the distribution in the case of gastropods.

To which extent such reasons also can explain the observed differences in the polychaete fauna, is difficult to answer. Since Thorson (1957) published his work on larval development of marine invertebrates, only little emphasis was laid on detailed studies of polychaete reproduction modes (Wilson, 1991). The role of development modes for ecology and zoogeography context is hardly studied (Jablonski & Lutz, 1983). In fact, our knowledge of reproductive modes in polychaetes includes only 3% of the total species known world-wide (Giangrande, 1997). Although I distinguish for my analysis only 2 reproduction modes, which I consider to be helpful for explanation of ecological and zoogeographical patterns of the polychaete fauna, my approach to include this criterium nevertheless, resulted in clear differences between entities – comparable to what was described above for gastropods. In the moment the observed distribution patterns in the polychaete fauna are difficult to explain by differences in their reproductive modes, because a lack of the knowledge in this field.

4.4 Zoogeographic patterns and endemisms

35% of the polychaete species (CAHO complex and FKLD complex) showed overlap with species inventories of Antarctic areas and the endemism levels in the 3 South American entities were rather low (3% in FKLD, 5 % in CAHO, and 13% in the HUMB entity). The relatively high species overlap between CAHO and HUMB on the Pacific side with Antarctic areas may be caused by the northward transport of larvae with Antarctic Intermediate Waters and the West Wind Drift. In consequence, we see a continuous replacement of Antarctic species by temperate species towards lower latitudes along the Pacific coast of South America (Viviani 1979, Brattström & Johanssen 1983, Manuscript III and Fig. 4). Following the hypothesis outlined in this thesis, the CAHO area was re-colonized after the last glacial maximum. From where was this new marine

DISCUSSION

habitat re-colonized? Firstly it is interesting to mention that polychaetes are successful colonizers in areas after disturbance events (Levin 1984, Homziak 1988, Snelgrove et al, 2001, cf. Manuscript I), and there are no reasons for a change in the last few thousand years. This colonization success may have several reasons. On the one hand the oceanographic circulation patterns favour a steady import of larvae from adjacent areas: from the easterly FKLD area, where an exchange of species through the Magellan Straits as a "new" oceanic corridor should be, theoretically, possible (Manuscript III), from ANTA and SANTA areas via currents of the West Wind Drift, and also from the northern HUMB entity at least during El Niño events. However, not only transport of larvae facilitates successful colonization of an area, but also its environmental settings such as substrate, which influence the survival of recruits substantially (Bhaud 1998). In this sense CAHO seems to meet demands of many species by presenting a very heterogeneous spectrum of different habitats as mentioned already before.

The proposed species exchange between the entities of South America also explains the low percentage of endemism levels found in my study – low especially in comparison to Antarctic communities, where endemism levels for polychaetes are as high as 57 % and even much higher for other taxa (Knox & Lowry 1977).

High species affinities between the Magellan region (CAHO) and Antarctic regions have been confirmed by other studies, too: peracarids, (Brandt 1999), molluscs (Linse et al 1999) and shrimp decapods (Gorny 1999) are examples. These authors argue that this high affinity between both sides of the Drake Passage originates from one common shallow water fauna (see Zinsmeister 1979) prior to opening of the Drake Passage (Barker & Thomas 2004). Later on survivors of last glaciations may have re-colonized shallow areas on both sides of the Drake Passage from deeper waters. Nevertheless, some taxa are under-represented on the Antarctic shelves. For example, reptantia (brachyuran and anomuran crabs) in Antarctic waters show an impoverishment of species numbers towards high Antarctic areas owing to physiological constraints of their sensitivity to high levels of Mg^{2+} in the haemolymph (Frederich et al. 2001, Thatje 2003).

The ecological and zoogeographical findings of this study indicate that the Magellan region cannot be considered as one single zoogeographic entity. The environmental settings with water currents from different origins, differences in continental shelf and slope topography between the east and west coast leads to communities with different species inventories and lifestyles. The complex channel and fjord system as a result of the retreat of ice after the last glacial maximum is especially typical for the CAHO entity and houses a rich and diverse polychaete fauna as compared to the FKLD entity.

5 Biodiversity & Ecology

5.1 Polychaete assemblages on the Magellan and Weddell Sea shelves: a comparative ecological evaluation.

Montiel A^{1,2*}, Gerdes D.¹, Hilbig B.¹ & Arntz W.E.¹

ABSTRACT: Similarities between the soft-bottom polychaete assemblages on either side of the Drake Passage and spatial patterns of these assemblages were analysed based on data from 273 corer samples collected in the Magellan region (42°S to 55°S, 254 m mean water depth) and on the Weddell Sea shelf (70°S to 71°S, 263 m mean water depth). Paraonidae, Ampharetidae and Maldanidae were the most abundant families in the Magellan region, while in the Weddell Sea Syllidae, Terebellidae and Spionidae were most abundant. The total species number found in the Magellan region (199) was higher than in the Weddell Sea (163), yet significantly higher values of heterogeneity diversity, species richness, and density were found in the Weddell Sea. At most of the Weddell Sea stations all three trophic guilds (suspension feeders, detritus feeders, and predators) were present, whereas suspension feeders were almost absent in the Magellan samples. The species abundance distribution showed high numbers of species represented by only one specimen in both regions. This causes low dominance and similar high values of evenness in both regions. We suggest that the polychaete assemblage structures in both regions are influenced by environmental stress through ice and physical complexity of the areas resulting in many different habitats.

Key words: polychaetes, species composition, diversity, geographic

distribution, trophic guilds, Magellan region, Weddell Sea.

INTRODUCTION

Soft bottoms are the most common habitats in the world's ocean (Wilson 1991, Snelgrove 1998). Traditionally, the understanding of community patterns in this kind of habitat has been an important task of marine ecology (Gray 2002). Many studies during the last 30 years compared community attributes along depth (Sanders 1968, Rex et al. 1993, Gray 1994, Cosson-Sarradin et al. 1998) or latitudinal gradients (Ellingsen 2001, Clarke & Johnston 2003, Valdovinos et al. 2003). Recently, interest has concentrated on once again diversity patterns (Gaston 1996, Foggo et al. 2003, Barnes & Brockington 2003). In the northern hemisphere, Petersen (1913) and Thorson (1957), pioneers in marine benthic ecology, compared shelf communities and showed that assemblages in different areas are seldom similar even when bottom type conditions are identical (Rosenberg, 2001). In the southern hemisphere, Arntz and Ríos (1999) compared the Magellan versus the Weddell Sea shelves with special focus on ecological and evolutionary relations. They described distinct differences in species composition and community structure between these ecosystems. However, the accuracy on species level for polychaete assemblages and their quantitative attributes requires improvement. For example, a quantitative study in shallow waters

performed in the northernmost part of the Magellan region yielded only 38 species belonging to 24 families, with Nereidae and Orbiniidae being the most speciose families (Cañete et al. 1999). Gambi & Mariani (1999) archived from the Straits of Magellan 119 polychaete species belonging to 34 families and identified Syllidae and Ampharetidae as the most speciose families. In both studies more than 50% of the species were shared by Magellan and Antarctic areas. The latter report suggests that no major differences between polychaete assemblages on either side of the Drake Passage exist.

The aims of the present study are: (1) to make a detailed description of shelf polychaete assemblages in the Magellan region (~42°S) and the high Antarctic Weddell Sea (~72°S) based on quantitative samples; (2) to use biodiversity and density values in order to elucidate potential faunistic and zoogeographical links of the polychaete assemblages between the Magellan and the Antarctic Weddell Sea shelves.

MATERIAL AND METHODS

Study areas

The biogeographic Magellan region *sensu* Camus (2001) extends from about 42°S to 55°S on the western coastal shelf of South America (Strub et al. 1998). The shelf has a mean width of 6.54 km (Gallardo 1984), whereas the Atlantic shelf extends to about 850 km width at 51°S (Piccolo 1998). Successive glaciation periods structured the west coast with more than 200 fjords and channels (Syvitski et al. 1987) with water depths frequently less than 150 m depth and maximum depths around 1050 m. Sediments are mostly characterized by silt and clay, but

coarser sediments such as pebbles and biogenic deposits from molluscs and barnacles are also present (Brambati et al. 1991). Three permanent ice fields exist, Campo de Hielo Norte (46 – 47 °S), Campo de Hielo Sur (48-52°S), and the Darwin mountain range (54-55°S, Naruse & Aniya 1992). The hydrographic regime is characterized by strong freshwater input due to high precipitation and concomitant runoff, producing a strong and shallow pycnocline (Dávila et al. 2002).

A mosaic of diverse soft-bottom habitats exist in the Magellan region (Arntz 1999). Taxa such as ascidians, brittle stars, decapods, and brachiopods dominate the megafauna (Gutt et al. 1999), whereas polychaetes, amphipods, and bivalves contribute considerably to the macrofauna (Montiel et al. 2001).

The Weddell Sea stations are located on the southeastern shelf (71°S - 10°W; 71°S - 12°W). Due to the continent's ice cover, the shelf is depressed to depths up to 800 m (Teixidó et al. 2002). The Weddell Sea shelf has a width range between 10 and 40 km, although a maximum up to 90 km can be observed (Carmack & Foster 1975). Near-bottom water temperatures are rather constant with values between -1.7 and -1.9°C, apart from common but unpredictable 'Warm Deep Water' intrusions, which occasionally may increase temperatures to 0.5 °C (Gerdes et al. 1992). The sediment is dominated by sand, gravel and biogenic substrates (sponge and bryozoan debris) with numerous drop stones in between being transported by the continental ice sheet.

During winter, the sea ice covers a maximum of almost 20×10^6 km² of

the Antarctic Ocean, in austral summer the coverage is reduced to less than 4×10^6 km² (Eicken 1992). Along the southeastern Weddell Sea shelf icebergs originating from the shelf ice often run aground and affect benthos communities in depths down to about 300 m. Due to this disturbance, the community structure of the Weddell Sea shelf benthos is the result of a combination of a rather constant temperature regime and considerable disturbance mainly by icebergs with all implications for the function and structure of benthic communities (Piepenburg et al. 2002; Teixidó et al. 2002; Gerdes et al. 2003; Knust et al. 2003).

Sampling

Samples in the Magellan region (MR) were collected during three expeditions: the Joint Chilean-German-Italian Magellan Campaign with RV "Victor Hensen" in 1994 the Cimar-Fiordo II Expedition with RV "Vidal Gormaz" in 1996 and the expedition ANT XIII/4 with RV "Polarstern" in 1996. The expeditions ANT XV/3 and ANT XVII/3 with RV "Polarstern" in 1998 and 2000, respectively, provided samples from the southeastern Weddell Sea shelf (WS).

A total of 257 cores from 59 stations were collected with a multibox corer (Gerdes 1990) and a Reineck box corer (Reineck 1958), 41 (171 cores) stations in MR and 18 (86 cores) stations in WS. The total area sampled was 4.3 m² in MR and 2.1 m² in WS. The mean depths at the MR and WS stations were 254 and 263 m, respectively (Tab. 1). The macrofauna was sieved on 0.5 mm mesh size, sorted and fixed in 4% buffered formaldehyde seawater solution prior to counting and

identification of all polychaetes to species level.

Data processing

For comparison of the polychaete assemblages we used the following attributes: density (ind. m⁻²) per station, dominance of species (%), trophic guild, species composition, diversity ($\exp H'$), and evenness (J). Additionally, point species richness and sample species richness (SR_p and SR_s , respectively) were calculated following the recommendations of Gray (2001a): SR_p is the species richness of a single sampling unit (core) and SR_s is the species richness of a number of sampling units from the same sampling location. According to Gray (2000) the heterogeneity of the species diversity (HD_i) was measured by the exponential form of the Shannon-Wiener index based on \log_2 density data.

For the analysis of the trophic guild distribution patterns, each species was classified into a feeding category following the classification of Fauchald & Jumars (1979) and Gaston (1983) modified according to Crame (1992): predators include carnivorous and omnivorous species; detritus feeders include all (sub-) surface deposit feeders and burrowing motile and sessile species, and suspension feeders were considered as a single group. According to this classification the percentage of each trophic category per station was calculated and plotted in a triangular chart.

To elucidate any potential zoogeographic links between both sides of the Drake Passage, we searched the literature for the distribution and depth ranges of those polychaete species found in

both areas under investigation (see Table 4).

Species accumulation curves were calculated in order to compare the polychaete inventory among the different sample sizes from each region (Gray 1981, Lawrence & Walters 1979) and to consider the high number of rare species in the samples (Cosson-Sarradin et al. 1998).

We established species-accumulation curves in the two regions according to the following procedure:

The accumulation of the number of species S with increasing number of individuals N was computed using the *EstimateS* programme (Colwell 2001). *EstimateS* generates n data pairs of average S , N (averages refer to 100 randomized runs with replacement), where n is the number of samples considered ($n = 171$ for MR; $n = 86$ for WS). Subsequently a simple exponential model was fitted to these n data pairs of average S , N .

Completeness of sampling of the species inventory was checked by computing the number of new species S_N to be expected if a further 1000 individuals would have been collected:

$$S_N = a * N^b \Leftrightarrow \ln(S_N) = \ln(a) + b * N$$

S_N is the smaller the more comprehensive the inventory has been performed, i.e. in this case the more specimens N are included.

An objective and comparable measure of species richness was derived by determining the points of equal slope in both species-individual curves, i.e. that number of individuals N at which the addition of a further X individuals would result in exactly 1 additional species, $P_{X,1}$:

$$S_{N+X} - S_N \leq 1$$

This equation had to be solved iteratively by minimising:

$$\text{abs}(N - (N + X)^b - 1/a)^{1/b}$$

N and the corresponding S which are computed from the exponential model define the point of equal slope:

$$P_{X,1} \sim \{N ; S\}$$

Confidence limits for the true mean of S_N were computed according to standard linear regression procedures (Draper & Smith 1981). Multidimensional scaling ordination MDS, based on 4th root transformed density values (Bray – Curtis similarity coefficients) was performed to identify differences between MR and WS. The multivariate statistical methods of classification and ordination used the software package PRIMER Version 5.2.1 (Clark & Warwick, 1994). The differences between the remaining community parameters were tested with a Mann – Whitney U-Test.

RESULT

Family composition

A total of 2974 polychaete individuals were collected, 1668 in MR and 1306 in WS. The percentage of polychaetes in the total macrofauna per station varied between 4.5% and 100% in MR and 30% and 60% in WS (Fig. 2).

Of the 334 species belonging to 179 genera identified 199 species were found in MR and 163 species in WS, 28 species and 58 genera occurred in both regions. Of the 44 families, 37 were found in MR and 36 in WS. Thirty-two families were common to both regions while Onuphidae, Cossuridae, Oeonidae, Eunicidae, Goniadidae, Sigalionidae, Magellonidae, and Sternaspidae were restricted to MR and

Lacydoniidae, Chrysopetalidae, Polygordiidae and Spintheridae have been recorded only from WS.

The most speciose families were Syllidae (10% of all polychaete species), Maldanidae (9%) and Paraonidae (7%) in MR and Terebellidae (12%), Syllidae (11%) and Polynoidae (9%) in WS (Fig. 3). The most abundant families were Paraonidae (21% of all individuals), Ampharetidae (9%) and Lumbrineridae (8%) in MR and Syllidae (20%), Spionidae (15%), and Lumbrineridae (10%) in WS (Fig. 4).

Structure of the polychaete species assemblage

The result of the MDS showed some degree of discrimination between MR and WS with a stress of 0.15 (Fig. 5). A Mann – Whitney U-Test was carried out separately and confirmed this result, showing the mean densities (Fig. 8a) were significantly different between MR and WS (Table 2; U-Test = 5873.0 $p = 0.0085$).

The species abundance distribution in both regions showed high numbers of species represented by only one specimen (Fig 6 a b). This led to high values of evenness (Table 2) and low dominance values on either side of the Drake Passage. In MR the maximum dominance value on species level was 9% of the total density for *Aricidia strelzovi* and the 50% cumulative dominance was achieved with 14 species in MR (Table 3). The remaining 185 species contributed only between 2 and 0.1% per species. In WS *Spiophanes tcherniai* accounted for the maximum dominance value (10%) on species level, and 14 species made up 54% of the cumulative dominance (Table 3). The remaining 149 species reached

percentages only between 2 and 0.1% per species.

Detritus feeders (57% of all individuals) constituted the dominant trophic guild in both regions, followed by predators (38%) and suspension feeders (5%). Suspension feeders were present at only 17% of the MR stations, whereas detritus feeders and predators prevailed at all stations. In contrast, at most of the WS stations all three trophic guilds were present (Fig. 7). Among the detritus feeders in MR the highest numbers of individuals were those of *A. strelzovi*, *Aricidea pisanoi* and *Prionospio orensanzi*, the predator guild was represented by *Glycera capitata* and *Aglaophamus peruana*, the suspension feeders consisted mainly of *Hypsicomus phaeotaenia*.

In WS *S. tchernia* contributed the highest individual number to the detritus feeders. The predator guild was represented mainly by *Syllis spongiphila* and *Glycera kerguelensis*, and among the suspension feeders, *Jasmineira crumenifera*, *Euchone pallida*, and *Galathowenia wilsoni* were dominating.

Mean point species richness (SR_s ; Fig. 8b) and the heterogeneity diversity (HD_1 ; Fig 8c) showed significantly lower values at the MR than at the WS stations (U-Test= 5336.0 and 5207.0, respectively; $p < 0.05$; Table 2). Evenness values of cores containing more than one individual per species were not significantly different (U-Test = 5471.0; $p > 0.05$) between the MR and WS stations (Table 2).

The randomised cumulative species plots (Fig. 9 a, b) for both regions showed significant differences. The shape of the curves did not reach an asymptote in either region, because

the individual numbers were low and both species inventories were not considered completely.

Twenty-eight common species occurred in both regions (Table 4). Four species are cosmopolitans; *Artacama proboscidea* has a bipolar distribution. Ten species show a circumpolar distribution around the (Sub-) Antarctic, e.g., *Augeneria tentaculata*, the remainder occur from low to high latitudes, for example *Aricidea strelzovi* and *Sphaerodoropsis parva* along the Chilean coast through the Drake Passage into the high Weddell Sea. Concerning the depth distribution of these species, 57% showed a eurybathic distribution or a wide depth range, whereas the remainder had stenobathic distribution patterns.

DISCUSSION

This study improves and updates the precision of the distribution limits of polychaete species on either side of the Drake Passage and presents empirical ecological data from two research areas in the Southern Ocean, where taxonomic information is still scarce and, as Clarke and Johnston (2003) concluded, a revision of polychaetes is urgently needed.

Polychaete species inventories and assemblages in WS and MR waters have been little studied in the last 30 years. The lack of descriptions of assemblages up to now complicates the establishment and comparison of polychaete assemblage patterns in both areas. This study is the most comprehensive approach to describe polychaete assemblages on species level on either side of the Drake Passage based on the same sampling methods, enabling us to compare data from these

ecosystems which remained closely together for some considerable time and became separated as last parts of Gondwana some 20 - 30 million years ago.

Our data suggest that today both areas differ significantly in terms of polychaete densities, diversity, species richness and affiliation to different trophic guilds.

The actual patterns derived from this study are based on 163 species/36 families in WS and 199 species/37 families in MR. The latter figures represent the highest numbers of species/families reported for the up to now little studied MR. Maurer & Williams (1988) reported for the Straits of Magellan 76 polychaete species belonging to 33 families, while Cañete et al. (1999) distinguished 38 species from 24 families in 39 corer samples from the northern border of MR. Bremec et al. (2000) found 119 polychaete species from 34 families in the Straits of Magellan and 36 species/ 20 families on the eastern Patagonian shelf in their qualitative and quantitative samples.

Comparable quantitative information from the high Antarctic WS is also very scarce, somewhat better is the available information from the Subantarctic Islands and the Antarctic Peninsula. From the high Antarctic WS Hartman (1978) described from just 2 van Veen grabs 37 polychaete species with Cirratulidae and Maldanidae being the most speciose families. Stiller (1996) reported from the WS and Lazarev Sea shelves 20 polynoid and 2 aphroditid species, additional information from WS reported by Hartman (1964, 1966) was obtained from qualitative sampling with towed gear.

From the Subantarctic Greenwich Island Gallardo et al. (1988) reported 206 polychaete species from 26 families. Terebellidae, Spionidae, and Phyllodocidae were the most speciose families on sublittoral soft-bottoms at this location. Recently, San Martin et al. (2000) recorded 29 families with 89 species off Livingston Island, Deception Island, and the South Shetland Islands; the most speciose families in their samples were Terebellidae, Syllidae, and Maldanidae.

Looking into the species composition per family of the WS the results resemble those reported by Clarke & Johnston (2003) for waters south of the Polar Front. The most speciose families Syllidae and Terebellidae are represented most dominantly by *Syllis spongiphila* and *Pista corrientis*, respectively, whereas in MR, the most speciose families Syllidae, Maldanidae, and Paranoidae were represented particularly by *Typosyllis hyalina*, *Maldane sarsi*, and *Aricidea strelzovi*.

Polynoidae occurred in our samples only in low species and especially low specimen numbers, possibly because the quantitative corers used in our study are known to capture more efficiently sessile organisms or those with low motility.

Significant differences between MR and WS polychaete assemblages also became evident by comparing the proportions of species representing different trophic guilds. The analysis of trophic guilds is a proper method to describe benthic communities, because they evidence the relationships of animals with their environment and / or interactions with other species (Muniz & Pires, 1999; Paiva, 1993).

In our study the trophic structures in MR and WS assemblages were dominated by detritus feeders and predators, whereas a higher percentage of suspension feeders (which were of minor importance in both areas) in WS made up the main difference in this parameter between both areas. These results resemble data commonly reported for benthic communities in WS, where suspension feeders from different taxa dominate high Antarctic shelf communities. The hydrographic regime with strong currents provides sufficient food via vertical flux and advection, thus allowing the existence of dense populations of suspension feeders (Teixidó et al. 2002).

Most of the MR stations were located in fjords and channels which typically form the MR and which are widely described in the literature (e.g. Syvitski et al. 1987). The prevailing environmental conditions with low water currents and exchange (Pinochet & Salinas, 1998) and frequently high sedimentation rates (Pickard & Stantor 1980, Heiskanen & Tallberg 1999) favour the existence of motile detritus feeders and predators – not only in case of polychaetes but also in other taxa, and suspension feeders are almost absent. This composition found in MR seems to be a typical feature for fjord and channel communities and is also reported from other regions worldwide (Rosenberg 2001).

No significant differences became obvious in the evenness values between both areas. Due to relatively high species numbers and low numbers of specimens per species evenness in both assemblages was high. In the polychaete related literature typically 1 or 2 species

contribute considerably to overall abundance with dominance values of 27 % (Gambi et al. 1997) or even 36 % (Gallardo et al. 1988). Contrasting in our study the maximum dominance values were lower and more species contributed to the 50% cumulative dominance value as compared to the literature data mentioned above. Hughes (1984) made similar observations in benthic invertebrate communities. Hughes' model based on his observations predicted a stable stage with a high dominance of a common species and few rare species, while high numbers of rare species with low abundance characterised early stages of colonization.

In our case, the resulting pattern could also reflect disturbance in the two assemblages under study: the impact of ice scouring in WS and the impact of a permanent ice field with salinity gradients and high rates of sedimentation in MR, could maintain the assemblages in both areas in permanent early recolonization stages (Gray 2001b, Gerdes et al. 2003). There clearly is some evidence to suggest a relationship between polychaete assemblage parameters and ice influence, but more quantitative documentation will be required to confirm this hypothesis.

In view of the common history of the Magellan region and the Antarctic and considering the fact, that they are neighbouring ecosystems, separated only by the Drake Passage and the Antarctic Convergence (which, however, acts like a filter for the dispersal of many aquatic organisms), the number of common species in both areas should be quite high. Surprisingly we found only 8% overlap of polychaete

species and 32% on genera level north and south of the Drake Passage. However, as shown by our randomized cumulative species plots our species inventory has to be considered incomplete, because the areas in MR and WS have not been adequately sampled for this purpose. In a recent paper Montiel et al (subm) reported a considerably higher overlap (>30%) of polychaete species based, however, on quantitative, qualitative samples and literature data. Although our present result brought up some further insights in polychaete distribution patterns. The nevertheless also demonstrate the need of that further studies on this item to answer the questions addressed in this study with more accuracy.

ACKNOWLEDGEMENTS

We are grateful to Dr. T. Brey for his help in the statistic analysis, C. Ríos for his useful comments on the manuscript and to E. Mutschke and the Comité Oceanográfico Nacional (CONA) for providing the biological material from the CIMAR-Fiordo expedition. Support by DAAD grant No A/00/10932 and DFG grant BR 1127 is gratefully acknowledged.

Legends

Figure 1. Study area in the Magellan region (South America) and the Weddell Sea (Antarctica), with indication of sampling locations.

Figure 2. Comparison of the percentage of polychaete individuals in the total macrofauna obtained at each station (In MR n = 5508 ind.; WS n = 4225 ind.). All plotted stations are arranged in a N-S direction; for code number see table 1. In black or full MR and WS in white or open.

PUBLICATION 1

Figure 3. Comparison of the total species number per polychaete family obtained from the study areas. Arrangement and symbols as in Fig. 2.

Figure 4. Comparison of total density values (ind m⁻²) per family obtained in the study areas. Arrangement and symbols as in Fig. 2.

Figure 5. MDS plot for $\sqrt{\sqrt{\quad}}$ transformation of the mean density data using group average linkage on Bray-Curtis similarities for differences between study areas. Arrangement and symbols as in Fig. 2.

Figure 6. Species abundance distribution (a) Magellan region (b) Weddell Sea (expressed on a log₂ scale).

Figure 7. Triangular chart showing polychaete feeding modes in the study areas. Values refer to percent per station in WS and MR. Symbols as in Fig. 2.

Figure 8. Plot showing the mean density (a) and species richness (SRs) per station in the study areas (b) (c) plot of HD₁ per station through the studies areas, where HD₁= exp (H'). Arrangement and symbols as in Fig. 2.

Figure 9. Estimated cumulative species richness using the Stimated S program (Colwell, 1997), with 50 randomisations and no replacement. (----) Standard deviation; Arrangement and symbols as in Fig.2.

PUBLICATION 1

Table 2. Mann-Whitney test for differences in density, species richness, diversity and evenness values (Means \pm SD) between the MR and WS regions at $\alpha = 0.05$. Significant p values are shown in bold.

	MR (n = 171)	WS (n = 86)	Mann-Whitney U-test	P values
Mean density (ind. m ⁻²)	352 \pm 319	582 \pm 448	5873.0	0.0085
Mean point species richness (SR _p)	5.0 \pm 3.9	8.9 \pm 7.0	5336.0	0.0003
Heterogeneity diversity (HD ₁)	4.7 \pm 3.0	7.5 \pm 5.4	5207.0	0.0001
Evenness (J')	0.7 \pm 0.3	0.9 \pm 0.04 *	5471.0	0.8056

(MR n = 145; WS = 77)

PUBLICATION 1

Table 3. Polychaete dominance patterns in MR and WS.

Species.MR	Density (ind. m ⁻²)	Dominance (%)	Cumulative dominance (%)	Species WS	Density (ind. m ⁻²)	Dominance (%)	Cumulative dominance (%)
<i>Aricidea strelzovi</i>	6613	9	9	<i>Spiophanes tcherniai</i>	5459	10	10
<i>Glycera capitata</i>	5119	7	16	<i>Syllis spongiphila</i>	4500	8	18
<i>Aricidea pisanoi</i>	3209	4	21	<i>Lumbrineris cf. kerguelensis</i>	3750	7	25
<i>Prionospio orensanzii</i>	3125	4	25	<i>Laonice weddellia</i>	2542	5	30
<i>Levinsenia gracilis</i>	2845	4	29	<i>Cirrophorus brevicirratus</i>	1833	3	33
<i>Monticellina sp</i>	2184	3	32	<i>Glycera kerguelensis</i>	1792	3	37
<i>Chaetozone sp2</i>	1917	3	35	<i>Chaetozone sp. 3</i>	1708	3	40
<i>Lumbrineris magelhaensis</i>	1833	3	37	<i>Sphaerosyllis antarctica</i>	1667	3	43
<i>Leitoscoloplos sp</i>	1708	2	39	<i>Augeneria tentaculata</i>	1583	3	46
<i>Ampharete kerguelensis</i>	1617	2	42	<i>Notomastus latericeus</i>	958	2	47
<i>Melinna cristata</i>	1565	2	44	<i>Scoloplos marginatus</i>	958	2	49
<i>Aglaophamus peruana</i>	1494	2	46	<i>Jasmineira crumenifera</i>	875	2	51
<i>Abyssoninoe abyssorum</i>	1327	2	48	<i>Harmothoe spinosa</i>	833	2	52
<i>Ninoe falklandica</i>	1308	2	50	<i>Typosyllis armillaris</i>	792	1	54

PUBLICATION 1

Table 4. List of polychaete species occurring in both regions (MR and WS) and their respective densities and bathymetric distribution patterns. LaD: Latitudinal distribution CiP: Circum (Sub) Antarctic BiD: Bipolar distribution CoD: Cosmopolitan distribution.

Species		Density (ind. m ⁻²)		Depth (m)	D
		MR	WS	min-max	
<i>Amphicteis gunneri</i>	(Sars, 1835)	83	208	5-7686 ^a	CoD
<i>Anobothrella antarctica</i>	(Monro, 1939)	292	167	40-4099 ^a	LaD
<i>Sphaerodoropsis parva</i>	(Ehlers, 1913)	167	42	128-3980 ^b	LaD
<i>Harmothoe spinosa</i>	Kinberg, 1855	83	42	55-3400 ^c	CiP
<i>Notoproctus oculatus antarcticus</i>	Arwidsson, 1811	296	208	218-3397 ^d	CiP
<i>Artacama proboscidea</i>	Malmgren, 1865	125	42	20-3380 ^a	BiD
<i>Paramphinome australis</i>	Monro, 1930	702	333	128-3197 ^e	LaD
<i>Ampharete kerguelensis</i>	MacIntosh, 1885	1617	83	64-2700 ^f	CiP
<i>Augeneria tentaculata</i>	Monro, 1930	226	1583	80-2350 ^g	CiP
<i>Travisia kerguelensis</i>	MacIntosh, 1885	208	42	40-1784 ^j	LaD
<i>Aricidea simplex</i>	(Day, 1963)	83	83	35-1615 ^h	CoD
<i>Aricidea strelzovi</i>	Hartmann-Schröder & Rosenfeldt, 1990	6613	83	300-1600 ⁱ	LaD
<i>Maldane sarsi antarctica</i>	Arwidsson, 1811	184	333	75-1116 ^j	CiP
<i>Aricidea antarctica</i>	Hartmann-Schröder & Rosenfeldt, 1988	42	125	20-1100 ^k	LaD
<i>Amage sculpta</i>	Ehlers, 1908	42	42	244-1080 ^b	LaD
<i>Aphelochaeta cincinnata</i>	(Ehlers, 1908)	570	458	61-1079 ^a	LaD
<i>Harmothoe magellanica</i>	MacIntosh, 1885	83	208	0-900 ^l	CiP
<i>Leodamas marginatus</i>	(Ehlers, 1897)	167	958	20-640 ^d	LaD
<i>Euphrosine antarctica</i>	Kudenov, 1993	101	500	60-494 ^e	LaD
<i>Phyllochaetopterus monroi</i>	Hartman, 1967	42	125	270-485 ^o	LaD
<i>Nereis eugeniae</i>	Kinberg, 1866	167	125	40-455 ^m	LaD
<i>Gyptis incompta</i>	Ehlers, 1897	202	500	300-445 ^m	?
<i>Axiothella antarctica</i>	Monro, 1930	119	42	207-344 ^d	CiP
<i>Lysilla loveni macintoshi</i>	Gravier, 1907	42	42	25-335 ^b	CiP
<i>Leitoscoloplos kerguelensis</i>	(MacIntosh, 1885)	375	292	3-276 ^l	LaD
<i>Scalibregma inflatum</i>	Rathke, 1843	500	42	110-247 ^d	CoD
<i>Autolytus charcoti</i>	Gravier, 1906	83	250	0-165 ^b	CiP
<i>Typosyllis armillaris</i>	Müller, 1776	167	792	0-100 ⁿ	CoD

a. Hartmann-Schröder & Rosenfeldt, 1989 **b** Rozbaczylo, 1985 **c:** Hartmann-Schröder & Rosenfeldt, 1988; **d:** Hartman, 1966 **e:** Kudenov, 1992 **f:** Knox & Cameron, 1998 **g:** Orensanz, 1990 **h:** Strelzov, 1973 **i:** Palma et al.(subm), **j:** Hartman, 1967 **k:** Montiel et al., 2002 **l:** Orensanz, 1974 **m:** this study **n** Licher, 2002 **o:** Parapar & San Martin, 1997.

PUBLICATION 1

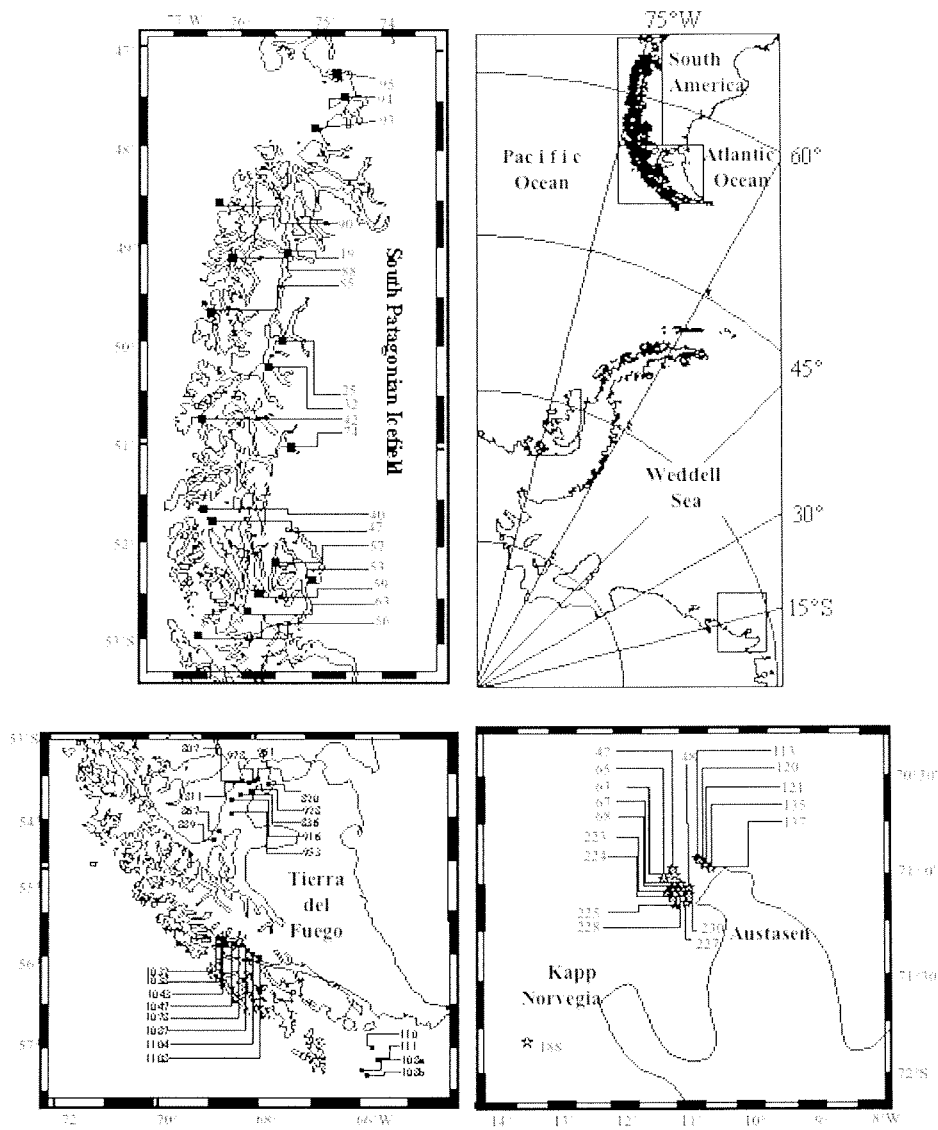


Figure 1. Study area in the Magellan region (South America) and the Weddell Sea (Antarctica), with indication of sampling locations.

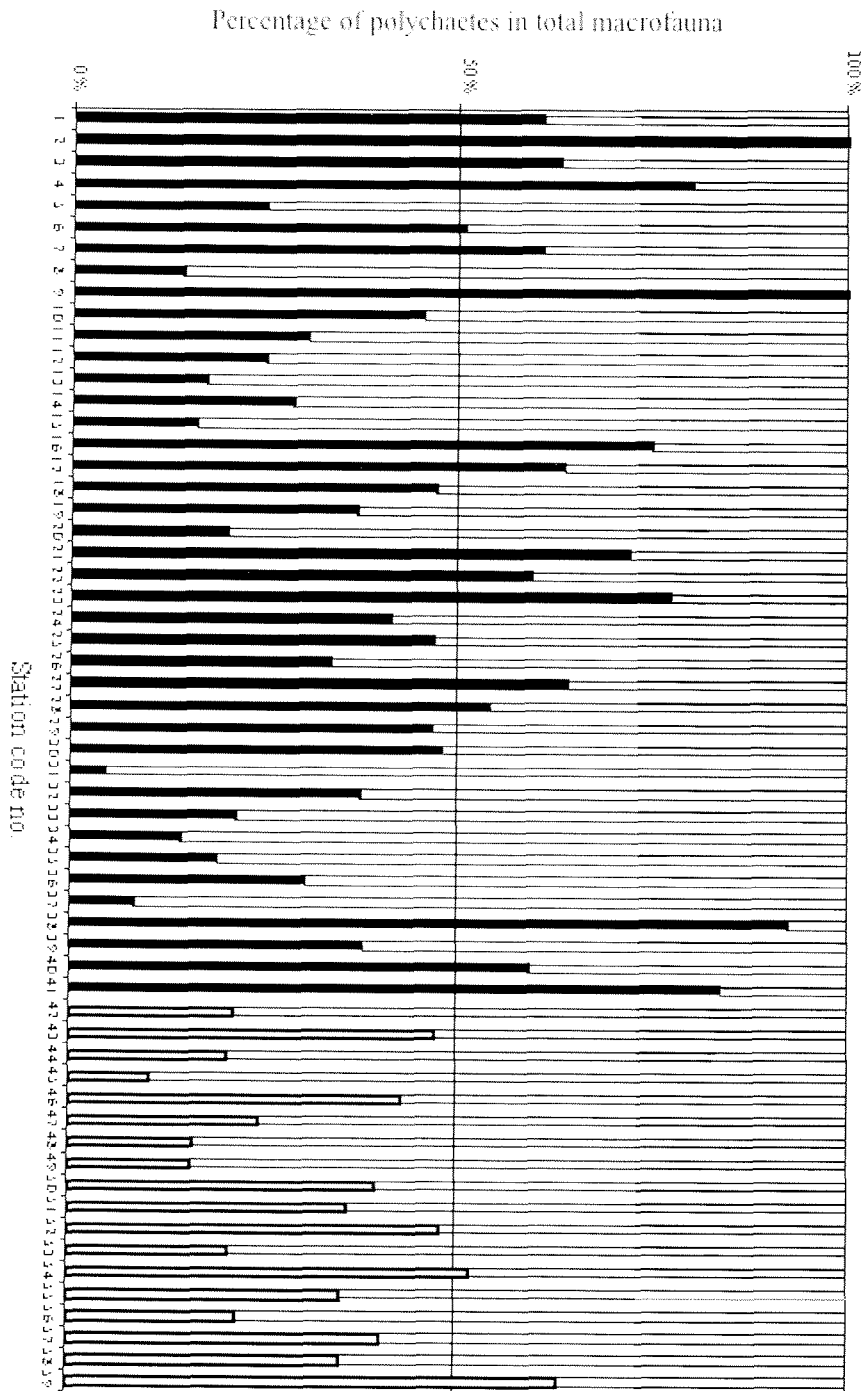


Fig 2. Figure 2. Comparison of the percentage of polychaete individuals in the total macrofauna obtained at each station (In MR n = 5508 ind.; WS n = 4225 ind.). All plotted stations are arranged in a N-S direction; for code number see table 1. In black or full MR and WS in white or open.

PUBLICATION 1

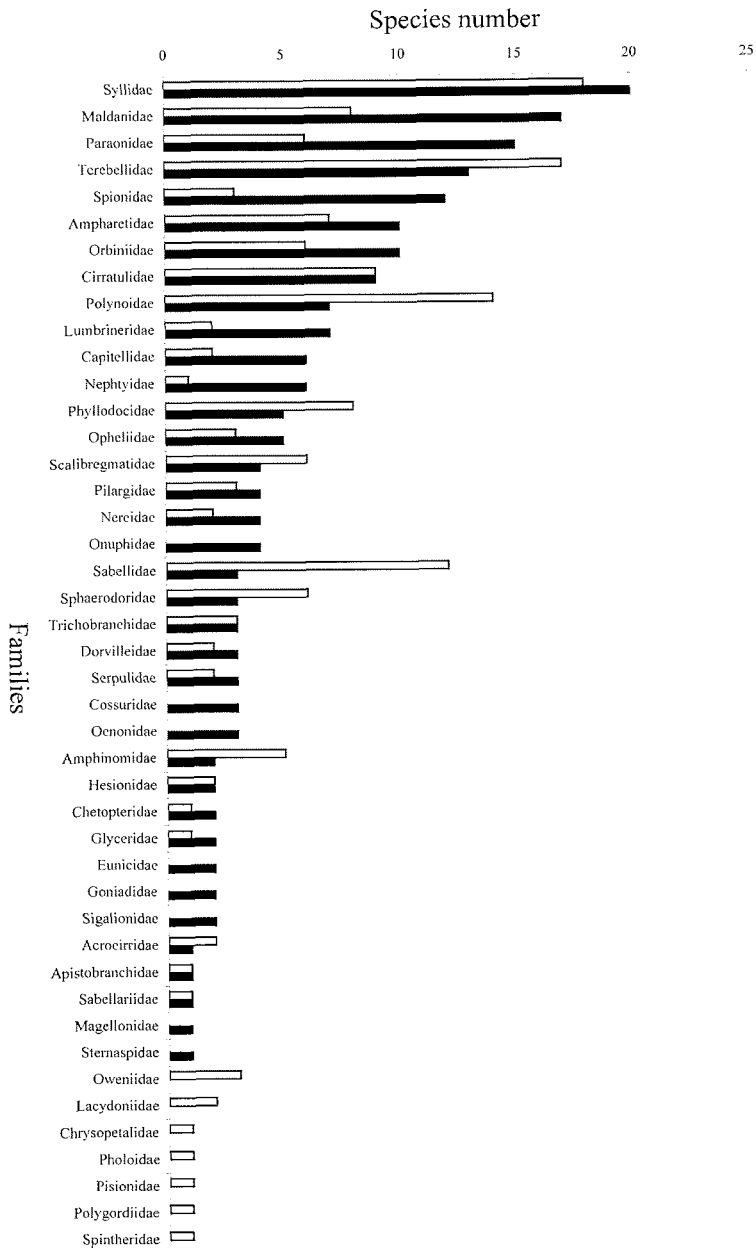


Figure 3. Comparison of the total species number per polychaete family obtained from the study areas. Arrangement and symbols as in Fig. 2.

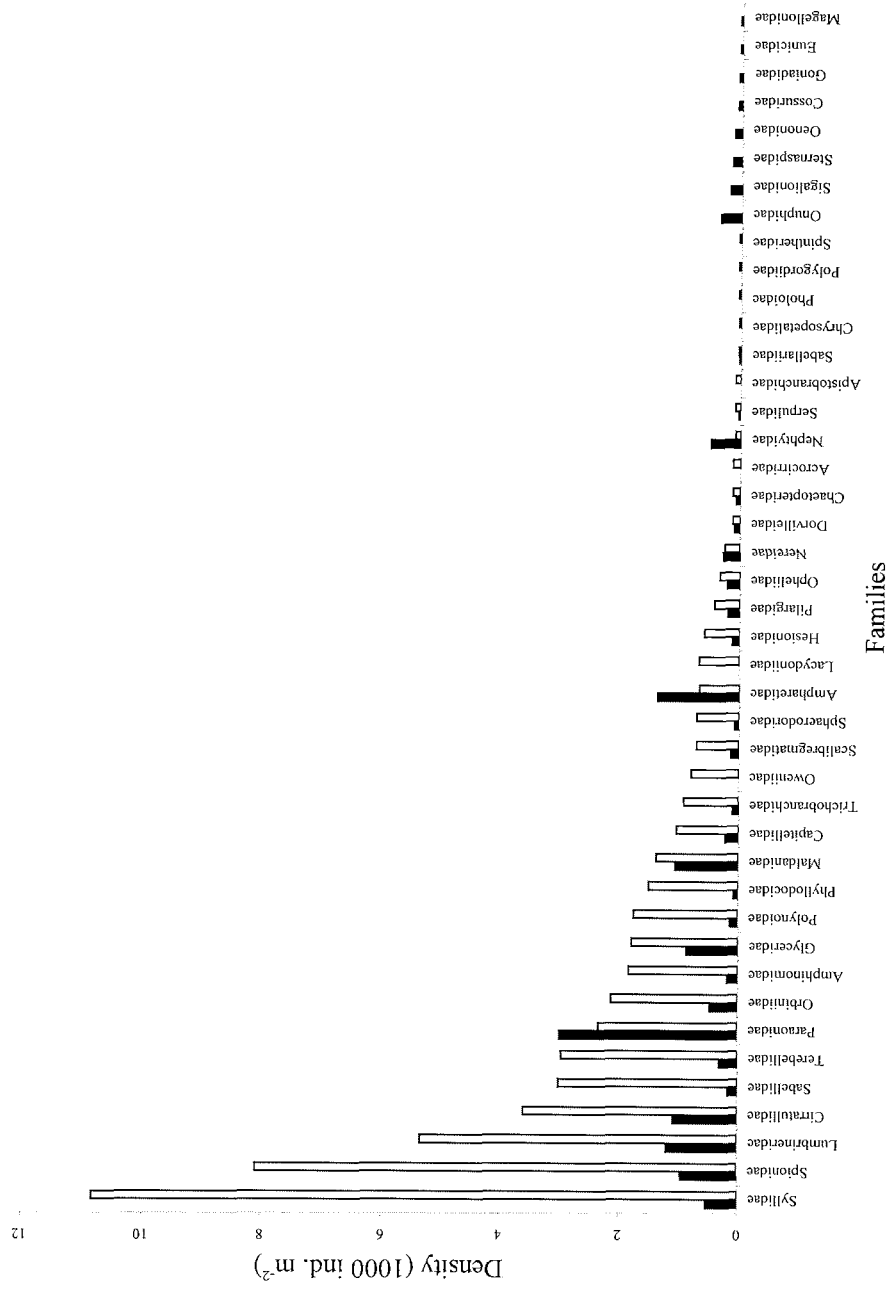


Figure 4. Comparison of total density values (ind m⁻²) per family obtained in the study areas. Arrangement and symbols as in Fig. 2.

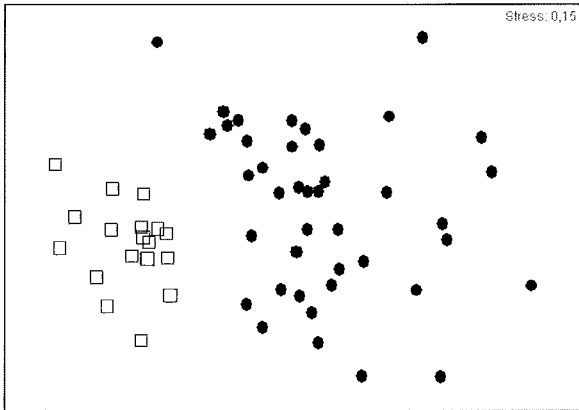
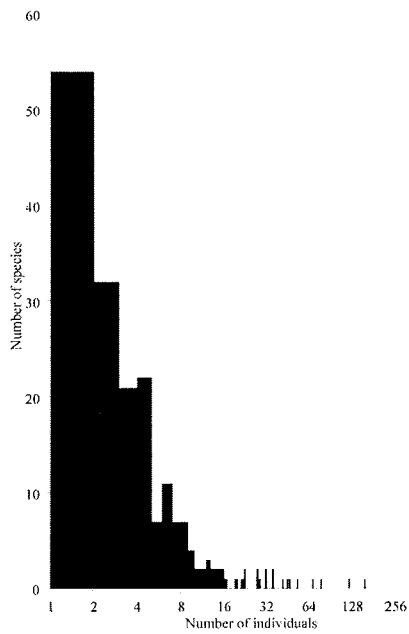
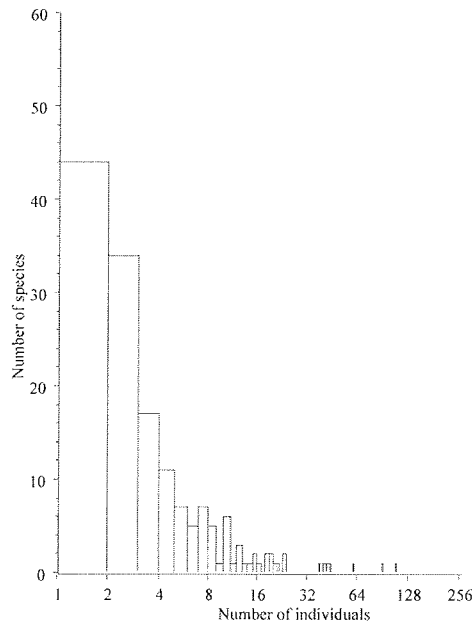


Figure 5. MDS plot for \sqrt{v} transformation of the mean density data using group average linkage on Bray–Curtis similarities for differences between study areas. Arrangement and symbols as in Fig. 2



A



B
Figure 6. Species abundance distribution (A) Magellan region (B) Weddell Sea (expressed on a log₂ scale).

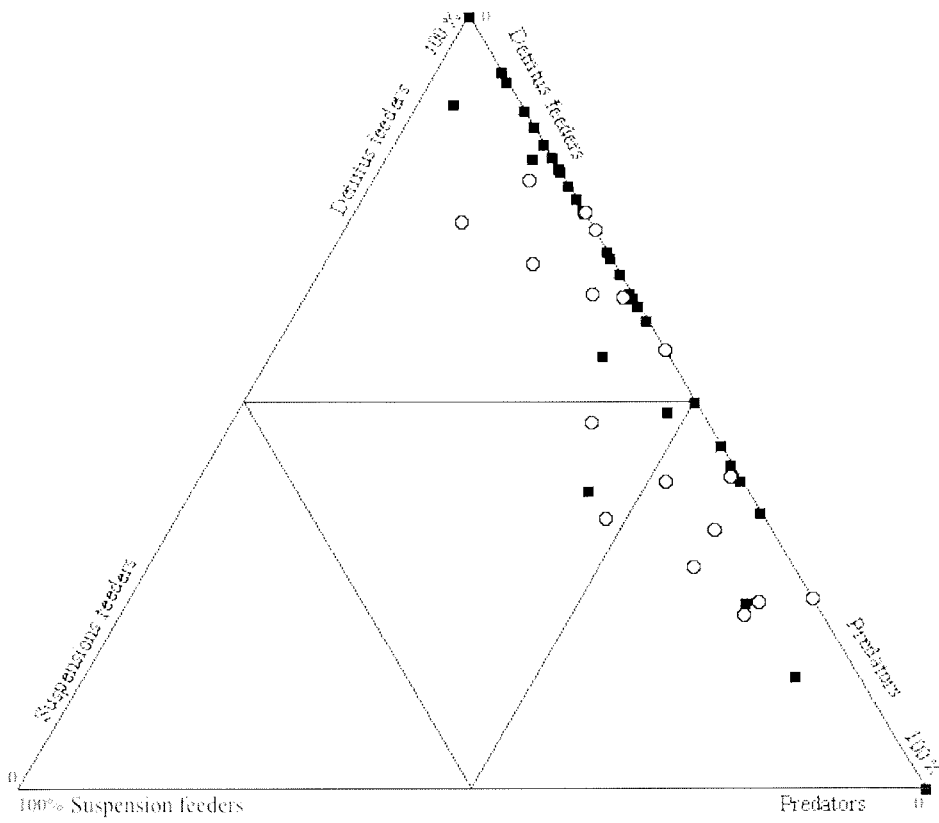
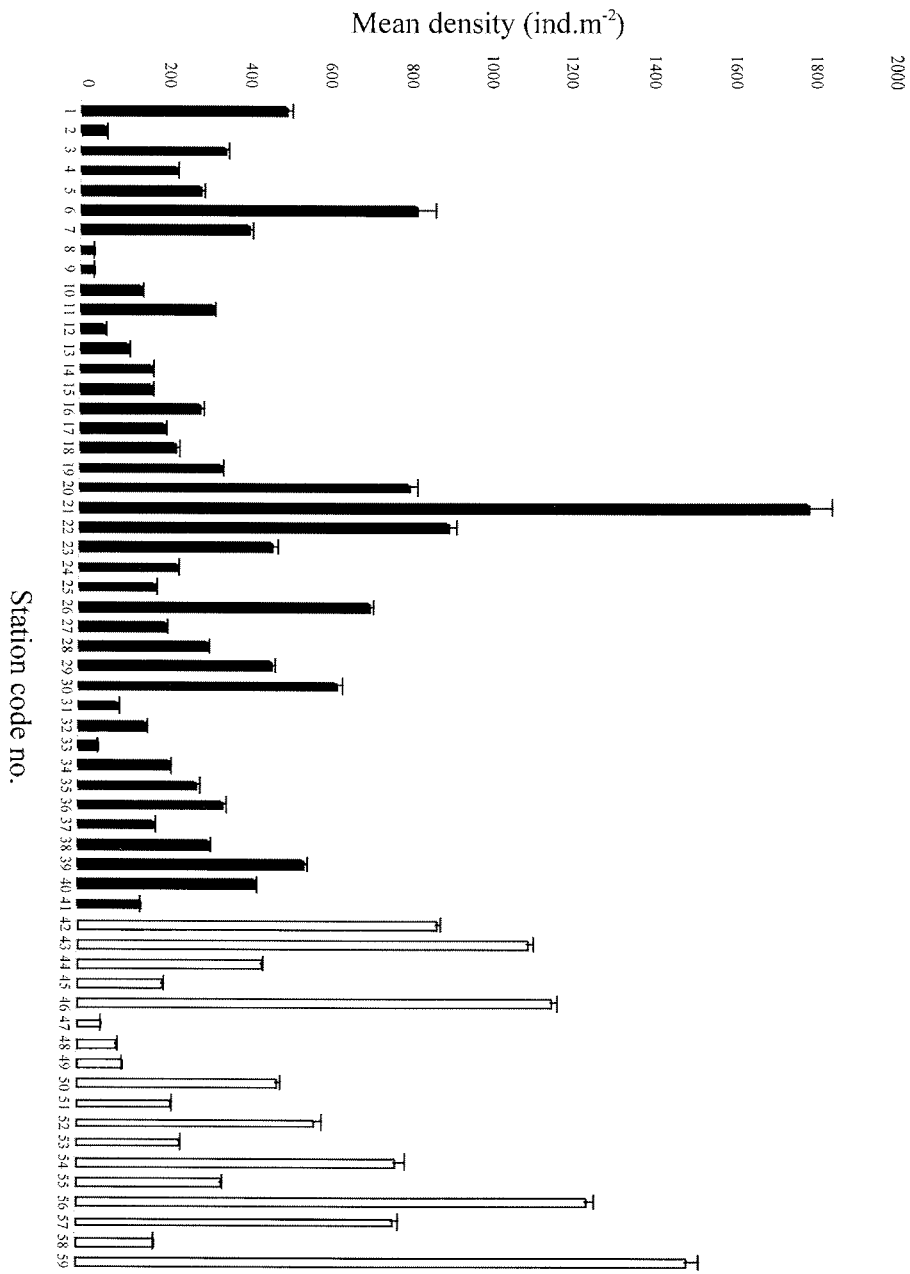


Figure 7. Triangular chart showing polychaete feeding modes in the study areas. Values refer to percent per station in WS and MR. Symbols as in Fig. 2.

PUBLICATION 1



PUBLICATION 1

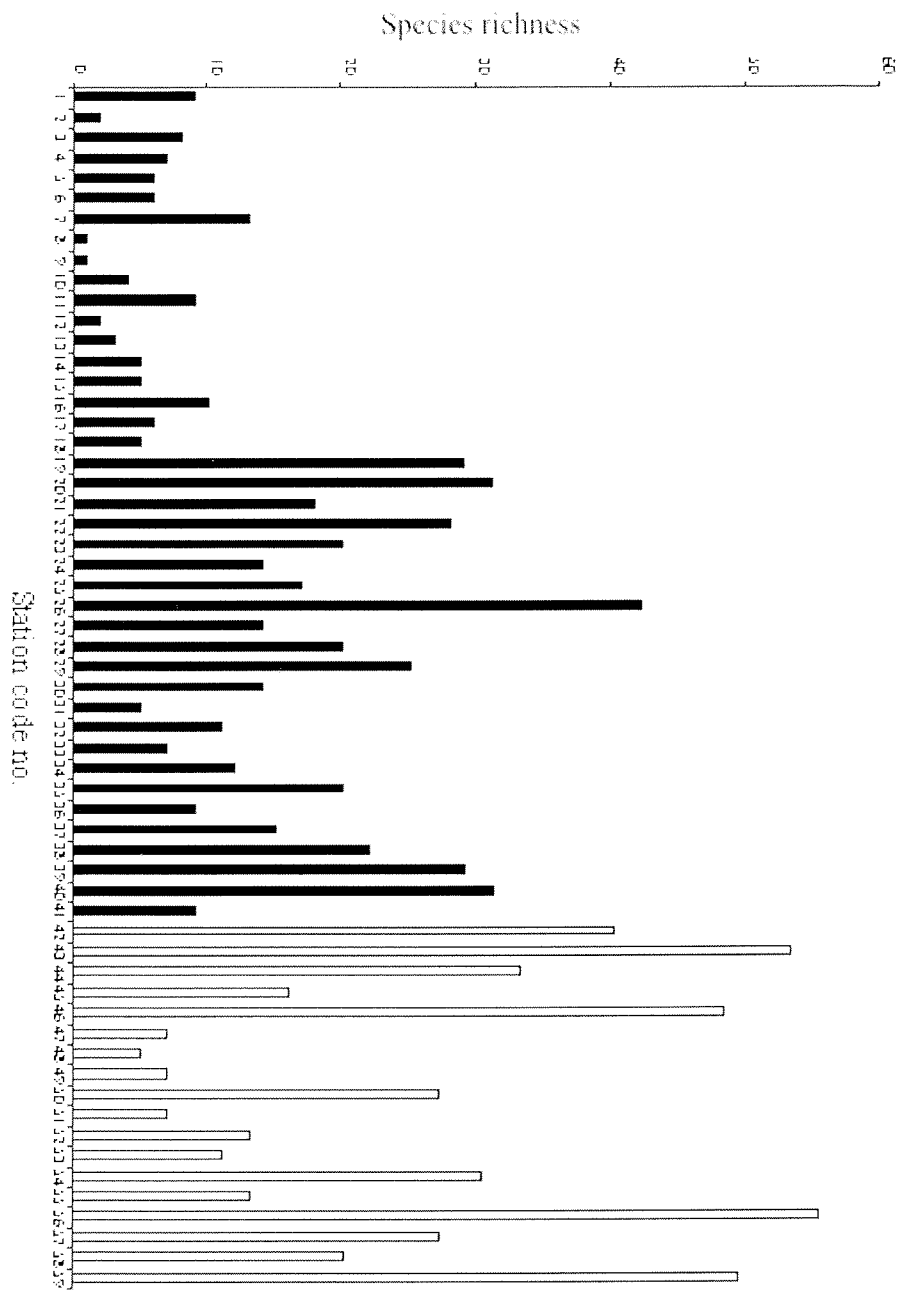


Fig. 8b.

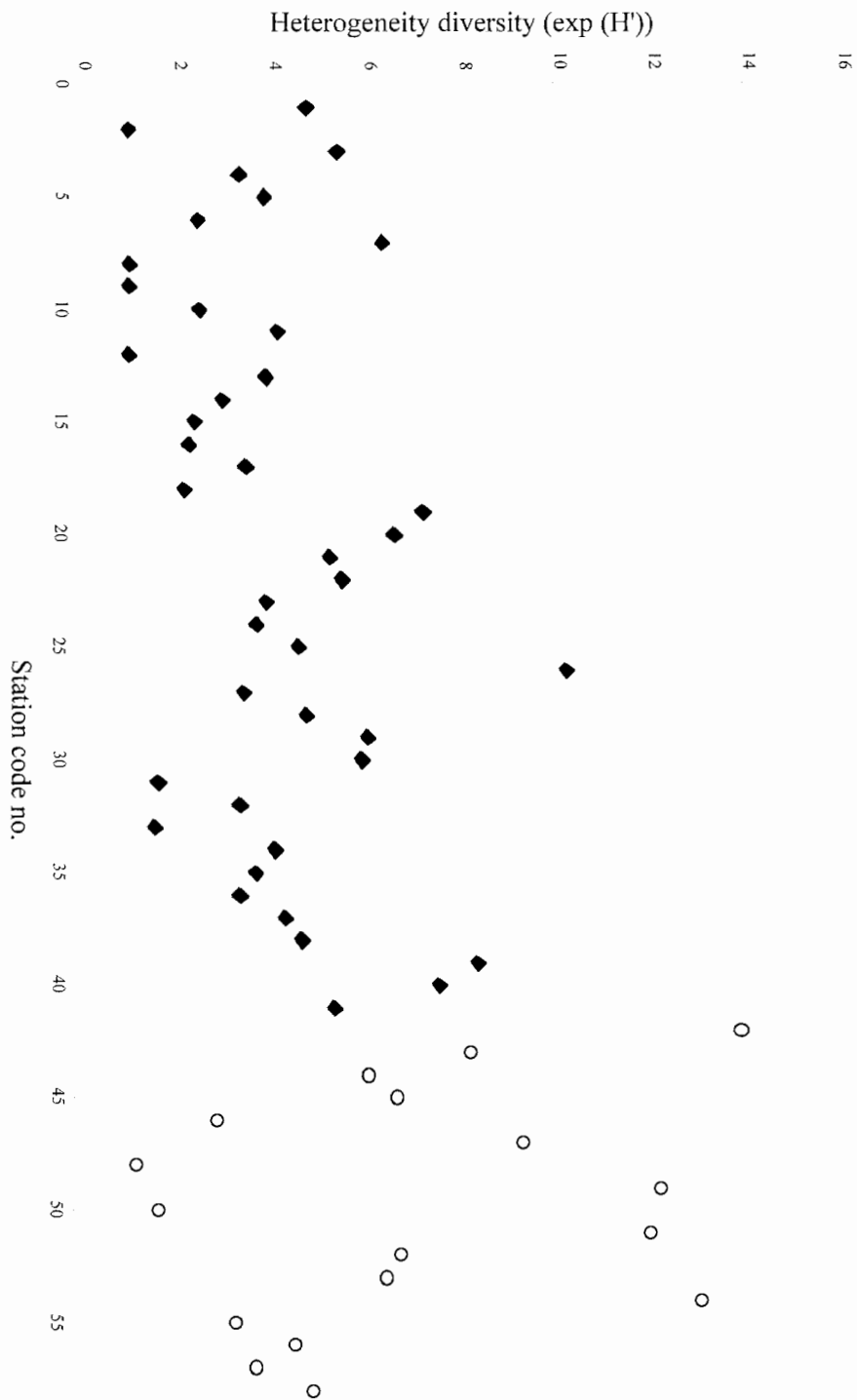
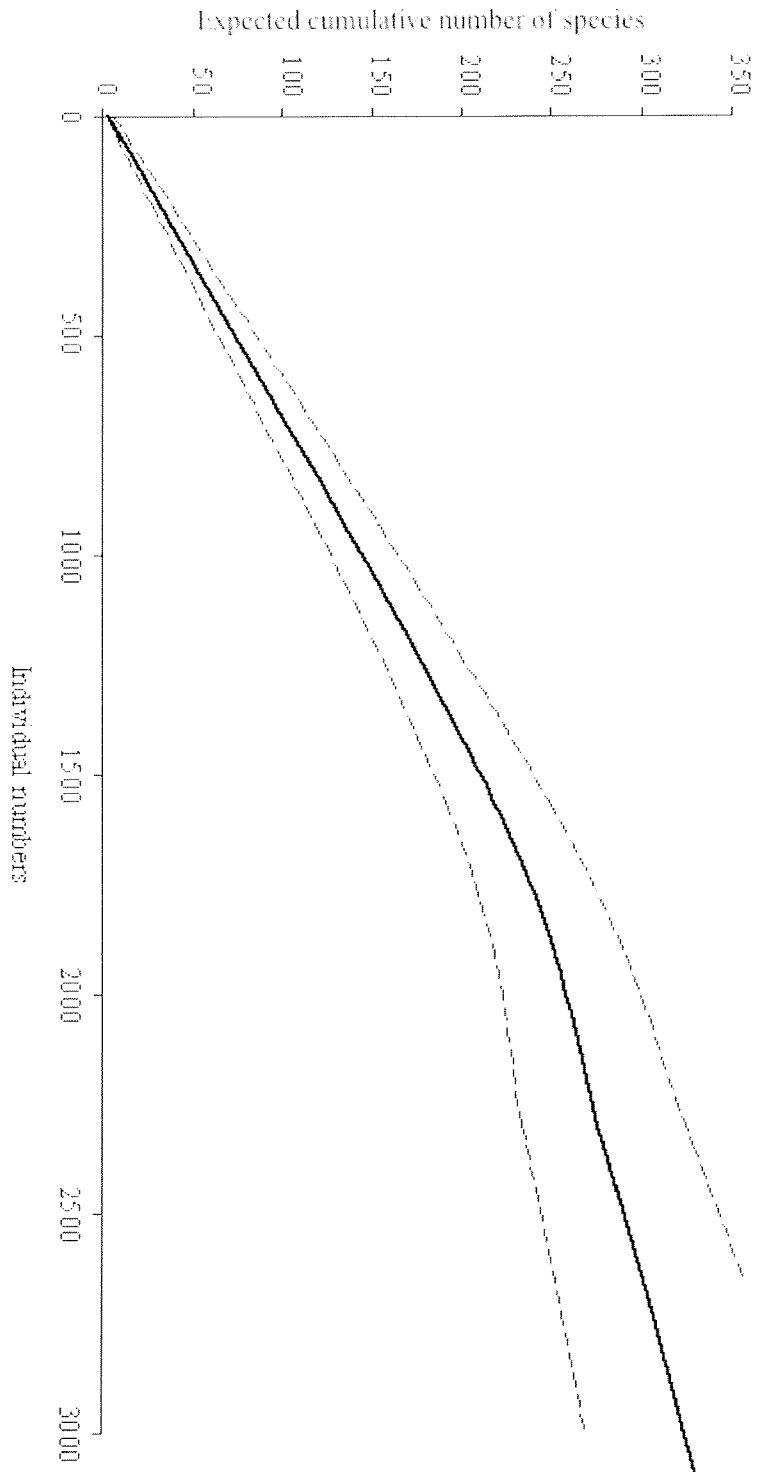


Figure 8. Plot showing the mean density (a) and species richness (SRs) per station in the study areas (b) (c) plot of HD_1 per station through the studies areas, where $HD_1 = \exp(H')$. Arrangement and symbols as in Fig. 2.



A.

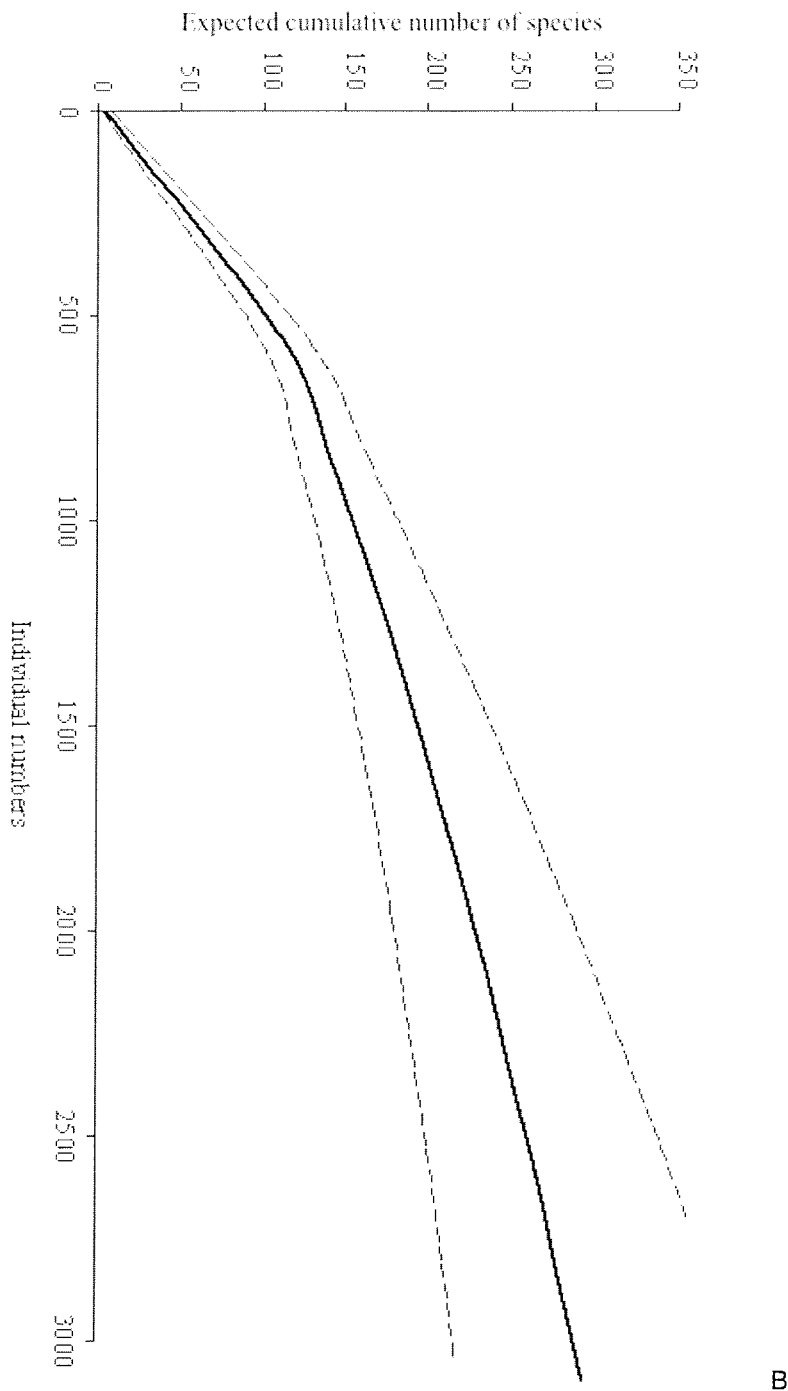


Figure 9. Estimated cumulative species richness using the Stimated S program (Colwell, 1997), with 50 randomisations and no replacement. (---) Standard deviation; Arrangement and symbols as in Fig.2.

D. Gerdes · B. Hilbig · A. Montiel

Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea

Received: 27 May 2002 / Accepted: 18 January 2003 / Published online: 5 March 2003
© Springer-Verlag 2003

Abstract UW-video guided multibox corer sampling in and outside iceberg scours provided quantitative macrozoobenthos samples for analyses of effects of grounding icebergs on infaunal benthic communities. These studies were performed on the southeastern Weddell Sea shelf off Kapp Norvegia and Austasen. Based on the UW-video sequences, stations were grouped a priori into two different “disturbance categories” and into undisturbed areas.

Average biomass of major taxa in the cores of undisturbed areas was significantly higher (14,716.5 g wet weight m^{-2}) than in old (405.3 g w. wt. m^{-2}) or in young scour marks (9.2 g w. wt. m^{-2}). The habitat taxon richness, too, was highest in undisturbed areas (on average, 11.8 taxonomic units occurred per core), decreased in old scour marks (9.0) and was lowest in young scours (6.8). In undisturbed areas, a higher developed community structure was reflected by a greater variety of taxonomic groups, some of which were principally absent in scours.

In young scours, the number of taxa was significantly reduced. Motile forms such as echinoderms and crustaceans, mainly amphipods, and juvenile polychaetes, in particular pioneering species of the family Spionidae, started the recolonization of the devastated areas. Burrowing organisms occurred in older scours where the initially overcompacted sediment had softened. In the course of the re-establishment of macrofaunal communities (after some years/decades), the faunal composition is expected to change towards a “normal” dominance of suspension-feeding organisms, mainly sponges and

bryozoans, being typical for wide areas on the southeastern Weddell Sea shelf.

A more detailed taxonomical approach, using 167 polychaete species as representatives of the macrozoobenthos, also revealed significant differences between undisturbed and affected areas. The mean abundances (784, 389, and 242 ind. m^{-2} , respectively), as well as habitat species richness (11.6, 5.5, and 3.1, respectively), decreased from undisturbed areas to old to young iceberg scours. Similarly, a large variety of motile and sessile forms was encountered among the polychaetes at undisturbed sites, whereas in scours, the polychaete fauna was impoverished in terms of species richness, abundance and variety of feeding types and lifestyles.

Introduction

Resilience of a system is defined as its capacity to return to a situation similar or identical to that before a disturbance. Resilience studies in aquatic and terrestrial ecosystems have gained worldwide interest since anthropogenic impacts on the environment have been monitored and evaluated. Natural disturbances have to be distinguished from anthropogenic ones, and the still poorly understood role of the former in the maintenance of biodiversity has further enhanced recent efforts to study resilience. Since the “Madrid Protocol” of the Antarctic Treaty has come into force, such studies are also of particular interest in the Antarctic.

One of the major disturbances for the high-Antarctic shelf fauna at water depths < 400 m is caused by grounding icebergs. From literature and previous expeditions, we know that approximately 5% of the Antarctic shelf is affected by grounding icebergs (Gutt 2000). Locally this figure may be much higher, for example, on the shelf off Austasen north of Kapp Norvegia, where high concentrations of grounded icebergs (“rest places”) can be observed regularly (Gutt et al. 1997, 1999). Statistically, once every 340 years, each square metre of

D. Gerdes (✉) · A. Montiel
Alfred Wegener Institute for Polar and Marine Research,
P.O. Box 120161, 27576, Bremerhaven, Germany
E-mail: dgerdes@awi-bremerhaven.de

B. Hilbig
Zoological Institute and Zoological Museum,
University of Hamburg, Martin Luther King-Platz 3,
20146 Hamburg, Germany

seafloor on the Antarctic shelf < 400 m is devastated by grounding icebergs (Gutt 2001).

The southeastern Weddell Sea shelf, especially the shelf area off Kapp Norvegia, has become one of the most intensely investigated Antarctic areas. The benthos has been described in numerous publications with respect to specific taxa and their ecological role in this environment (e.g. Hain 1990; Gutt 1991; Klages 1991; Stiller 1996), species composition, densities and biomass (Galéron et al. 1992; Gerdes et al. 1992), as well as benthic production and productivity (Brey and Gerdes 1998a, 1998b). Thus, studies on the resilience of southeastern Weddell Sea shelf communities are based on almost a decade of intense benthological work.

The current knowledge on effects of grounding icebergs on different benthic community fractions and demersal fish was summarized in a preliminary synopsis by Knust et al. (2003). On the southeastern Weddell Sea shelf, most impact studies were performed by means of imaging methods (ROV, UW-camera), and analyse especially the effects on the mega-epibenthos.

Another paper, based on Agassiz trawl and bottom trawl catches, described the role of iceberg scours for niche separation within the Antarctic fish genus

Trematodus (Brenner et al. 2001). The response of meiofauna to iceberg disturbance based on quantitative samples from corers has been studied once in this area (Lee et al. 2001b) and macrobenthos response, especially of the smaller fraction and the infauna, is analysed in the present study.

Based on UW-video, we classified our stations "a-priori" into two different disturbance categories and undisturbed areas. Significance of differences between these hypothetical categories was tested by means of abundance and biomass values of 31 macro-zoobenthos taxa, the abundance of 166 polychaete species, the composition of the benthos communities and groups, and their diversity and evenness.

Materials and methods

During the "Polarstern" expeditions ANT XV/3 in 1988 and ANT XVII/3 in 2000, 86 quantitative macrobenthos samples were obtained from disturbed and undisturbed shelf areas off Austasen and Kapp Norvegia (Fig. 1) by means of a multibox corer guided by a UW-video system (Gerdes 1990).

The 86 cores from 18 stations were treated as separate samples for macrobenthic community analyses (Table 1). According to visual checks by means of UW-video prior to sampling, 8 of these

Fig. 1 Sampling stations in disturbed (●) and undisturbed (○) locations on the southeastern Weddell Sea shelf off Austasen and Kapp Norvegia

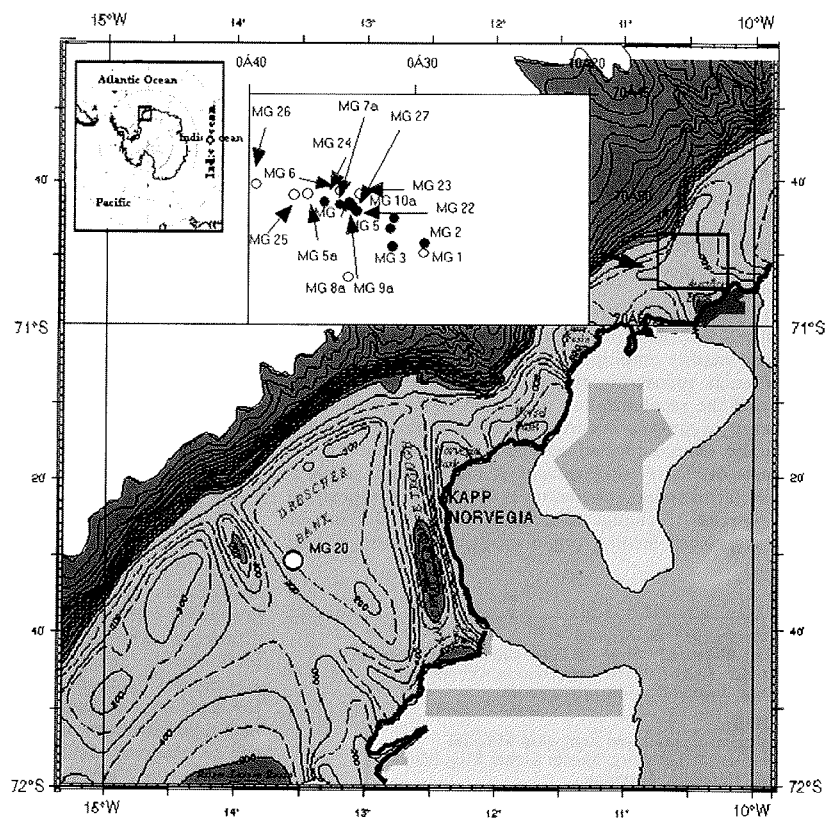


Table 1 List of sampling stations on the south eastern Weddell Sea shelf

Date	Lat./Long. (S/W)	Depth (m)	Gear no.	No. of cores	A priori classification
30.01.1998	70°52.15/10°29.26	234	MG1	7	Undisturbed
30.01.1998	70°52.15/10°29.26	245	MG2	5	Undisturbed
31.01.1998	70°52.10/10°32.40	234	MG3	5	Old scour
31.01.1998	70°51.90/10°32.20	227	MG5	2	Undisturbed
01.02.1998	70°49.90/10°36.70	305	MG6	7	Undisturbed
01.02.1998	70°50.30/10°38.10	269	MG7	3	Old scour
15.02.1998	71°31.50/13°30.30	225	MG20	5	Undisturbed
19.02.1998	70°50.19/10°35.39	273	MG22	4	Young scour
19.02.1998	70°49.79/10°34.40	279	MG23	7	Undisturbed
19.02.1998	70°50.15/10°35.03	276	MG24	4	Young scour
20.02.1998	70°49.32/10°38.84	360	MG25	6	Undisturbed
20.02.1998	70°49.83/10°37.53	293	MG26	7	Undisturbed
20.02.1998	70°50.94/10°32.18	229	MG27	6	Old scour
06.04.2000	70°49.91/10°36.77	275	MG5a	4	Undisturbed
08.04.2000	70°50.34/10°35.04	271	MG7a	4	Old scour
08.04.2000	70°53.63/10°34.21	249	MG8a	5	Undisturbed
10.04.2000	70°50.16/10°34.52	256	MG9a	2	Young scour
10.04.2000	70°50.20/10°34.70	272	MG10a	3	Young scour

stations (31 cores) were situated in iceberg scours of different age, and 10 stations (55 cores) belonged to undisturbed areas. Definitions used to classify a priori the different categories of disturbed and undisturbed areas were:

- young scours (MG nos. 22, 24, 9a, 10a; 13 cores): an abrupt change in megabenthic species composition with a sharp boundary between disturbed and undisturbed areas. In the often slightly depressed scours, hardly any epifauna was visible.
- old scours (MG nos. 7, 7a, 27, 3; 18 cores): impoverished epifauna. Sessile forms, e.g. young sponges, bryozoans, ascidians, occur sporadically and often patchily; higher species number than in young scours.
- undisturbed sites (MG nos. 1, 2, 5, 6, 20, 23, 25, 26, 5a, 8a; 55 cores): biomass rich and diverse; three-dimensional benthos community with large hexactinellid sponges and without obvious borders in between.

All samples were sieved over 500- μ m mesh-size screens and stored in 4% formaldehyde solution buffered with hexamethylenetetramine.

In the laboratory, the whole material was separated into 31 major taxonomic groups. Abundance (ind. m⁻²) and wet biomass (g m⁻²) values were determined for each taxon and core. Furthermore, the polychaetes were counted and determined to species level (data available on request from the first author).

Diversity [Shannon Wiener H' (log e)] and evenness (Pielou, J') of the biomass/abundance values of taxa and abundance values of polychaete species were calculated for each core. Significance of differences between the cores of the three categories was tested by nonparametric Kruskal-Wallis tests. The terms "habitat taxon richness" for the taxonomic units and "habitat species richness" for the polychaete species, according to Gray (2001), describe the category means.

The taxon biomass and polychaete species abundance data were ordinated by non-metric multidimensional scaling (MDS) using PRIMER v5 software of Clarke and Gorley (2001); the similarity matrices were based on the Bray-Curtis Similarity Index. All data were 4th root transformed; for clustering, the "Group Average" methodology was used.

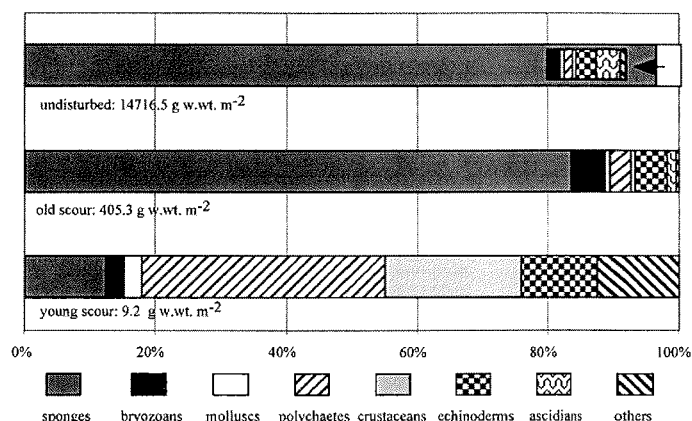
Results

The three categories of stations were significantly different in all tested parameters (Table 2). The Kruskal-Wallis tests showed highly significant differences in abundance, biomass, and habitat taxon richness in the case of taxonomic units ($\alpha \leq 0.001$), as well as in polychaete species richness and abundance ($\alpha \leq 0.0005$). Diversity (H') and evenness (J') based on biomass values

Table 2 Statistical data based on 31 taxonomic units and 167 polychaete species considered for the separation of stations into two different disturbance categories and undisturbed locations on the south eastern Weddell Sea shelf

A priori category	Undisturbed	Old scour	Young scour
MG nos.	1, 2, 5, 6, 20, 23, 25, 26, 5a, 8a	3, 7, 27, 7a	22, 24, 9a, 10a
No. of cores per drop	7, 5, 2, 7, 5, 7, 6, 7, 4, 5	5, 3, 6, 4	4, 4, 2, 3
Taxonomic units			
Mean w.wt m ⁻² category ⁻¹ (SD)	14716.5(35362.9)	405.3 \pm 638.5	9.2 \pm 4.2
Mean ind. m ⁻² category ⁻¹ (SD)	2435 (1146)	875 \pm 246	670 \pm 404
Mean sponge biomass category ⁻¹	12713.1	501.6	1.2
Habitat taxon richness	11.8 \pm 3.4	9.0 \pm 3.0	6.8 \pm 3.8
Mean H' (based on biomass)	0.714	1.092	1.383
Mean J' (based on biomass)	0.287	0.493	0.729
Polychaete species			
Mean ind. m ⁻² category ⁻¹	784 \pm 475	389 \pm 248	242 \pm 239
Habitat species richness	11.3 \pm 7.5	6.0 \pm 3.6	3.1 \pm 2.7
Total species number	143	39	38
Mean H'	1.677	1.340	1.108
Mean J'	0.755	0.826	0.892

Fig. 2 Taxonomic composition of benthic communities (wet biomass proportions) in disturbed and undisturbed locations on the south eastern Weddell Sea shelf



of 31 taxonomic units (Table 2) also differed significantly ($\alpha \leq 0.007$). Both increased from undisturbed areas to old scours and were highest in young scours. In contrast, polychaete diversity and evenness decreased from undisturbed areas to old scours and were lowest in young scours; these differences, too, were significant ($\alpha \leq 0.004$).

Striking differences were also obvious from the composition of the communities (Fig. 2).

Young scours differed from all other areas by the absence of large-sized sessile epifauna; instead, motile organisms such as polychaetes, crustaceans and ophiuroids predominated. In the undisturbed areas, the overwhelming role of sponges as community structuring elements—off Austasen more pronounced than off Kapp Norvegia—was reflected by a biomass share of more than 95% (cf. also Table 2). Two undisturbed stations (MGs 5a, 8a) were characterized by exceptionally high sponge biomass values of more than 10 and 100 kg m⁻², respectively. In contrast to

the old scours and to the undisturbed areas, the young scour community biomass was much more evenly distributed among the taxa. Sponges contributed less than 20% whereas motile forms such as echinoderms, crustaceans and polychaetes gained considerable importance. Bryozoans, which are said to be pioneers (Gutt et al. 1996), also occurred quite frequently in scours.

In total, 167 polychaete species were separated from the samples. Polychaete communities of rich and three-dimensional undisturbed areas showed highest diversity and were dominated by species representing a variety of feeding types and life-styles (Table 3). In contrast, the impoverished polychaete fauna in young scours consisted mainly of discretely motile or sessile deposit feeders belonging to the infauna, with one or few species dominating. In old scours, where sponges and other sessile epifauna provided an already more structured substratum, the polychaete community still appeared impoverished, but comparable to undisturbed sites,

Table 3 Dominant polychaete species, their feeding behaviour and their motility in disturbed and undisturbed locations on the south-eastern Weddell Sea shelf (ecological role, motility: *a* motile forms, *b* sessile forms, *c* discretely motile; feeding type: *I* predators/scavengers, *II* suspension feeders, *III* deposit feeders)

Undisturbed ^a		Old scour ^a		Young scour ^a	
<i>Syllis spongiphila</i>	Ia	<i>Spiophanes tcherniai</i>	IIIc	<i>Spiophanes tcherniai</i>	IIIc
<i>Lumbrineris cf. kerguelensis</i>	Ia	<i>Lumbrineris cf. kerguelensis</i>	Ia	<i>Laonice weddellia</i>	II/IIIc
<i>Spiophanes tcherniai</i>	IIIc	<i>Laonice weddellia</i>	II/IIIc	<i>Lumbrineris cf. kerguelensis</i>	Ia
<i>Cirrophorus brevicirratu</i>	IIIa	<i>Syllis spongiphila</i>	Ia	<i>Neosabellides elongatus</i>	IIIb
<i>Glycera kerguelensis</i>	Ia	<i>Augeneria tentaculata</i>	Ia	<i>Phyllocomus crocea</i>	IIIb
<i>Laonice weddellia</i>	II/IIIc				
<i>Chaetozone</i> sp. 3	IIIa				
<i>Sphaerosyllis antarctica</i>	Ia				
<i>Augeneria tentaculata</i>	Ia				
<i>Scoloplos marginatus</i>	IIIc				
<i>Notomastus latericeus</i>	IIIb				
<i>Typosyllis armillaris</i>	Ia				
<i>Jasmineira crumenifera</i>	IIb				
<i>Polycirrus insignis</i>	IIIb				

^aSpecies contributing 50% to total polychaete abundance

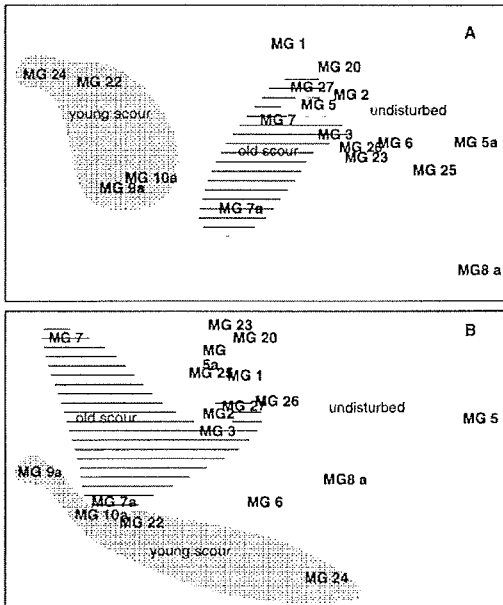


Fig 3A, B MDS plots of sampling stations based on biomass data of 31 macrobenthic taxonomic units (A) and abundance data of 167 polychaete species (B) from 18 stations on the southeastern Weddell Sea shelf

motile scavengers and predators contributed a higher percentage to the fauna.

Multidimensional scaling based on biomass of taxonomic units and abundance of polychaete species did not allow a clear differentiation among categories. The exception was the separation of young scour stations based on biomass of taxonomic units (Fig. 3A), whereas old scour stations and undisturbed ones intermingled with the former showing more affinity with the undisturbed sites. The special composition of these "sponge stations" was reflected by the somewhat isolated position outside the cloud of undisturbed stations.

Ordination of polychaete species did not result in any unequivocal station groups (Fig. 3B), indicating that polychaetes are less useful discriminators of disturbed faunal communities, most likely because their distribution is strongly influenced by the presence of large sessile epifauna.

Discussion

Depending on the iceberg size, scour marks may have widths varying from a few metres to 50 m or even more. Sampling of organisms out of these relatively small but extremely different structured areas has to be very pre-

cise, and the UW-camera guided multibox corer has proved on several expeditions to be an excellent gear for controlled sampling of benthic fauna in scour marks. However, sampling by grabs and corers is likely to underestimate the abundance of rare, large or highly motile specimens, which might recognize the approaching gear and escape. For the multibox corer, such potential underestimates in abundance and biomass by a factor of 3 were documented by Dahm (1996) for ophiuroids. As no correction factors are available for affected benthic groups, our data have to be regarded as minimum estimates, especially in the case of ophiuroids, crinoids or motile, epifaunal crustaceans. However, the multibox corer allows multiple simultaneous sampling of up to nine cores per drop, each covering an area of 240 cm². However, inside scour marks the sediment often appeared highly overcompacted, thus complicating penetration of corers and leading to an average of only 4.0 cores per station, whereas in undisturbed "normal" sediments, the multibox corer provided 5.5 cores on an average.

Previous quantitative benthos studies with the multibox corer on the southeastern Weddell Sea shelf showed the area off Kapp Norvegia to be the richest in terms of organism density and biomass (Gerdes et al. 1992). The mean benthic biomass of 358.3 g w.wt. m⁻² recorded in these investigations, however, was about 22 times lower than that found off Austasen during the present survey. Off Kapp Norvegia, minimum and maximum biomass values (39 and 1,673 g w.wt. m⁻², respectively; cf. Gerdes et al. 1992) varied considerably, but this variability was even higher off Austasen. Outstanding high sponge biomass at several stations with a maximum value > 100 kg m⁻² explains the rather high mean biomass. Without this value, which is the highest recorded so far for high-Antarctic areas, the mean biomass at the 17 stations off Austasen would decrease to a more "normal" value of 1,923 g w.w. m⁻². Grounding icebergs cause a patchy distribution of benthos organisms on the narrow Antarctic shelf, with pronounced differences between affected and undisturbed areas. The region off Austasen can be regarded as one of the most disturbed shelf areas in the Weddell Sea. Effects of grounding icebergs on mega-epibenthos were reported in > 70% of about 50-km video transects analysed by Gutt (2001).

The contrasting results concerning diversity on the gross taxa and species levels, respectively, were somewhat surprising at first sight. However, diversity expressed as Shannon-Wiener index should be interpreted with caution, as the index depends on relative abundances or, in our case, contribution to total biomass. The characteristic eastern Weddell Sea shelf assemblages dominated by very large hexactinellid sponges can certainly be regarded as climax communities, with other taxa contributing no more than a few percent to total biomass. Mats of sponge spicules accumulating over centuries lead to communities that are depauperate in terms of infauna because few organisms are adapted to

this very harsh environment. The high diversity in young scours is therefore not necessarily a result of a greater variety of organisms, but rather of the absence of the true dominant, i.e. scouring icebergs cause increased diversity in cases where different succession stages co-exist.

A diverse pattern of different succession stages of recolonization in disturbed areas may exist. Fundamental questions that still have to be solved include the aging of benthic succession stages and the identification of successional pathways and timescales of recovery after disturbance. Meiofauna may serve as a biological marker for recent disturbance events. Lee et al. (2001a) estimated a recovery time of 30–80 days in a shallow-coast meiofauna community at Signy Island. It is uncertain yet whether these results can be applied to the offshore Weddell Sea shelf. In another study, Lee et al. (2001b) described decreased meiofauna abundance and diversity as typical effects after iceberg disturbance, but they could not provide good estimates of the recovery time. This study also considered samples of MG 24, and the scour was characterized as being recently disturbed, thus coinciding exactly with our classification based on macroinfauna.

Based on Dayton and Robilliard's (1971) assumption that "...almost all sponges are certainly much older than*Odontaster validus* which.....could reach ages of over 100 years", the age of undisturbed areas with dense sponge associations as the other extreme can be assumed to be more than 100 years. The age of different successional stages lies between these two extremes, and growth rates of sessile key species like bryozoans or sponges have to be used as proxies for age determination. Some data are available (e.g. Brey et al. 1999; Gatti et al. 2003) but generally the database of life-histories of Antarctic benthos organisms is still rather small.

In conclusion, our results indicate that grounding icebergs have a significant impact on benthic assemblages in Antarctic regions. From Arctic sites, similar effects are reported by Conlan et al. (1998). Icebergs extinguish bottom fauna and create new space for opportunistic species, thus increasing the between-habitat diversity (β -diversity) and probably also the overall gamma-diversity of the eastern Weddell Sea shelf. The quantification of these parameters is still in a beginning stage due to the incomplete breakdown of most taxa to species level, but the polychaete data presented in this paper support this assumption.

The significance of iceberg disturbance is likely to increase in the future due to global warming and accelerated melting of Antarctic ice shelves. This implies the necessity of further studies, which should aim to better understand the effects of this physical disturbance on benthic systems in high polar environments, and their importance for biodiversity.

Acknowledgements Our thanks are due to the crew of the RV "Polarstern" for help and assistance at sea. An unknown reviewer is thanked for many helpful comments that greatly increased the

quality of this paper. The second author was supported by the "Deutsche Forschungsgemeinschaft", grant no. BR 1121-7.

References

- Brenner M, Buck BH, Cordes S, Dietrich L, Jacob U, Mintenbeck K, Schröder A, Brey T, Knust R, Arntz WE (2001) The role of iceberg scours in niche separation within the Antarctic fish genus *Trematodus*. *Polar Biol* 24:502–507
- Brey T, Gerdes D (1998a) High Antarctic macrobenthic community production. *J Exp Mar Biol Ecol* 231:191–200
- Brey T, Gerdes D (1998b) Benthic community productivity in the Magellan region and in the Weddell Sea. *Sci Mar* 63 [Suppl. 1]:145–148
- Brey T, Gerdes D, Gutt J, Mackensen A, Starmans A (1999) Growth and age of the Antarctic bryozoan *Cellaria incula* on the Weddell Sea shelf. *Antarct Sci* 11:408–414
- Clarke KR, Gorley RN (2001) Primer v5: user manual/tutorial. Primer-E, Plymouth
- Conlan KE, Lenihan HS, Kvitek RG, Oliver JS (1998) Ice scour disturbance to benthic communities in the Canadian high Arctic. *Mar Ecol Prog Ser* 166:1–16
- Dahm C (1996) Ecology and population dynamics of Antarctic ophiuroids. *Ber Polarforsch* 194:1–289
- Dayton PK, Robilliard GA (1971) The benthic community near McMurdo station. *Antarct J US* 6:54–56
- Galéron J, Herman RL, Arnaud PM, Arntz WE, Hain S, Klages M (1992) Macrofaunal communities on the continental shelf and slope of the southeastern Weddell Sea, Antarctica. *Polar Biol* 12:283–290
- Gatti S, Brey T, Arntz WE (2003) The Antarctic lollipop sponge *Stylocordyla borealis* (Lovén, 1868). 1. Morphometrics and reproduction. *Mar Ecol Prog Ser* (in press)
- Gerdes D (1990) Antarctic trials with the multibox corer, a new device for benthos sampling. *Polar Rec* 26:35–38
- Gerdes D, Klages M, Arntz WE, Herman RL, Galéron J, Hain S (1992) Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. *Polar Biol* 12:291–301
- Gray JS (2001) The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *J Exp Mar Biol Ecol* 250:23–49
- Gutt J (1991) On the distribution and ecology of holothurians in the Weddell Sea (Antarctica). *Polar Biol* 11:145–155
- Gutt J (2000) Some "driving forces" structuring communities of the sublittoral Antarctic macrobenthos. *Antarct Sci* 12:297–313
- Gutt J (2001) On the direct impact of ice on benthic communities, a review. *Polar Biol* 24:553–564
- Gutt J, Starmans A, Dieckmann G (1996) Impact of iceberg scouring on polar benthic habitats. *Mar Ecol Prog Ser* 137:311–316
- Gutt J, Buschmann A, Dimmler W, Frey N, Gerdes D, Bohlmann H, Grünwald T, Lee HJ, Niederjaspert F, Schickan T, Vanhove S (1997) The impact of iceberg on benthic assemblages. *Ber Polarforsch* 249:35–41
- Gutt J, Buschmann A, Dijkstra J, Dimmler W, Piepenburg D, Teixidó N (1999) Study on benthic resilience of the macro- and megabenthos by imaging methods. *Ber Polarforsch* 301:17–22
- Hain S (1990) Die beschalteten benthischen Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. *Ber Polarforsch* 70:1–181
- Klages M (1991) Biologische und populationsdynamische Untersuchungen an ausgewählten Gammariden (Crustacea; Amphipoda) des südöstlichen Weddellmeeres, Antarktis. PhD Thesis, University of Bremen
- Knust R, Arntz WE, Boche M, Brey T, Gerdes D, Gutt J, Mintenbeck K, Schröder A, Starmans A, Teixidó N (2003) Iceberg scouring on the eastern Weddell Sea shelf (Antarctica). A benthic system shaped by physical disturbances. VIII. SCAR International Biology Symposium, Amsterdam 2001 (in press)

PUBLICATION 2

301

- Lee HJ, Vanhove S, Peck LS, Vincx M (2001a) Recolonisation of meiobenthos after catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biol* 24:918-925
- Lee HJ, Gerdes D, Vanhove S, Vincx M (2001b) Meiofauna response to iceberg disturbance on the Antarctic continental shelf at Kapp Norvegia (Weddell Sea). *Polar Biol* 24:926-933
- Stiller M (1996) Verbreitung und Lebensweise der Aphroditen und Polynoiden (Polychaeta) im östlichen Weddellmeer und im Lazarevmeer (Antarktis). *Ber Polarforsch* 185:1-200

6 Zoogeography

6.1 Distributional patterns of shallow-water polychaetes in the Magellan region: a zoogeographical and ecological synopsis.

Montiel A.,^{1,2} Gerdes D.¹ & Arntz W.E.¹

SUMMARY: The biogeography of polychaete annelids was described for the Magellan Region. This work considered information available from 19 expeditions carried out in the last 124 years of polychaete taxonomic research in the southernmost tip of South American continental shelf. The polychaete fauna of the Magellan region constituted of a total of 431 species belonging to 108 genera and 41 families. MDS and ANOSIM analyses showed the Magellan region to be divided into two entities, one on the Pacific side of the tip of South America and one on the Atlantic side. These entities presented a low percentage of "endemic species" (< 10%) and more than 70% of the species recorded for the Magellan region showed a wide distribution range. Especially high affinities existed with Antarctic and Subantarctic areas. We suggest dispersion through larval transport via easterly directed water currents of the West Wind Drift to play an important role for the actual distribution patterns of the polychaete fauna around the tip of South America. We suggest that the opening of the Straits of Magellan created a new pathway for enhanced exchange of faunal elements between the Pacific and the Atlantic and vice versa.

Key words: Polychaete zoogeography, Antarctic affinities, species composition, Magellan Region.

RESUMEN: Se describe la biogeografía de los poliquetos anelidos para la región de Magallanes, la cual hace referencia a la información disponible de 19 expediciones llevadas a cabo durante los últimos 124 años de investigación taxonómica en la plataforma del cono sur de Sudamérica. La fauna de poliquetos de la región de Magallanes está constituida por un total de 431 especies perteneciente a 108 géneros y 41 familias. El resultado de análisis de MDS y ANOSIM mostró que la región de Magallanes se puede dividir en dos entidades biogeográficas, una de las cuales se ubica en el lado Pacífico, mientras la otra en el lado Atlántico del cono sur de Sudamérica. Estas entidades biogeográficas se caracterizaron por un bajo porcentaje de especies endémicas (< 10%). Aproximadamente el 70% de las especies registradas en ambas entidades mostró un amplio rango de distribución, especialmente una alta afinidad con áreas Antárticas y Subantárticas fue encontrada. Estos sugiere que el proceso de dispersión a via transporte larvario a través de la corriente de deriva del oeste estaría jugando un rol preponderante en el actual patrón de distribución de la fauna de poliquetos en el región de Magallanes. Mientras que la apertura del estrecho de Magallanes significó un nuevo pasaje de intercambio de especies entre la el Pacífico – Atlántico y vice versa.

Palabras clave: Zoogeografía de poliquetos, afinidades antárticas, composición de especies, Región de Magallanes.

INTRODUCTION

Polychaetes have been considered for zoogeographical analyses in South America only in the last decade (Lancelotti & Vásquez, 1999; Fernandez *et al.*, 1998; Camus, 2001; Glasby & Alvarez, 1999). They are thought to be no proper indicators for zoogeographical purposes because of their wide geographical range on all taxonomic levels and especially because of their long-distance dispersal capabilities. Paradoxically, polychaetes worldwide make up a large portion of the total macrofauna in soft-bottoms (Hutchison, 1998) and with more than 16,000 species known so far, they are the fourth major group of marine invertebrates (Blake, 1995; Bouchet, 2000). Although most polychaete families, except a few poor-known, are known to occur in all oceans and at all depths, studies on species level, which would be required for zoogeographic analysis, are scarce in the polychaete literature, and the Magellan region is by no way an exception in this (e.g. Hartmann-Schröder & Hartmann, 1974; Knox & Lowry, 1977). According to Knox (1957) more than 40% of the southern hemisphere polychaete species are thought to be cosmopolitans, but the poor knowledge of the polychaete taxonomy and the low level of quantitative data might well be one reason for this unusually high percentage of "cosmopolitan" species.

Zoogeography of the Magellan region has been reviewed several

times, but despite these studies the gain of knowledge remained comparative poor. Balech (1954) was the first to propose a scheme for the Magellan region, subdividing it into 5 districts: two on the Atlantic side (Santacruceño and Chubutiano), two on the Pacific side (Valdiviano and Chiloense) and the Fuegino district, which connects both sides at the tip of South America. Fifty-six years later and after several reviews (Viviani, 1979; Brattström & Johanssen, 1983; Carreto, 1983; Stuardo & Valdovinos, 1992; Lancelotti & Vásquez, 1998) Camus (2001) questioned, whether the Magellan region as a zoogeographic entity should be extended into the Atlantic area off the South American coast.

In another recent study Longhurst (1998), based on oceanographic and phytoplankton data, considered only two divisions at the tip of South America, the Humboldt Current Coastal Province, stretching over the entire Chilean Pacific coast, and the Falkland Coastal Province on the Atlantic side.

In this context the purpose of this investigation was to analyse, based on all available polychaete data, whether the traditional subdivisions of the Magellan region also are recognizable on the basis of distribution patterns of polychaete species. Certainly the amount of information on polychaete distribution patterns is considerable and bases on almost 120 years of descriptive taxonomy. However, to our knowledge no one has ever tried to synthesize this bulk of data. Our paper thus is an attempt to check existing zoogeographical subdivisions in the Magellan region by using polychaete data (presence/

absence of species in the different regions) obtained on several own expeditions and data available from literature.

MATERIAL AND METHODS

Source of polychaete data

Benthic polychaetes with exact catch positions (georeferences) were considered from continental shelf areas in and around the Magellan Region. In total data from 519 stations provide the basis for our analyses. Forty-two of these stations were sampled by ourselves during three expeditions with RVs "Victor Hensen" in 1994 (Arntz & Gorny, 1996), "Vidal Gormaz" in 1995 (Mutschke, 1996) and "Polarstern" in 1996 (Fahrback & Gerdes, 1997). The origin of the remaining data is summarized in Table 1.

Study area

Based on oceanographic conditions and on the topography the tip of South America can be divided into three major areas:

- channels and fjords on the Pacific side extend from about 42°S to 55°S and are located in the section with a wider shelf of the South American coastline (Strub *et al.*, 1998); the mean width of the continental shelf is about 6.54 km (Gallardo, 1984). This area is under the oceanic influence of the Humboldt Current and at the southern tip of the Cape Horn Current, both of which are branches of the West Wind Drift Current (WWD). The Subantarctic water can penetrate into the inlets (Silva *et al.*, 1998). The hydrographical regime is characterized by strong fresh water input, due to high precipitation and concomitant runoff, all producing a strong and shallow pycnocline (Dávila *et al.*, 2002). Successive

glaciation periods structured this coast with more than 200 fjords and channels (Syvitski *et al.*, 1987). Water depths vary from < 150 m to maximum depths around 1050 m. The sediments are characterized by silt and clay (Murray, 1895), but coarser sediments such as pebbles/gravels and biogenic gravel from molluscs and barnacles also are present (Brambati *et al.*, 1991). Three permanent ice fields exist, Campo de Hielo Norte (46 – 47 °S), Campo de Hielo Sur (48-52°S), and the Cordillera Darwin (54-55°S; Naruse & Aniya, 1992).

- the second area, the Straits of Magellan (52°58'S, 70°55'W and 53°43'S, 70°17'W), is a natural seaway connecting the Pacific with the Atlantic Ocean. Water depths vary between 8 and 1,200 m in the western entrance on the Pacific side (Antezana *et al.*, 1992). Currents decrease from 100 cm s⁻¹ on the Atlantic side of the Straits to 20 cm s⁻¹ in the Paso Ancho (Michelato *et al.*, 1991). Primary production ranges seasonally between 282 and 1000 mg C m⁻² day⁻¹ (Guglielmo & Iacona, 1997). The sediments mainly consist of sand and gravel with varying proportions of mud and shell debris; the distribution patterns appear considerably heterogeneous, especially in the shallower parts of the Straits (Brambati *et al.*, 1992).

- the Atlantic shelf of the Magellan Region as the third area extends from the Rio de la Plata to Tierra del Fuego. This province between 38°S and 55°S comprises the Argentine Patagonian shelf and the Falkland plateau. The continental shelf widens to a maximum of about 850 km at 51°S (Piccolo, 1998). The coast presents the Peninsula Valdés,

Bahía Blanca, San Matías and San José. The hydrographical regime includes the confluence region of the Falkland and Brazil currents. The mean annual temperature in the Falkland Current is 10°C and primary production varies between 150 and 500 mg C m⁻² day⁻¹ (Longhurst, 1995). The Brazil Current shows a higher annual mean temperature of 22°C with variations in the primary production between 115 to 830 mg C m⁻² day⁻¹ (Boltovskoy, 1999). In general, the bottom sediments are characterized by sand (fine to median size) and silt (< 2mm; Bastida *et al.*, 1981). The coarse fraction > 2 mm prevails near the coast (< 50 m) and in the embayments mentioned above, this fraction is characterized by high percentages of biogenic gravel of mollusc, brachiopod and barnacle shells (Bastida *et al.*, op.cit.).

Data treatment

The zoogeographical analysis was based on 19 different expeditions with 445 stations.

The total polychaete species number used for this analysis includes all species records with exact georeferences and more than 1 finding (Fig. 1). A map of the marine realm around the tip of South America was divided into 96 quadrants, each one degree longitude and one degree latitude in size. Quadrants without polychaete findings per station were not considered and quadrants with only one station were homologated with the neighbour quadrant. With this division quadrants 1 to 66 plus quadrant 71 represented the Atlantic entity, the Straits of Magellan is represented by quadrants 72-75 and quadrants 67 to 70 and 76 to 96 make up the Pacific entity (cf. Fig. 1).

To check, whether or not polychaete distribution patterns coincide with the traditional (sub-) divisions of the Magellan region *sensu* Balech (1954), Carreto (1983), Longhurst (1998), Lancelloti & Vásquez (2000) and Camus (2001). The following acronyms were used by the different authors for the traditional division of the Magellan Region:

A : Atlantic, **AU** : Austral, **C**: Chubutiano, **CAHO**: Cape Horn Province *sensu* Longhurst (1998), **CS**: Chiloense, **CE**: Chiloé, **CH**: Cape Horn *sensu* Lancelloti & Vásquez (1998), **CI**: Chonos Inlet, **F**: Fueguino, **FKLD**: Falkland Province, **MS**: Magellan Straits, **PI**: Pacific Inlets, **S** : Santacruseño, **SA**: Subantarctic (*sensu*, Camus, 2001). For comparison with the adjacent Subantarctic and Antarctic areas south and temperate areas north, additional acronyms (**ANTA**, **SANT** and **HUMB**, respectively) were introduced according to Longhurst (1998).

ANOSIM and MDS plots on the basis of 216 species records from the 96 quadrants were performed to evaluate the dissimilarity between quadrant groups representing and coinciding with these traditional divisions. In a next step the similarity percentage breakdown analysis (SIMPER; Clarke, 1993) describes the contribution of each species to the dissimilarity between the obtained groups of quadrants. All analyses were carried out using the software PRIMER version 5.2.1. (Clark & Warwick, 1994) with standardized polychaete presence/absence data.

Many of the polychaete species used as discriminators for entities in the Magellan Region also occurred in adjacent and other parts of the world

oceans. In order to take into consideration also the large-scale distribution of specific polychaetes, we consulted the fundamental taxonomic studies of Hartman (1959 a, b) and Rozbaczylo (1985). In addition the most recent taxonomical reviews for the species distribution of the eunicemorph polychaetes of Orenzáns (1990), the Spionidae families (Blake, 1983), the Syllidae (Licher, 2000) and Glyceridae (Böggemann, 2002) were consulted.

RESULTS

Up to now a total of 431 polychaete species are recorded for the Magellan region summarizing 124 years of polychaete research in this part of the world. These species can be divided into 108 genera and 41 families. The most speciose families were Syllidae, contributing 11 % to total polychaete species, followed by Polynoidae (9%), Terebellidae (8%), Spionidae (6%) and Lumbrineridae (4%), whereas other families were of minor importance (< 4%, Fig. 2).

Out of the 431 polychaete species, one hundred species were reported without exact catch position and another 111 species occurred as single findings, i.e. these species were not considered for this purpose. The remaining 220 species thus provided the basis for the numerical and statistical analyses.

Do polychaete distribution patterns agree with traditional patterns?

To prove, whether or not polychaete distribution patterns coincide with the traditional (sub-) divisions of the Magellan region referred to above, ANOSIM on the basis of 220 species records from 96 quadrants was performed prior to the following zoogeographical divisions. The

results are summarized in Table 2 and clarify that splitting of the Magellan region in more than two entities, as done by most of the investigators mentioned above, not always make obvious significant differences on the basis of polychaete presence/absence data between the specific entities. Based on our data the subdivision of the Magellan Region into two distinct entities, one on the Atlantic and another one on the Pacific side resembles mostly the results obtained by Longhurst on the basis of satellite pictures of phytoplankton in surface waters. ANOSIM of the CAHO versus FKLD data revealed a significant difference between both entities, as shown by the fairly low R value ($R = 0.4$, $P < 0.001$; cf. Table 2). The MDS plot confirms the observation of the ANOSIM test (Fig. 3) by presenting two distinct quadrant groups, standing for the Pacific and the Atlantic shelves of the tip of South America.

SIMPER analysis (Tab. 3) identified the main contributor species for the average dissimilarity (average = 94.75) between the established entities. In the quadrant group representing FKLD main contributor species with highest frequency of occurrence were e.g., *Idanthyrsus macropaleus*, *Serpula narconensis*, *Perkinsiana antarctica* and *Chaetopterus variepedatus*, whereas in the CAHO group species such as *Glycera capitata*, *Onuphis pseudoiridescens*, *Leanira quaterfagesi* and *Ninoe falklandica* were better discriminators between both entities.

Distribution patterns of polychaetes in the Magellan Region and affinities with Antarctica.

The distribution patterns of the polychaete fauna are shown in Fig. 4 a, b. This figure considers 354 of the 431 species known from the Magellan region; 77 species appearing with disjunctive findings worldwide were not considered. Forty-eight (14 %) of the 354 species showed a cosmopolitan distribution. Only rather low percentages of the polychaete species of the present study were restricted to just one of the distinguished entities: 4 % to the Atlantic side and 7 % to the southern Pacific coast, whereas another 1% occurred exclusively along the northern Pacific coast of South America north of 42° S. The major part of remaining species (74 %) showed an overlapping distribution pattern everywhere along the South American coasts and down to Antarctica. Because of the complexity and a high degree of species with overlapping distribution patterns we divided the remaining species into three arbitrary groups representing the best fit to our above mentioned results (Fig. 4b).

The biggest of these groups was that showing affinities to the CAHO complex (123 species; 35%); these species were distributed along the Pacific coast of South America towards high Antarctic waters, and some species also extend their northern distribution limit over 42 °S into more temperate regions of the Pacific coast. The smallest group showed closest affinities between FKLD (6.5%), on the Atlantic side, and south of the Antarctic Convergence. A more distinct group of species was restricted to the coast

of South America, some of them even extended beyond 42°S latitude northwards into the Pacific, and other species were also found on the Atlantic side.

DISCUSSION**Species numbers and structure of the polychaete fauna in the Magellan region**

Based on 431 species considered in this study, the polychaete fauna was dominated by the families Syllidae, Polynoidae, and Terebellidae. This dominance was described before in the classical polychaete reviews of Orensanz (1974) and Knox & Lowry (1977) on the basis of 397 and 223 species, respectively. In our study Spionidae followed as the next important family in the 4th position, whereas Phyllodocidae occupied this rank in the studies of Orensanz (1974) and Knox & Lowry (1977). The later sequence also resulted in the studies of Clark & Johnston (2003) for the whole Southern Ocean and of Rozbaczylo (1995) for the southeastern Pacific coast.

From these data it is obvious that the number of species in the Magellan region increased quite a lot since the studies of Lowry & Knox and Orensanz (loc. cit.) in the middle of the 1970s. This increase may be explained to some part by new expeditions in the 1980s and 1990s, which brought up quite a number of new records. Many of these species, however, occurred as "single findings" or "disjunctive species", i.e. due to few and scattered records, wide distribution ranges, and/or uncertain taxonomical status they did not have much value for zoogeographical analyses. Therefore

our data basis for the zoogeographical analysis consisted in less species numbers than the 431 species described for the Magellan region in total. This agrees with the analysis of the macroinvertebrate fauna along the Chilean coast of Lancellotti & Vásquez (1998). Our results also showed for the cold temperate regions at the tip of South America the highest percentage of single records, which may be a result of insufficient numbers of surveys in this region.

Zoogeographical patterns of the polychaete fauna

Based on polychaete presence/absence data the Magellan region can clearly be subdivided into a Pacific and an Atlantic entity. A similar picture results from the satellite plankton discrimination of Longhurst (1998), although his study area only coincides with the northernmost of our Pacific quadrants up to about 45°S. The composition of the polychaete fauna within the Humboldt entity quadrants and the Pacific quadrants further south down to Cape Horn looks very much the same and occurs as one entity in our analysis, named Cape Horn entity (CAHO).

In the last decade conscious marine zoogeographical studies based on macro-invertebrates from the Pacific coast of South America have been performed exclusively with old literature data (Fernandez *et al.*, 1998, Lancellotti & Vasquez, 1998, 1999; Camus, 2001). These authors have given strong emphasis to the traditional zoogeographical barriers along the Chilean coastline, as proposed by Viviani (1979) and Brattström & Johanssen (1983), for example the 42°S barrier between the Magellan region in the south and

the adjacent temperate region directly north. However, this traditional barrier does not exist for many polychaete species, as is obvious from the high percentage of overlapping species with a wide range of distribution and the high number of common species north and south of 42°S. One reason could be an enormous ecological capacity and tolerance of polychaetes to very different environmental conditions, as is typical for organisms of phylogenetic old lineage (Fauchald, 1984).

The marine realm is a dynamic system, i.e. fixed borderlines hardly occur. Absolute barriers in aquatic systems are almost impossible, and for many species borders probably act more as filters than as barriers, allowing species exchange in both directions (Dell, 1972; Scheltema, 1988; Boltovskoi, 1999; Hilbig, 1994).

Do our arbitrary groups (cf. Fig. 4) correspond to polychaete distribution patterns and how could these patterns be explained? We distinguished two groups with species showing a high affinity to Antarctic waters and one group being restricted to South American shelf areas. Within the first two groups, one group contained 34.7% of species, showing affinity between Pacific and Antarctic, and another smaller group (6.5 %) showed affinity between Atlantic and Antarctic waters. The processes and mechanisms behind these patterns are controversially discussed in the literature (Orensanz, 1990). Two different explanations are under discussion: a) common species in both areas occur due to the common history of the areas as parts of Gondwana (*vicariance*) and b)

common species occur due to dispersion of meroplanktonic larvae (*dispersalism*). We suggest dispersion through larval transport via easterly directed water currents of the WWD to play an important role for the actual distribution patterns of the fauna around the tip of South America. This hypothesis is supported by a major proportion of species with higher affinities to the Pacific coast as compared to the relatively small amount of species with affinities to the Atlantic side, although according to Bhaud (1998) the spreading potential of polychaete larvae does not necessarily predict the adult distribution; key processes for the establishment of a successful population in a new habitat are especially the recruitment conditions and substrate choice of settling larvae. However, the presence of common species on both sides of the Drake Passage gives strong evidence to argue that dispersion might be an important process for faunal exchange between the Magellan region and Antarctica. The polar front, thus does not function as a strict barrier for many species. In fact, several of the dominating polychaete species in the Magellan area as defined by SIMPER (*I. macropaleus*, *S. narconensis*, *C. variepedatus*, *L. quetrefagesi*) reproduce via meroplanktonic larvae (Giangrande, 1997). Another hypothesis includes the adjacent deep-sea areas as possible sources for shelf species. However, potential pathways of recolonisation of shelf communities from the deep sea are still under study and hardly understood. The results of the recent "ANDEEP" and "LAMPOS" expeditions (Fütterer *et al.*, 2003; Arntz & Brey, 2003) might be

particularly important to present keystones in the overall Antarctic-Magellan puzzle.

Finally, we suggest the third group occurring exclusively in South American waters and its high number of common species on the Pacific and Atlantic side to be a result of the glaciation history of the southern parts of South America. The southeastern Magellan Region is a geologically young system (Pisano, 1990), which was ice covered until the last maximum glaciation period some 12,000 years BP (Clapperton *et al.*, 1995; Benn & Clapperton, 2000). The polychaete species present today in Magellan waters all colonized this area by species flux from adjacent Atlantic and Pacific areas and the Magellan Straits probably have been an important corridor for species exchange between both sides since their opening 7000 year BP (McCulloch & Davies, 2001). The oceanography of this area reflects the intrusion of oceanic waters from both sides of the continent and the mixture of these water masses in the Paso Ancho in the middle of the Straits. We suggest that the opening of the Straits of Magellan created a new pathway for enhanced exchange of faunal elements between the Pacific and the Atlantic and vice versa.

ACKNOWLEDGEMENTS

We are grateful to Prof. Erika Mutschke and the Comité Oceanográfico Nacional (CONA) for providing the biological material from the CIMAR-Fiordo expedition. This work was supported by DAAD grant No A/00/10932.

PUBLICATION 3

Table 1. Chronological and synoptic list of expeditions carried out in Magellan waters.

Campaign	Research Vessel	Station per expedition	Source
HMS Challenger	"Challenger"	6	McIntosh, 1885
Swedish Antarctic Expedition	"Antarctic"	28	Hartman, 1953
Discovery Expedition	"Discovery"	1	Monro, 1930-36
Discovery Expedition	"William Scoresby"	112	Monro, 1930-36
Lund Univ. Chile Expedition	"Arauco II" & Galvarino"	95	Wesenberg-Lund, 1962
Mission du Cap Horn	"Romanche"	23*	Fauvel, 1941
Mar Chile I	"Chipana"	6	Hartmann-Schröder, 1965
USNS Eltanin	"Eltanin"	26	Hartman, 1967
Akademic Knipovich	"Akademic Knipovich"	20	Averince, 1972
Akademic Knipovich	"OB"	4*	Averince, 1972
Walther Herwig 15 th , 36 th & 76 th	"Walther Herwig"	71	Hartmann-Schröder, 1983
Allan Hancock Pacific Expedition	"Vema"	25*	Maurer & William, 1988
Italian Oceanographic expedition	"Cariboo"	16	Gambi <i>et al.</i> , 1999
Shinkai Maru 4 th , 5 th , 10 th & 11 th	"Shinkai Maru"	22*	Bremec <i>et al.</i> , 2000
CIMAR Fiordos	"Vidal Gormaz"	19	Montiel <i>et al.</i> , in press
UMAG, data base.	"Lenga"	3	Ríos <i>et al.</i> , 2003
Joint Magellan Campaign	"Victor Hensen"	20	Present study
CIMAR Fiordos	"Vidal Gormaz"	18	Present study
ANT XIII/4	"Polarstern"	4	Present study

* Information on species per station or station georeference not available.

PUBLICATION 3

Table 2. ANOSIM pairwise test of presence/absence data of polychaete species from quadrants according to the division by the different authors. **A**: Atlantic **AU**: Austral **C**: Chubutiano **CAHO**: Cape Horn province **CS**: Chilense **CE**: Chiloe **CH**: Cape Horn **CI**: Chonos inlet **F**: Fueguino **FKLD**: Falkland province **MS**: Magellan Straits **PI**: Pacific Inlets, **S**: Santacruseño **SA**: Subantarctic. * significant difference.

Hypothetical group <i>sensu</i> different authors	Pairwise test		
	<i>R</i>	P (%)	Number \geq observed
Balech, 1954			
S - C	0.2	0.2	1
S - F	* 0.321	0.1	0
S - CS	* 0.557	0.1	0
C - F	0.151	0.9	8
C - CS	* 0.564	0.1	0
F - CS	* 0.263	0.1	0
Lancelloti & Vásques 2000			
A - CE	0.342	1.5	14
A - MS	* 0.455	0.1	0
A - CI	* 0.617	0.1	0
A - CH	* 0.86	0.1	0
CE - MS	0.329	2.9	28
CE - CI	0.026	51.4	18
CE - CH	0.476	0.6	2
MS - CI	0.244	7.5	74
MS - CH	* 0.524	0.1	0
CI - CH	0.31	3.3	11
Carreto 1988			
III - IV	0.179	0.4	3
PI - III	* 0.428	0.1	0
PI - IV	* 0.45	0.1	0
Camus 2001			
SA - AU	0.112	5.9	58
A - SA	* 0.353	0.1	0
A - AU	* 0.517	0.1	0
Longhurst 1998			
FKLD - COHO	* 0.447	0.1	0
Present study			
PI - A	* 0.482	0.1	0
PI - MS	-0.034	5.3	52
A - MS	0.237	57.8	577

PUBLICATION 3

Table 3. Results of the SIMPER analysis of presence/absence data of polychaete species from the CAHO and FKLD quadrants. Species are listed in the order of their contribution to the average dissimilarity between both groups after Longhurst (1998). Diss: Dissimilarity; SD: Standar desviation.

Species	Mean Diss	Diss / SD	Contribution (%)	Cumulative contribution (%)
<i>Idanthyrsus macropaleus</i>	2.65	0.79	2.80	2.80
<i>Serpula narconensis</i>	2.38	0.75	2.51	5.31
<i>Perkensiana antarctica</i>	2.05	0.71	2.16	7.47
<i>Chaetopterus variopedatus</i>	1.77	0.61	1.87	9.34
<i>Glycera capitata</i>	1.72	0.62	1.81	11.15
<i>Onuphis pseudoiridescenes</i>	1.60	0.63	1.69	12.84
<i>Leanira quatrefagesi</i>	1.57	0.68	1.66	14.50
<i>Ninoe falklandica</i>	1.55	0.56	1.64	16.14
<i>Polyeunoa laevis</i>	1.54	0.61	1.63	17.77
<i>Eunice magellanica</i>	1.52	0.53	1.61	19.38
<i>Maldane sarsi</i>	1.51	0.57	1.59	20.96
<i>Aglaophamus praetiosus</i>	1.49	0.60	1.57	22.54
<i>Harmothoe spinosa</i>	1.47	0.65	1.55	24.09
<i>Nicon maculata</i>	1.47	0.58	1.55	25.64
<i>Platynereis australis</i>	1.28	0.47	1.35	26.99
<i>Melinna cristata cristata</i>	1.27	0.52	1.34	28.33
<i>Harmothoe magellanica</i>	1.19	0.53	1.26	29.59
<i>Abyssoninoe abyssorum</i>	1.17	0.54	1.24	30.82
<i>Perinereis nuntia vallata</i>	1.16	0.39	1.22	32.05
<i>Gymnonereis hartmannschroederiae</i>	1.15	0.53	1.22	33.27
<i>Amphitrite kerguelensis</i>	1.13	0.56	1.19	34.46
<i>Eunereis patagonica</i>	1.06	0.51	1.12	35.58
<i>Syllis (Syllis) sclerolaema</i>	1.05	0.46	1.10	36.68
<i>Kinbergonuphis dorsalis</i>	0.92	0.45	0.97	37.65
<i>Trypanosyllis gigantea</i>	0.90	0.47	0.95	38.60
<i>Glycinde armata</i>	0.90	0.42	0.95	39.55
<i>Sternaspis scutata</i>	0.89	0.43	0.94	40.49
<i>Harmothoe campoglacialis</i>	0.88	0.45	0.92	41.41
<i>Thelepus plagiostoma</i>	0.85	0.43	0.90	42.31
<i>Hyalinoecia artifex</i>	0.85	0.33	0.89	43.21
<i>Austrolaenilla antarctica</i>	0.82	0.41	0.86	44.07
<i>Typosyllis armillaris</i>	0.78	0.36	0.83	44.90
<i>Nereis eugeniae</i>	0.78	0.48	0.83	45.72
<i>Lumbrineris cingulata</i>	0.77	0.52	0.82	46.54
<i>Nothria anoculata</i>	0.75	0.37	0.79	47.33
<i>Nicolea chilensis</i>	0.74	0.42	0.79	48.12
<i>Lumbrineris magalhaensis</i>	0.72	0.45	0.76	48.88
<i>Autolytus charcoti</i>	0.70	0.35	0.74	49.62
<i>Marphysa aenea</i>	0.70	0.30	0.74	50.36
<i>Aphelochaeta cincinnata</i>	0.69	0.39	0.73	51.09
<i>Phylo felix</i>	0.67	0.46	0.71	51.80
<i>Aphrodita longicornis</i>	0.65	0.29	0.69	52.49

PUBLICATION 3

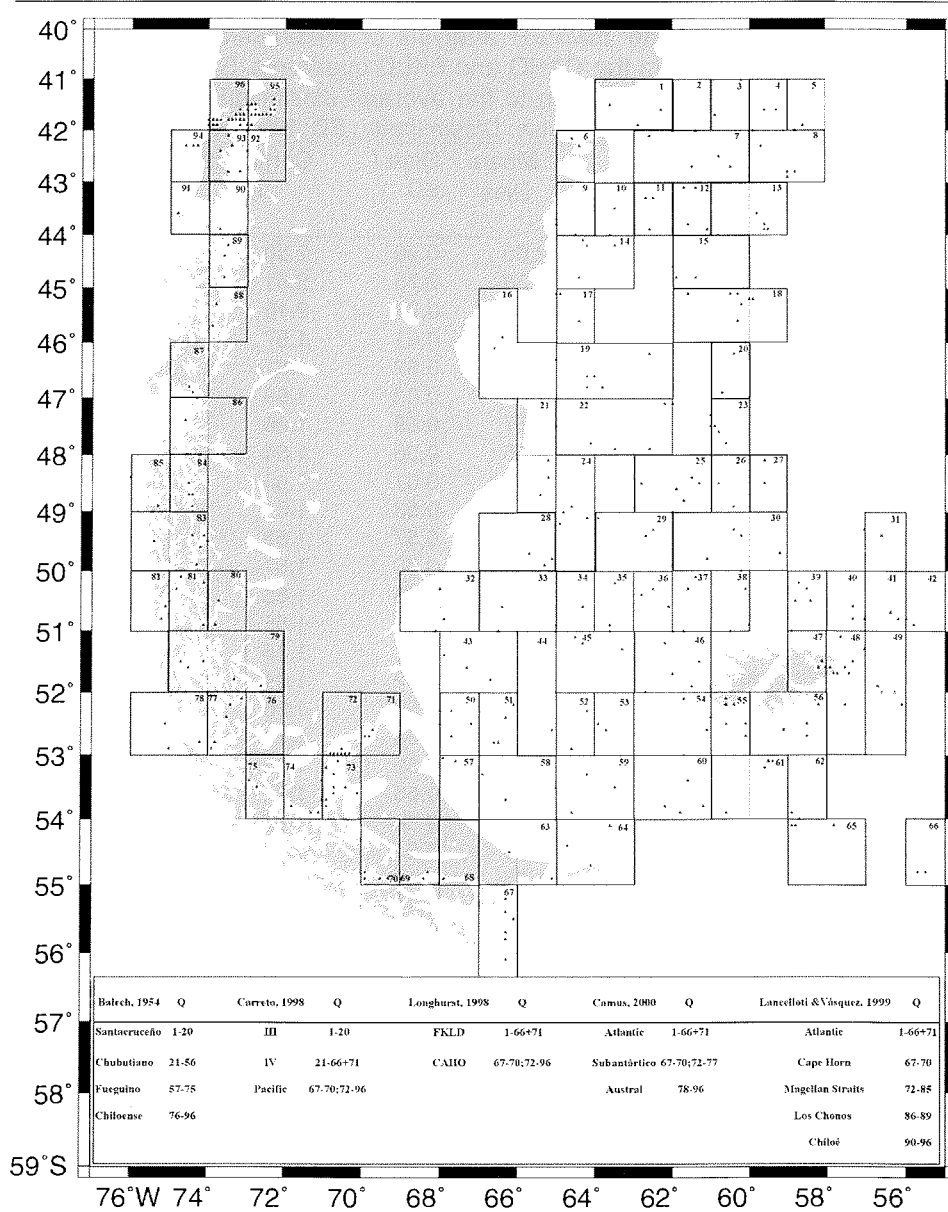


Figure 1. Grid of the marine realm of the tip of South America with indication of sampling locations and quadrant numbers and traditional divisions of the Magellan Region according to the different authors as considered in the analysis.

PUBLICATION 3

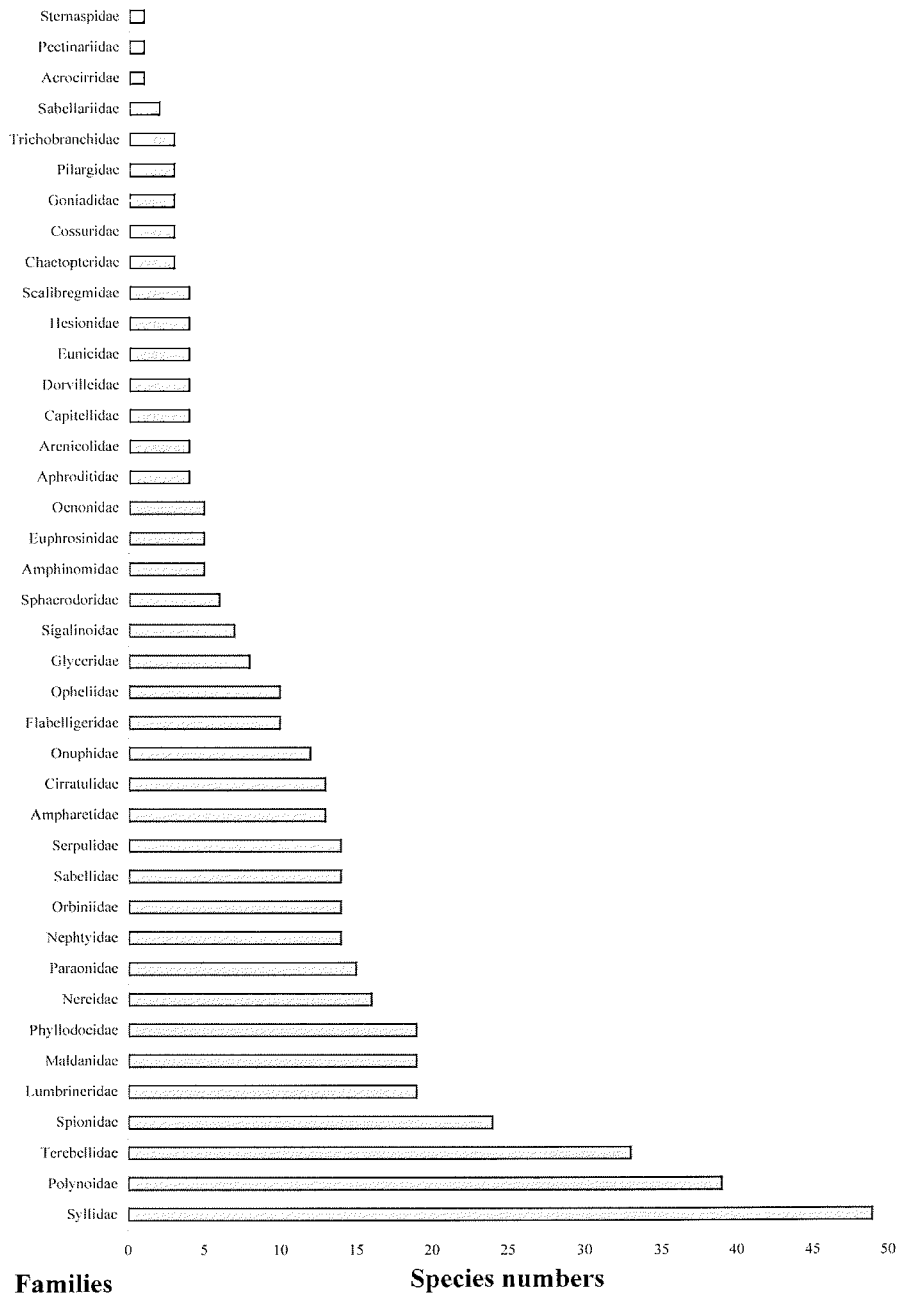


Figure 2. Total species number per polychaete family obtained from the study (n = 431)

PUBLICATION 3

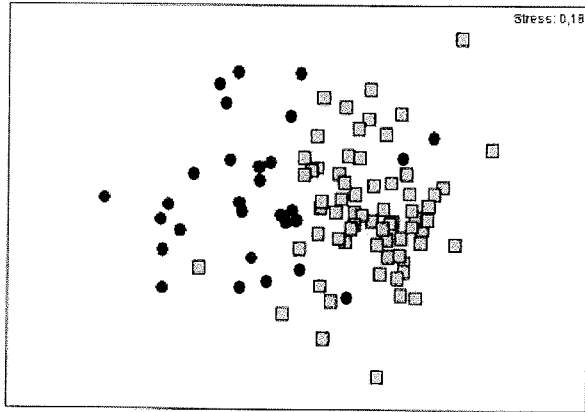


Figure 3. MDS ordination plot for the CAHO (circle) and FKLD (squares) entities.

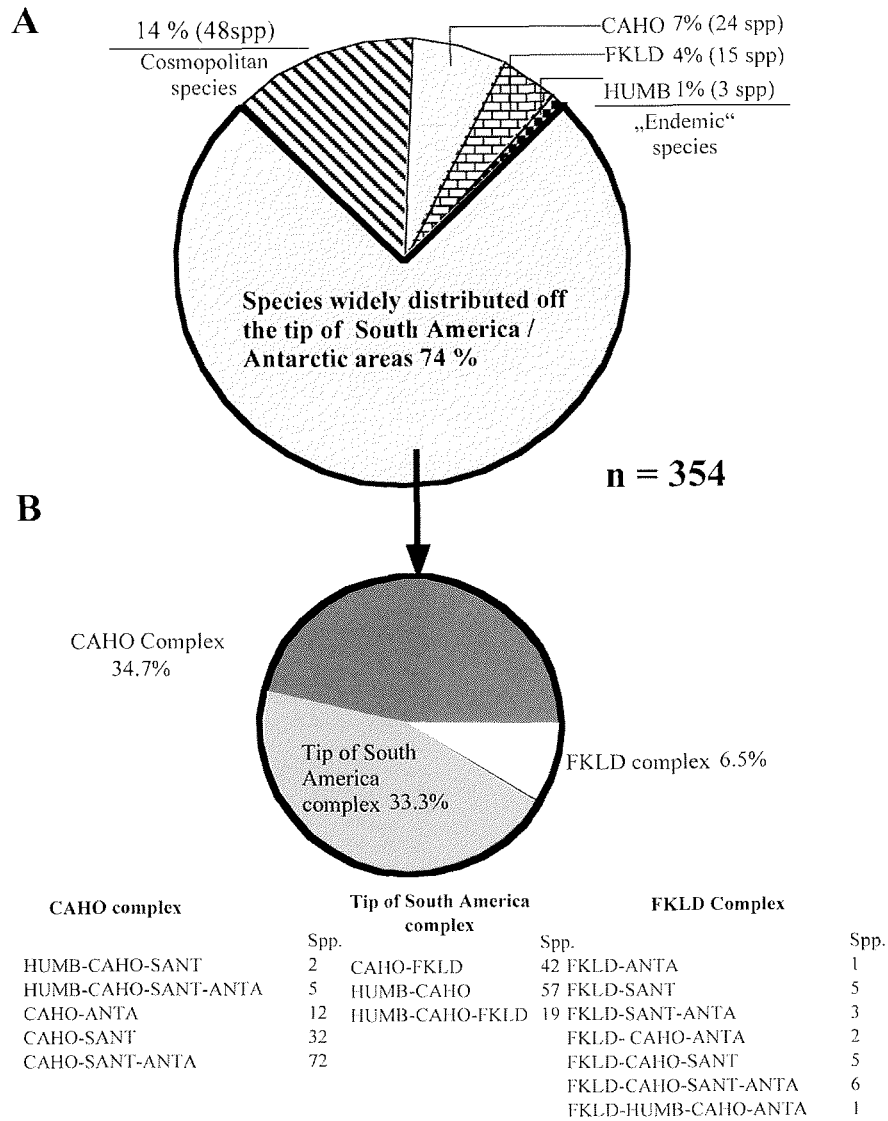


Figure 4. Graph A shows the percentage of polychaete species numbers in different entities of the Magellan region and the percentage of arbitrary group of species widely distributed off the South America and in the Antarctic, B shows further subdivisions of the arbitrary species group and absolute species number of each arbitrary subdivision.

7 Taxonomy

Aricidea pisanoi (Annelida: Polychaeta), a new species of
 Paraonidae from the southernmost waters of South America
 (Chile)

Américo Montiel*[†] and Brigitte Hilbig[†]

*Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile.

Present address: Alfred Wegener Institute for Polar and Marine Research; Bremerhaven, Germany.

[†]Ruhr University Bochum, Bochum, Germany.

[†]Corresponding author, e-mail: amontiel@awi-bremerhaven.de

Aricidea (Allia) pisanoi sp. nov. (Annelida: Polychaeta), is described from southern Chile. The new species was recorded from the Strait of Magellan (52°S) south to the continental slope of the Drake Passage (56°S). This new species is distinguishable from other species of the subgenus by only having capillary setae on postbranchial segments.

INTRODUCTION

The family was recognized by Mesnil & Caullery (1898); the currently used family was first introduced by Cerruti (1909). The genus *Aricidea* has been defined by the single antenna and a terminal sensory organ and the subgenus *Allia* differed by the capillary neurosetae of postbranchial parapodia being markedly thicker than the capillary notosetae (Strelzov, 1973). Recently, Rouse & Pleijel (2001) included the family Paraonidae to belong to clade Scolecida. World wide paraonids includes 87 known species while in Chilean waters 16 species are known (Rozbaczylo, 1985; Montiel et al., 2002).

The Paraonidae Cerruti, 1909, include polychaetes of small size mostly between 2 and 3 mm length and 0.1 to 2 mm width. The body is usually slender, divided into three regions (cephalic, branchial and postbranchial) (Strelzov, 1973). Parapodia are biramous include capillaries, hooks, or otherwise modified setae. The prostomium is simple, subconical with an occipital single antenna present or absent. The typical habitat of this infaunal species is mud and/or sand. They belong to deposit feeders and feed on meiofauna or meioflora (Levin et al., 1999). They are distributed from the Arctic to the Antarctic and in almost all deep-water regions of the world and only a few species are found in intertidal areas (Hartley, 1984; Rouse & Pleijel, 2001).

MATERIALS AND METHODS

The specimens of *A. (Allia) pisanoi* have been collected in the Magellan region (Chile) with a multibox corer (Gerdes, 1990) during the 'Joint Chilean-German-Italian Magellan Victor Hensen Campaign' in 1994 (Arntz & Gorny, 1996) and during the expedition 'ANT XIII/4' aboard RV 'Polarstern' in 1996 (Fahrbach & Gerdes, 1997). The three sampled areas included the Strait of Magellan, the Beagle Channel, and the continental shelf and slope south off Tierra del Fuego.

A total of 59 specimens were collected. The holotype is deposited in the 'Sala de Sistemática de la Pontificia Universidad Católica de Chile', Santiago, Chile (SSUC) and a paratype in the Zoologisches Institut der Universität Hamburg, Germany (ZMH).

SYSTEMATICS

Family PARAONIDAE

Genus *Aricidea* Wedster, 1879

Subgenus *Allia* Strelzov, 1973

Aricidea (Allia) pisanoi sp. nov.

(Figure 1A–D)

Type material and distribution

Holotype: 12.0 mm long, 0.5 mm wide. Type locality Drake Passage (55°44.7'S 66°15'W), depth 382 m, Station no. 109. Collection code SSUC-6.900.

Paratype: 4.0 mm long, 0.5 mm wide. Strait of Magellan, Laredo Bay (52°58.4'S 70°47.2'W), depth 14 m, Station no. 807. Collection code ZMH-24393.

Description

Complete specimen, 12 mm long and 0.5 mm wide. Orbinideform with 85 segments and 15 branchiae. Body anteriorly inflated, posteriorly cylindrical.

Prostomium triangular, as wide as long, nuchal organs gently curved, antenna fastened to the mid-dorsal surface of prostomium, conical, with numerous ciliates extending to the third segment (Figure 1A). On the ventral side, posterior lip of mouth on second segment, eyes absent.

Setae of prebranchial and branchial segments in dense fascicles (Figure 1A). Setae of two kinds: one limbate, thick, tapering abruptly to fine tip, strongly curved; the other slender capillary, longer than limbates, beginning at fourth segment; setae arranged in three vertical rows on each parapodium (Figure 1A). Postbranchial noto- and neurosetae all capillary, neurosetae very long, modified setae absent (Figure 1B).

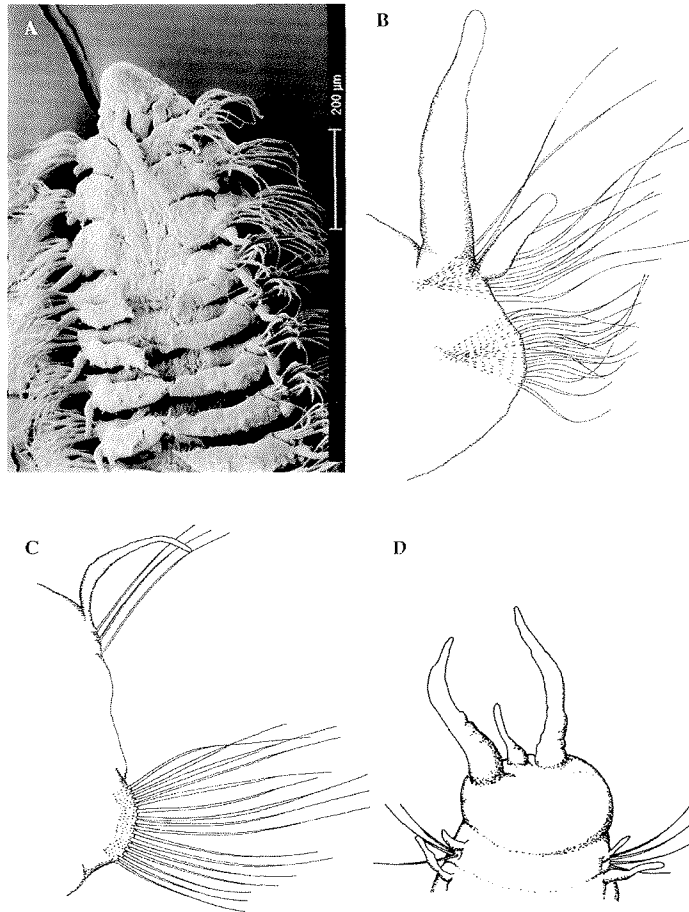


Figure 1. *Aricidea (Allia) pisanoi* sp. nov. Scanning electronic microscopy (SEM) micrograph of (A) the prostomium, prebranchial and branchial area, dorsal view; (B) branchial setiger; (C) post-branchial setiger; and (D) pigidium.

Branchiae on segments 4 to 19 digitiform and distally blunt tipped. Longest branchiae half as long as segmental width. First and second dorsal podial lobe tubercle-shaped, others cirriform and becoming thinner but the same length as on the postbranchial segments. Length of dorsal podial lobes on third segment and on large part of branchial segments equal to approximately half length of branchiae. Ventral podial lobes absent (Figure 1C). Anal segment dorsally truncate at almost right angle with two long lateral pygidial cirri (Figure 1D).

Remarks

Of the 16 species of Paraonidae known to occur in Chilean waters three species belong to *Cirrophorus*, two to *Levinsenia* and 11 to *Aricidea*. The subgenus *Allia* is represented by five species: *A. antarctica* Hartmann-Schröder & Rosenfeldt, 1988, *A. albatrossae* Pettibone, 1957, *A. quadrilobata* Webster & Benedict, 1887, *A. suecica* Eliason, 1920 and *A. ramosa* Annenkova, 1934.

Aricidea (Allia) pisanoi is distinguishable from another *Allia* species that occur in Chilean waters by the length of the antennae that arise at the third segment, being longer than in the case of *Aricidea (Allia) antarctica*, *Aricidea (Allia) albatrossae* and *Aricidea (Allia) ramosa* and shorter than *Aricidea (Allia) quadrilobata* and *Aricidea (Allia) suecica*. The key difference between *A. pisanoi* and *A. quadrilobata*, *A. suecica*, *A. ramosa* and *A. albatrossae* is the absence of the neuropodial lobes and the presence of only capillary setae in the post-branchial segment.

In the case of *Aricidea (Allia) antarctica*, *Aricidea (Allia) pisanoi* can be distinguished by the absence of eyes and the shape of the brachiae, which in *A. antarctica* are foliaceous and shorter than *A. pisanoi*'s brachiae.

Aricidea (Allia) pisanoi resembles *A. (Allia) suecica sensu* Hartley, 1984. However, both species differ by the shape of and number of branchiae: cirriform and with a maximum of 30 pairs; and digitiform and with a maximum of 24 pairs in *A. suecica* and *A. pisanoi* respectively.

PUBLICATION 4

A new species of paraonids A. Montiel and B. Hilbig 45

Table 1. Station list and meristic counts for *Aricidea* (*Allia*) *pisanoi*.

Station No.	Longitude S	Latitude W	Depth (m)	No. specimens	Length (mm)	Width (mm)	No. segments	No. branchiae
807	52°58.4'	70°47.2'	14	7	3.0–10.0	0.5	37–83	15–18
811	52°58.4'	70°42.2'	122	10	3.0–10.0	0.4–0.5	26–89	10–18
928	52°57.8'	70°25.6'	44	5	4.0–13.0	0.5	26–70	20–24
953	52°59.8'	70°33.0'	80	26	3.0–11.0	0.4–0.5	14–69	10–20
961	52°57.9'	70°43.5'	38	1	4.0	0.5	42	15
108	55°44.1'	66°16.7'	202	3	0.8–4.0	0.4–0.5	30–52	15
109	55°44.7'	66°15.3'	382	4	4.0–12.0	0.5	45–85	15
111	55°28.8'	66°04.4'	1162	3	5.0–7.0	0.5	40–67	15

The major difference between *A. (Allia) ramosa* and *A. (Allia) pisanoi* is the protomial antenna, which in the case of *A. pisanoi* has a fusiform antenna, and *A. ramosa* has a branched antenna.

The prostomium of *Aricidea (Allia) albatrossae* and *Aricidea (Allia) pisanoi* appears similar, but can be separated on the basis of branchial shape and the size of the antenna.

Aricidea (Allia) quadrilobata is bigger (up to 2.1 mm width) than *A. (Allia) pisanoi* (up to 0.5 mm width, e.g. in Table 1). The protomial antenna in *A. quadrilobata* is elongated until segment 9 and ventral podial lobe are present. They are rounded in anterior segment, becoming elliptical posteriorly up to cirriform (Strelzov, 1973).

Aricidea (Allia) pisanoi inhabits gravely to muddy bottoms with varying salinity from 31 to 33 psu. Like many other paraonid species, *A. (Allia) pisanoi* was found to be of eurybathial distribution (14 to 1162 m depth) in southern Chile.

We thank Professor Dr h.c.W. Arntz and Dr D. Gerdes, Alfred Wegener Institute for Polar and Marine Research, Germany (AWI), for providing the biological material. Mrs K. Beyer kindly helped with the SEM micrographs and Dr S. Thatje (AWI) for comments on the manuscript. Financial support was provided by the International Bureau of the BMBF, project no. CHL CIAIA and CEQUA of the University of Magellan, and by a DAAD grant no. PKZ A/00/10932.

REFERENCES

Arntz, W. & Gorny, M., 1996. Cruise report of the Joint "Chilean-German-Italian Victor Hensen" Campaign in 1994. *Berichte zur Polarforschung*, **190**, 1–113.

Cerruti, A., 1909. Contributo All'anatomia, biologia e sistematica delle Paraonidae (Levinseniidae) con particolare riguardo alle specie del golfo di Napoli. *Mitteilungen aus der Zoologischen Station zu Neapel*, **19**, 459–512.

Fahrbach, E. & Gerdes, D., 1997. Die Expedition ANTARKTIS XIII/4-3 des Forschungsschiffes "Polarstern" 1996. *Berichte zur Polarforschung*, **239**, 1–126.

Gerdes, D., 1990. Antarctic trials of the multi-box corer, a new device for benthos sampling. *Polar Records*, **26**, 35–38.

Hartley, J.P., 1984. Cosmopolitan polychaete species: the status of *Aricidea belgicae* (Fauvel, 1936) and note on the identity of *A. suecica* Eliason, 1920 (Polycheta; Paraonidae). In *Proceedings of the First International Polychaete Conference, Sydney, Australia, July 1983* (ed. P.A. Hutchings), pp.7–20. Sydney, Australia: Linnecan Society of New South Wales.

Levin, L.A., Blair, N.E., Martin, C.M., Demaster, D.J., Plaia, G. & Thomas, C.J., 1999. Macrofauna processing of phytodetritus at two sites on the Carolina margin: *in situ* experiment using super (13)C-labeled diatoms. *Marine Ecological Progress Series*, **182**, 37–54.

Montiel, A., Hilbig, B. & Rozbaczylo, N., 2002. New records to Chile of the family Paraonidae (Annelida: Polychaeta). *Helgoland Marine Research*, **56**, 134–139.

Rouse, G. & Pleijel, F., 2001. *Polychaetes*. Oxford: Oxford University Press.

Strelzov, V.E., 1973. *Polychaete worms of the family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria)*. Akad. Nauk SSSR, Leningrad: Amerind Publishing. [English translation published in 1979 by Smithsonian Institution.]

Submitted 10 January 2003. Accepted 5 September 2003.

Américo Montiel · Brigitte Hilbig
 Nicolás Rozbaczylo

New records to Chile of the Family Paraonidae (Annelida: Polychaeta)

Received: 13 March 2001 / Revised: 12 February 2001 / Accepted: 13 February 2002 / Published online: 23 May 2002
 © Springer-Verlag and AWI 2002

Abstract The Paraonidae are a polychaete family of small body size which have not been reported for Chile until recently. Mainly due to improved sample-processing methods, research campaigns carried out in 1994 and 1996 on three areas off southern Chile have yielded numerous records. Several species proved to be new to the Chilean polychaete fauna, including species that have been known previously only from Antarctic areas. These new records and range extensions are reported in this paper.

Keywords Polychaeta · Paraonidae · New records · Chile

Introduction

The Paraonidae of Chile have only very recently been reported; Rozbaczylo (1985) listed six species in three genera, recorded for Chile between 1965 and 1978. Maurer and Williams (1988) and Mariani et al. (1996) provided a few additional records of paraonids sampled off the Chilean coast, but they did not provide exact data on the collection sites. Recent analyses of benthic corer samples taken between 1994 and 1996 in three areas off southern Chile have yielded numerous paraonids, including several species that have been reported from adjacent

areas along the Chilean coast and Antarctica but not for the Magellan area, and some species that, until now, have not been found off Chile at all. The new records for Chile and range extensions of some additional species are presented here. The systematics follow Strelzov (1973) and Hartley (1981, 1984).

Methods

The specimens were collected in the Magellan Region with a Reineck corer (Reineck 1958) and multibox corer (Gerdes 1990), respectively, during the Joint Chilean–German–Italian campaign of RV Victor Hensen in 1994 (Arntz and Gorny 1996), expedition ANT XIII/4 of RV Polarstern in 1996 (Fahrbach and Gerdes 1997), and the Chilean expedition aboard AGOR Vidal Gormaz (Mutschke et al. 1996). The three areas sampled included the Strait of Magellan and Beagle Channel, the channels and fiords off the South Patagonian Icefield, and the continental shelf and slope south of Tierra del Fuego (Table 1, Fig. 1).

Results

Aricidea (Allia) albatrossae Pettibone, 1957

Sta. PS 108a (1), Sta. PS 108b (1).

Both specimens incomplete, 6.0 and 13.0 mm long, respectively, both 0.5 mm wide and consisting of 66 and 78 segments, respectively (Fig. 2a–b). Branchiae 19 pairs, not meeting along dorsomedian line of body; modified setae present from setiger 37 onwards.

Previous records for Chile: none.

Previous records for the Magellan Region: none.

Distribution outside of Chile: northwest Atlantic: Massachusetts to Chesapeake Bay (Pettibone 1957); South Africa (Day 1963, as *Aedicira belgicae*); northeast Atlantic: Great Britain (Hartley 1984); Pacific: Caroline Islands.

This new record of *A. albatrossae* for the southern hemisphere may reopen the discussion about the possible synonymy of *A. albatrossae* and *Paraonis belgicae* Fauvel, 1936, a species described from Antarctica. Monro (1939) redescribed the species and referred it to *Aricidea* based on three specimens from Antarctica, which

Communicated by H.-D. Franke

A. Montiel (✉)
 Instituto de la Patagonia, Universidad de Magallanes,
 Casilla 113-D, Punta Arenas, Chile
 e-mail: amontiel@awi-bremerhaven.de
 Tel.: +49-471-48311712

A. Montiel
 Alfred Wegener Institute for Polar and Marine Research,
 Columbusstrasse 27568, Bremerhaven, Germany

B. Hilbig
 Zoologisches Institut und Zoologisches Museum,
 Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

N. Rozbaczylo
 Departamento de Ecología, Facultad de Ciencias Biológicas,
 P. Universidad Católica de Chile, Santiago, Chile

Fig. 1 Study area and stations sampled

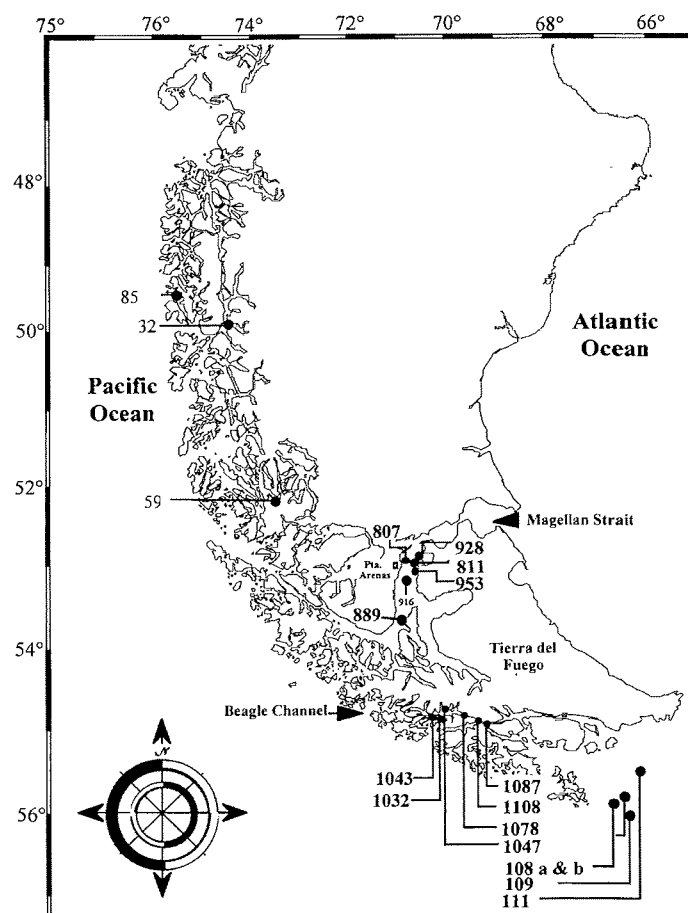


Table 1 List of stations from which new records or range extensions of Paraonidae are reported. VG: Vidal Gormaz, VH: Victor Hensen, PS: Polarstern. ND = no data

Cruise, Station	Location	Position	Depth(m)	Sediment
VG 32	South Patagonian Icefield, Seno Penguin	49°54.3'S, 74°18.6'W	711	ND
VG 59	South Patagonian Icefield, Canal Kirke	52°10.3'S, 73°21.7'W	238	ND
VG 85	South Patagonian Icefield, Canal Picton	49°28.9'S, 75°25.2'W	98	ND
VH 807	Strait of Magellan, Laredo	52°57.9'S, 70°47.2'W	14	ND
VH 811	Strait of Magellan, Laredo	52°58.4'S, 70°42.2'W	122	ND
VH 889	Strait of Magellan, Bahía Voces	53°42.7'S, 70°57.3'W	114	ND
VH 916	Strait of Magellan, off Punta Arenas	53°10.2'S, 70°52.3'W	26	Sand and shell hash
VH 928	Strait of Magellan, Laredo	52°57.8'S, 70°25.6'W	44	Sand and gravel
VH 953	Strait of Magellan, Paso Ancho	52°59.8'S, 70°33.0'W	80	Sand and gravel
VH 1032	Beagle Channel, Garibaldi	54°52.7'S, 69°54.5'W	330	Sand and gravel
VH 1043	Beagle Channel, Garibaldi	54°51.9'S, 69°55.2'W	216	Sand and gravel
VH 1047	Beagle Channel, Garibaldi	54°50.1'S, 69°56.6'W	101	Sand and gravel
VH 1078	Beagle Channel, Romanche	54°53.5'S, 69°31.0'W	348	silt and sand
VH 1087	Beagle Channel, Francia	54°55.3'S, 69°19.7'W	169	Sand and silt
VH 1108	Beagle Channel, Francia	54°55.0'S, 69°19.5'W	100	Sand and gravel
PS 108a	Continental shelf off Tierra del Fuego	55°44.1'S, 66°16.7'W	202	ND
PS 108b	Continental shelf off Tierra del Fuego	55°44.1'S, 66°16.7'W	204	ND
PS 109	Continental shelf off Tierra del Fuego	55°44.7'S, 66°15.3'W	382	ND
PS 111	Continental slope off Tierra del Fuego	55°28.8'S, 66°04.4'W	1162	ND

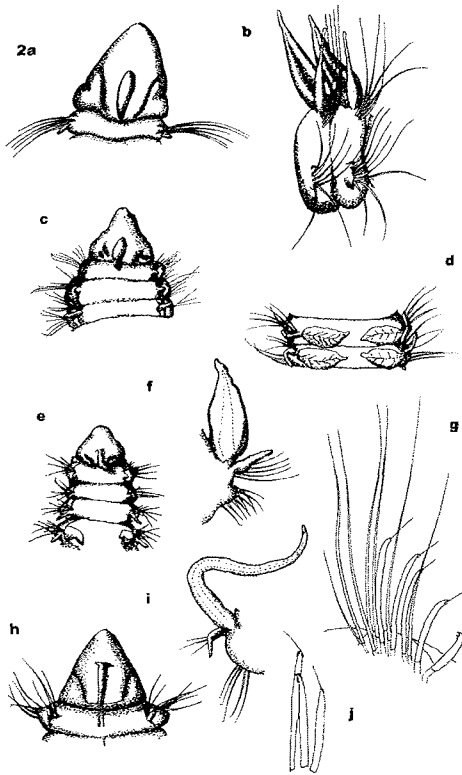


Fig. 2 a–b *Aricidea albatrossae*: a anterior end, dorsal view; b branchial segments, lateral view; c–d *Aricidea antarctica* (after Hartmann-Schröder and Rosenfeldt 1988): c anterior end, dorsal view; d branchial segments, dorsal view; e–g *Aricidea catherinae* (after Strelzov 1973): e anterior end, dorsal view; f branchial segments, lateral view; g neupodium with modified setae, view from above; h–j *Aricidea finitima* (after Strelzov 1973): h anterior end, dorsal view; i branchiferous parapodium, posterior view; j modified setae

were later determined by Hartley (1984) to re-present two species. In that same paper, Hartley (1984) redescribed the type of *P. belgicae* and returned the species to its original genus, although he indicated that further revision might result in a different generic assignment. The occurrence of *A. albatrossae* in the Magellan region may strengthen Hartman's (1959, 1965) position that *A. albatrossae* Pettibone and *P. belgicae* Fauvel are the same species.

Aricidea (Allia) antarctica
Hartmann-Schröder & Rosenfeldt, 1988

Sta. PS 111 (1)

Single specimen incomplete, 3.0 mm long, 0.5 mm wide and with 40 setigers (Fig. 2c–d). Branchiae of similar length throughout, with wide base and acute tip, 10 pairs. Modified setae of similar thickness to other neuro-

setae but shorter, more strongly bent, and tapering to very fine, hairlike tip, beginning on setiger 22. Specimen ovigerous; eggs large, two per segment, of creamy color, filling body cavity from segment 25.

Previous records for Chile: none.

Previous records for the Magellan Region: none.

Distribution outside of Chile: Antarctic: Bransfield Strait (type locality), Elephant Island.

Aricidea antarctica has not been reported in the literature since its original description, but is likely to have a wider Antarctic distribution (B. Hilbig, unpublished data). The single specimen found just south of Tierra del Fuego indicates that the northern boundary of this species lies outside of Antarctica.

Aricidea (Acmira) catherinae Laubier, 1967

Sta. VH 916 (2), Sta. VH 953 (1), Sta. VH 1047 (7), Sta. VH 1087 (3), Sta. VH 1108 (4).

All specimens incomplete, 3.5–10.0 mm long, 0.3–0.6 mm wide; segment numbers varied between 38 and 68 (Fig. 2c–g). Antenna reaching back to segment 3–5 where present. Twelve to 18 pairs of branchiae; modified setae first present on setiger 20, occasionally not until setiger 28–32.

Previous records for Chile: none.

Previous records for the Magellan Region: none.

Distribution outside of Chile: Arctic: Kurile Islands, Barents Sea (Strelzov 1968, as *Aricidea zelenzovi*); northeast Atlantic: Gulf of St. Lawrence to Chesapeake Bay (Pettibone 1963, as *Aricidea jeffreysii*); Uruguay; northeast Pacific: California; Mediterranean Sea (type locality) (Laubier 1967).

The specimens found in the Strait of Magellan and Beagle Channel are the first recorded from the southern hemisphere. *Aricidea catherinae* may have a much wider southern distribution, which may have remained undetected because one of the most important diagnostic characters for this species, the antenna, easily breaks off if specimens are not handled carefully during sample processing.

Aricidea (Acmira) finitima Strelzov, 1973

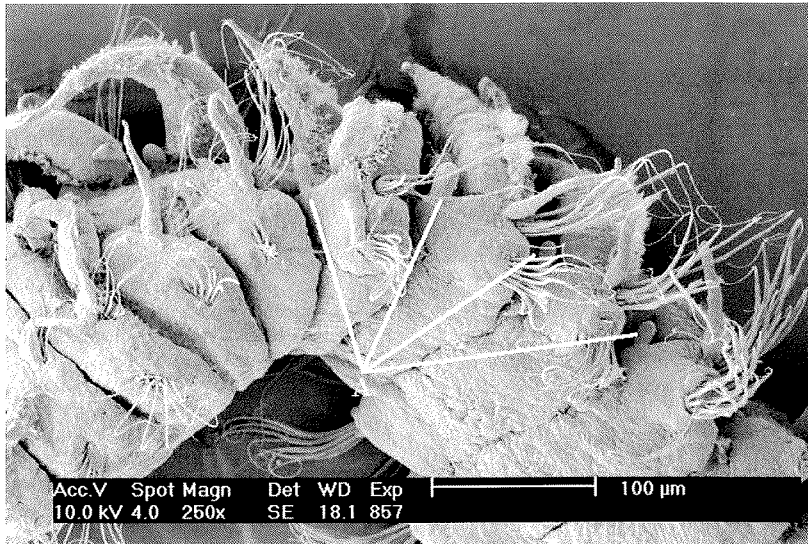
Sta. VH 807 (5), Sta. VH 820 (1), Sta. VH 928 (1), Sta. VH 953 (1).

All specimens incomplete, 1.5–6.0 mm long, 0.15–0.4 mm wide, the largest has 45 segments (Fig. 2h–j, Fig. 3). Branchiae 8–15 pairs, increasing in length from anterior to posterior, last two pairs much shorter than preceding ones. Modified setae first present from setiger 23–27, terminal spine not observed. Up to four pairs of dorsal papillae, located posterior to dorsal postsctal lobes, present between setigers 11 and 15. One specimen with eggs from segment 10.

Previous records for Chile: none.

Previous records for the Magellan Region: none.

Fig. 3 *Aricidea finitima*, scanning electron microscopy photograph of branchiferous setigers bearing dorsal papillae (A)



Distribution outside of Chile: eastern Pacific: California (Hartman 1957, as *Aricidea neosuecica*); western Pacific: Japan; western Atlantic: Uruguay; South Africa (Day 1963, as *Aricidea longobranchiata*); Antarctica: Scotia Sea (type locality).

This species may have a wide distribution but may never be abundant, which may account for its scattered occurrence. Moreover, the morphological feature that is the most characteristic for *A. finitima*, the papillae behind the dorsal postsetal lobes, can only be detected by careful examination of the specimens under a microscope and may have been overlooked in the past. The sea off the South Patagonian Icefield is fairly close to the type locality so that additional records can be expected from this area.

Aricidea (Allia) ramosa Annenkova, 1934

Sta. VG 32 (1), Sta. VG 59 (1), Sta. VH 889 (1), Sta. VH 1078 (6), Sta. VH 1087 (3), Sta. PS 108a (1).

Single complete specimen 4.0 mm long, 0.5 mm wide with 58 segments, other specimens incomplete, 3.0–12.0 mm long, 0.4–0.9 mm wide; segments numbers varied between 27 and 100 (Fig. 4a–c). Antenna with 3–13 terminal branches; 13–20 pairs of branchiae present; modified setae starting on setiger 35.

Previous records for Chile: questionably Maurer and Williams (1988, as *Aedicira* nr. *ramosa*),

Previous records for the Magellan Region: see above,

Distribution outside of Chile: Arctic: Gulf of Peter the Great, Bering Island (type locality) (Annenkova 1934); western Pacific: Japan (Annenkova 1937); eastern Pacific: Washington to California (Hartman 1957; Banse

and Hobson 1968); possibly (?) Peru and Ecuador (Maurer and Williams 1988).

The occurrence of *A. ramosa* on the continental shelf south of Tierra del Fuego represents a range extension of this species to the south, and a bipolar distribution is here established for this species. If *Aedicira* nr. *ramosa sensu* Maurer and Williams (1988) is a different species, the present records are the first for the southern hemisphere.

Aricidea (Acmira) strelzovi

Hartmann-Schröder & Rosenfeldt, 1990

Sta. VG 85 (2), Sta. VG 93 (2), Sta. VH 807 (112), Sta. VH 811 (32), Sta. VH 916 (11), Sta. VH 953 (1), Sta. PS 109 (2).

Complete specimens about 4.0–13.0 mm long (coiled), 0.2–0.5 mm wide; segments numbers varied between 68 and 141 (Fig. 4d–f). Branchiae 13–15 pairs, occasionally 17 pairs, continuously lengthening from anterior to posterior segments, last few pairs with long slender tips. Modified setae first present on setigers 20–29, conspicuous, with short arista. Many specimens with dorsolateral brown pigment spots and sometimes also with narrow segmental bands.

Previous records for Chile: none.

Previous records for the Magellan Region: none.

Distribution outside of Chile: Antarctica: Elephant Island (type locality).

There are no records in the literature of this species except for the original description, and the specimens collected off the South Patagonian Icefield and the Strait of Magellan represent a range extension for *A. strelzovi* into waters north of the Antarctic Convergence.

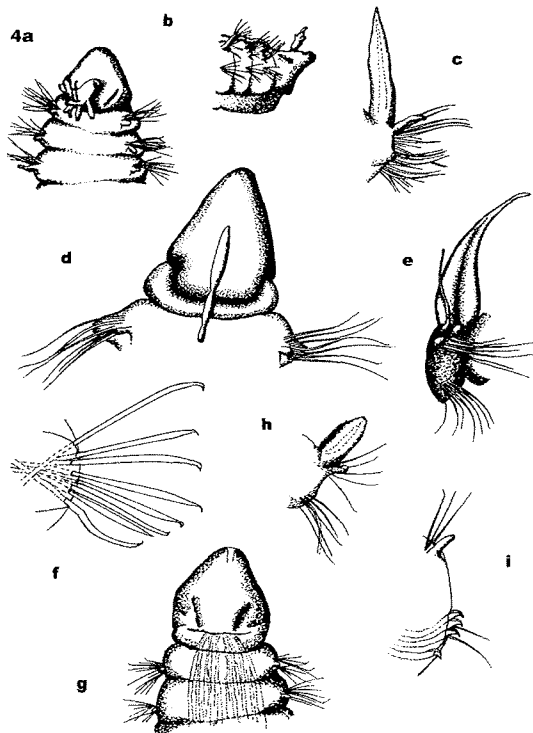


Fig. 4 a–c *Aricidea ramosa* (after Strelzov 1973): a anterior end, dorsal view; b lateral view; c branchiferous parapodium, posterior view; d–f *Aricidea strelzovi*: d anterior end, dorsal view; e branchial segment, lateral view; f fascicle of modified setae, lateral view; g–i *Levinsenia antarctica* (after Strelzov 1973): g anterior end, dorsal view; h branchial segment, posterior view; i posterior segment with modified setae

Levinsenia antarctica (Strelzov, 1973)

Sta. VH 1032 (1), Sta. VH 1043 (1), Sta. VH 1047 (4), Sta. VH 1078 (9), Sta. VH 1087 (5), Sta. PS 111 (2).

All specimens incomplete, 3–18 mm long, 0.15–0.3 mm wide, the largest has 99 setigers and the smallest has 32 setigers (Fig. 4g–i). Branchiae about twice as long as wide, starting on setiger 7 or 8, 3–5 pairs.

Previous records for Chile: none.

Previous records for the Magellan Region: none.

Distribution outside of Chile: Antarctica: Kemp coast (type locality) (Strelzov 1973); Weddell Sea, King George Island (B. Hilbig, unpublished data).

This species may have a more northerly distribution outside of Antarctic waters; but because of its small size, it may not have been sampled in the past or may have remained undetermined.

Discussion

The main taxonomical information for the Magellan region is based on often inadequately treated qualitative or quantitative samples which generally did not cover the whole size range of polychaetes.

The number of recorded from Chilean shelf areas has increased in the recent years because exploration has increased in this area (Bremec et al. 2000; Arntz and Ríos 1999), and fine mesh screens (0.5 or 0.3 mm) were used (Blake 1996).

Seven genera are currently accepted: *Sabidius*, *Paraonis*, *Paraonella*, *Paradoneis*, *Levinsenia*, *Cirrophorus*, and *Aricidea*, with four subgenera (Blake 1996). The last three genera from the Southwest Pacific and six species from the Chilean coast have been recorded by Rozbaczylo (1985). Including those records, the number of paraonid species described from Chilean waters increased to 17. The occurrence of two species of *Aricidea* and one species of *Levinsenia* which were only known from the Antarctic until now may point to faunistic affinities between Antarctica and the Magellan region.

Our results suggest that the influence of intensified sampling and finer sieves, rather than ecological changes, increased the reported species number in these areas.

Acknowledgements We thank Prof. Dr. Wolf Arntz and Dr. Dieter Gerdes, Alfred Wegener Institute for Polar and Marine Research, Germany, for providing the biological material and critical reading of the manuscript, respectively. Thanks also to Kerstin Beyer for help with the REM micrographs. This study was in part supported by the International Bureau of BMBF, Germany, project number CHLC1A1A.

References

- Annenkova NP (1934) Paraonidae of the far-eastern seas of the USSR. Dokl Akad Nauk SSSR 3:8–9
- Annenkova NP (1937) Polychaete fauna of the northern part of the Japan Sea. Issled Morei SSSR 23:139–216
- Arntz WE, Gorny M (eds) (1996) Cruise report of the joint Chilean–German–Italian Magellan “Victor Hensen” campaign in 1994. Ber Polarforsch 190
- Arntz WE, Ríos C (1999) Magellan–Antarctic: ecosystems that drifted apart. Sci Mar 63 [Suppl 1]
- Bansic K, Hobson KD (1968) Benthic polychaetes from Puget Sound, Washington, with remarks on four other species. Proc US Natl Mus 125:1–53
- Blake J (1996) Family Paraonidae Cerruti, 1909. In Blake J, Hilbig B, Scott P (eds) Taxonomic atlas of the benthic fauna of the Santa Maria basin and western Santa Barbara channel, vol 6. Santa Barbara Museum of Natural History, Santa Barbara, Calif. pp 27–66
- Bremec C, Elias R, Gambi C (2000) Comparison of the polychaete fauna composition from the Patagonian shelf and the Strait of Magellan. Preliminary results from cruises Shinkai Maru IV, V, X and XI (1978–1979) and second Italian oceanographic cruise (1991). Bull Mar Sci 67(1):189–197
- Day JH (1963) Polychaete fauna of South Africa. Part 7. Species from depths between 1.000 and 3.330 metres, west of Cape Town. Ann South African Mus 46:353–371
- Fahrbach E, Gerdes D (1997) The Expedition ANTARKTIS XII(4-5) of the Research Vessel Polarstern in 1996. (Reports on Polar Research 239) Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany

- Gerdes D (1990) Antarctic trials of the multi-box corer, a new device for benthos sampling. *Polar Rec* 26:35–38
- Hartley JP (1981) The family Paraonidae (Polychaeta) in British waters: a new species and new records with a key to species. *J Mar Biol Assoc UK* 61:133–149
- Hartley JP (1984) Cosmopolitan polychaete species: the status of *Aricidea belgicae* (Fauvel, 1936) and notes on the identity of *A. suecica* Eliason, 1920 (Polychaeta; Paraonidae). In: Hutchings PA (ed) Proceedings of the first international polychaete conference, Sydney, Australia, July 1983. The Linnean Society of New South Wales, Sydney, pp 7–20
- Hartman O (1957) Orbiniidae, Apistobranchidae, Paraonidae and Longosomidae. *Allan Hancock Pac Exped Publ* 15:211–393
- Hartman O (1959) Catalogue of the polychaetous annelids of the world. (Occasional paper of the Allan Hancock Foundation 23) Allan Hancock Foundation Publications, University of Southern California, Los Angeles
- Hartman O (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. (Occasional paper of the Allan Hancock Foundation 28) Allan Hancock Foundation Publications, University of Southern California, Los Angeles
- Hartmann-Schröder G, Rosenfeldt P (1988) Die Polychaeten der "Polarstern"-Reise ANT III/2 in die Antarktis 1984. Teil 1: Euphrosinidae bis Chaetopteridae. *Mitt Hamb Zool Mus Inst* 85:25–72
- Laubier L (1967) Sur quelques Aricidea (Polychètes, Paraonidae) de Banyuls-sur-Mer. *Vie Milieu Ser A* 18:99–132
- Mariani S, Gambi M, Lorenti M, Mazzella L (1996) Benthic population of the soft bottoms in the Strait of Magellan (South America): biodiversity, distribution and biogeography of polychaeta and crustacean isopods. *Biol Mar Medit* 3(1):155–158
- Maurer D, Williams S (1988) Deep-sea polychaetous Annelida from central America to the Antarctic Peninsula and south Sandwich Islands. *Int Rev Ges Hydrobiol* 73:659–701
- Monro CCA (1939) Polychaeta. *Rep BANZ Antarct Res Exp (1929–1931) (B)* 4:89–156
- Mutschke E, Ríos C, Hromic T, Gorny M, Montiel A, Rauschert M, Gerdes D (1996) Estudios bentónicos en fiordos y canales de los Campos de Hielo sur (450–530S). *Result Crucero CIMAR-FIORDO 2*: 91–98
- Pettibone M (1957) A new polychaetous annelid of the family Paraonidae from the North Atlantic. *J Wash Acad Sci* 47:354–356
- Pettibone M (1963) Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *Bull Smithsonian Inst US Nat Hist Mus* 227:1–356
- Reineck HE (1958) Kastengreifer und Lotröhre "Schnepfe", Geräte zur Entnahme ungestörter, orientierter Meeresgrundproben. *Senckenb Lethaea* 39:42–48, 54–56
- Rozbaczylo N (1985) Los Anelidos Poliquetos de Chile. *Monogr Biol* 3:1–284
- Strelzov VE (1968) Polychaetous annelids of the family Paraonidae (Polychaeta, Sedentaria) of the Barents Sea (in Russian). *Tr Murmansk Morsk Biol Inst* 17(21)
- Strelzov VE (1973) Polychaete worms of the family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria). *Akad Nauk SSSR, Leningrad* (English translation published in 1979 by Smithsonian Institution)

8 Acknowledgement, appendix & references

8.1 Acknowledgements

Many people have been part of my scientific education, some as teachers, some as colleagues, and some as friends. I have to thank all of them but for some I would like to express my gratitude, because without their support and assistance this thesis could not be realized.

Thanks to Prof. Dr. W.E. Arntz (Alfred Wegener Institute for Polar and Marine Research, AWI) for never trying to change my way to make science, who just helped me to improve what had to be improved.

Thanks to Dr. D. Gerdes (AWI); my mentor and friend since 1995. Thank you very much for pushing me! He guided me patiently and helped me to find my way through the jungle of marine ecology.

Dr. B. Hilbig (Ruhr University Bochum) guided me and showed me the door to rigorous and systematic work in polychaete taxonomy, many thanks to you!

I further would like to thank Dr. habil. T. Brey (AWI) for his always helpful comments and corrections and

Dr. S. Thatje (AWI) for many discussions and corrections in manuscripts.

To Prof. Dr. A. Brandt (University Hamburg) many thanks for supporting me always in a positive manner.

I thank Dr. R. Knust and his "crew" I. Suck, K. Mintenbeck, E. Brodte, C. Hasemann for patience and many questions in German language, and for providing a nice neighbourhood in the Columbus Center. Special thanks to Dr. C. Orejas for many discussions and helpful comments on the manuscripts.

Not to forget many people who supported me from the very first beginning of my career as a young and unexperienced student during expeditions on board RVs 'Polarstern', 'Victor Hensen', and 'Vidal Gormaz': thanks to the crews!

I'm also grateful to K. Beyer for technical support with the REM photography and to the staff of the AWI-library.

Beside my "every day work" I met some colleagues creating my "treue Mensa Gemeinschaft": Drs J. Ragua, M. Cledon, J. Herjes and J. Velez.

My "Schnorchel-Gemeinschaft" tried on our Wednesday meetings to give me the feeling of a 'polychaete underwater', K. Barz S. Grabbert J. Laudien, M. Assmann thank you.

Personally I'm grateful to MSC. Ing. M. Pokorná, who walked together with me the last difficult year of my Ph. D. Many Thank also to Drs. Texido and E. Isla.

The way to science is a long way and I will not forget where everything started: many thanks to my teachers MSC. C. Ríos and Lic. E. Mutschke from the Universidad de Magallanes.

I gratefully acknowledge support of this work by DAAD grant No. A/00/10932 and the International Bureau of the BMBF, Germany (project no. CHL01/010) and the Centro de Investigación del Cuaternario de la Universidad de Magallanes, Chile.

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

8.2 Appendix 1. Station data of sampling locations. BC: Reineck box corer, MG: multibox corer, VG: Vidal Gormaz, VH: Victor Hensen, PS: Polarstern.

Code number	Cruise	Leg	Station	Gear	No of cores	Date	Location	Lat	Long	Depth (m)
1	VG	Leg b	95	BC	2	07.11.1996	B. San Quintín	46°48.85	74°26.9	20
2	VG	Leg b	94	BC	2	07.11.	Golfo de Penas	46°57.50	74°15.0	92
3	VG	Leg b	93	BC	2	07.11.	Golfo de Penas	47°22.20	74°38.7	130
4	VG	Leg b	90	BC	2	06.11.	C. Fallos	48°23.40	75°06.5	550
5	VG	Leg a	19	BC	2	20.10.	C. Messier	48°39.10	74°27.2	410
6	VG	Leg b	88	BC	2	.05.11	C. Ladrilleros	48°56.60	75°02.0	630
7	VG	Leg b	85	BC	2	04.11.	C. Pícton	49°28.90	75°25.2	98
8	VG	Leg a	25	BC	2	21.10.	C. Ice	49°33.60	74°12.4	538
9	VG	Leg a	32	BC	2	24.10.	Seno Penguin	49°54.29	74°18.6	711
10	VG	Leg a	42	BC	2	25.10.	C. Concepción	50°35.70	75°04.5	532
11	VG	Leg b	74	BC	2	.02.11	Estero Calvo	50°37.90	73°37.4	385
12	VG	Leg a	40	BC	2	.24.10	C. Concepción	50°9.55	74°42.1	323
13	VG	Leg a	47	BC	2	26.10.	Estrecho Nelson	51°35.00	74°31.0	615
14	VG	Leg b	57	BC	2	31.10.	E. las Montañas	51°49.00	73.19.4	136
15	VG	Leg a	53	BC	2	27.10.	S.Ult. Esperanza	51°54.30	72°33.7	32
16	VG	Leg b	59	BC	3	27.10.	C. Kirke	52°10.30	73°21.7	238
17	VG	Leg b	63	BC	2	31.10.	C. Smith	52°26.40	73°29.5	175
18	VG	Leg b	56	BC	2	30.10.	C. Kirke	52°5.66	73°07.5	136
19	VH	Leg 1	928	MG	6	28.10.1994	Magellan Straits	52°57.8	70°25.6	44
20	VH	Leg 1	961	MG	6	31.10.	Magellan Straits	52°57.9	70°43.5	38
21	VH	Leg 1	807	MG	6	18.10.	Magellan Straits	52°57.9	70°47.2	14
22	VH	Leg 1	811	MG	6	18.10.	Magellan Straits	52°58.4	70°42.2	119
23	VH	Leg 1	953	MG	8	31.10.	Magellan Straits	52°59.8	70°33.0	80
24	VH	Leg 1	820	MG	8	18.10.	Magellan Straits	53°02.5	70°17.1	8
25	VH	Leg 1	836	MG	8	23.10.	Magellan Straits	53°08.4	70°38.4	120
26	VH	Leg 1	916	MG	8	28.10.	Magellan Straits	53°10.2	70°52.3	26
27	VH	Leg 1	978	MG	8	01.11.	Magellan Straits	53°32.7	70°39.3	459
28	VH	Leg 1	867	MG	8	25.10.	Magellan Straits	53°40.7	70°54.6	445
29	VH	Leg 1	889	MG	5	26.10.	Magellan Straits	53°42.7	70°57.3	114
30	VH	Leg 2	1047	MG	4	04.11.	Beagle C	54°50.1	69°56.6	101
31	VH	Leg 2	1038	MG	6	04.11.	Beagle C	54°50.9	69°55.7	38
32	VH	Leg 2	1043	MG	4	04.11.	Beagle C	54°51.9	69°55.2	216
33	VH	Leg 2	1032	MG	8	04.11.	Beagle C	54°52.7	69°54.5	330
34	VH	Leg 2	1104	MG	7	06.11.	Beagle C	54°53.1	69°30.3	91
35	VH	Leg 2	1078	MG	8	05.11.	Beagle C	54°53.5	69°31.0	348
36	VH	Leg 2	1108	MG	6	06.11.	Beagle C	54°55.0	69°19.5	100
37	VH	Leg 2	1087	MG	8	05.11.	Beagle C	54°55.3	69°19.7	169
38	PS	XIII/4	110	MG	7	17.05.1996	Continental shelf	55°26.1	66°15.5	102
39	PS	XIII/4	111	MG	6	17.05.	Continental slope	55°28.8	66°04.4	1162
40	PS	XIII/4	108	MG	4	16.05.	Continental shelf	55°44.1	66°16.7	202
41	PS	XIII/4	108	MG	3	16.05.	Continental shelf	55°44.1	66°16.7	204

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

8.3 Appendix 2: List of species determined from the quantitative samples.

Terebellidae	<i>Artacama cf. crassa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20.8
Terebellidae	<i>Artacama proboscidea</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.6
Trichobranchidae	<i>Artacameia sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Euthelepus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Hauchiella sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Laphania sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Lysilla macintoshi</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Lysilla pacifica</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Neoleprea sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9
Terebellidae	<i>Pista cristata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Pista sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Polycirrus cf. kerguelensis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9
Terebellidae	<i>Polycirrus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	29.6	0.0	0.0
Terebellidae	<i>Proclea cf. graffi</i>	59.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	39.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Streblosoma nr. intestinalis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichobranchidae	<i>Terebellides stroemii kerguelensis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	29.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichobranchidae	<i>Trichobranchus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

8.3 Appendix 2: List of species determined from the quantitative samples.

Terebellidae	<i>Artacama cf. crassa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Artacama proboscidea</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichobranchiidae	<i>Artacamella sp</i>	20.8	20.8	0.0	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Euthelopus sp</i>	0.0	0.0	0.0	0.0	6.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Hauchiella sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.9
Terebellidae	<i>Laphania sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.9
Terebellidae	<i>Lysilla macintoshi</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.9
Terebellidae	<i>Lysilla pacifica</i>	0.0	0.0	0.0	0.0	13.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Neoleprea sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Pista cristata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Pista sp</i>	0.0	0.0	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.4	0.0	6.9
Terebellidae	<i>Polycirrus cf. kerguelensis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Polycirrus sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Prodea cf. graffi</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Terebellidae	<i>Streblosoma nr. intestinalis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Trichobranchiidae	<i>Terebellides stroemii kerguelensis</i>	0.0	0.0	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0
Trichobranchiidae	<i>Trichobranchius sp</i>	0.0	0.0	8.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

8.4 Appendix 3. Results of the SIMPER analysis of presence/absence data of polychaete species from the CAHO, FKLD and HUMB quadrants. Species are listed in the order of their contribution to the average dissimilarity between three groups. Diss: Dissimilarity; SD: Standar desviation. Entities FKLD & CAHO (Average dissimilarity = 95.32)

Species	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Idanthyrus armatus</i>	2.46	0.79	2.58	2.58
<i>Serpula narconensis</i>	2.20	0.75	2.30	4.89
<i>Perkinsina antarctica</i>	1.91	0.71	2.00	6.89
<i>Chaetopterus variopedatus</i>	1.64	0.60	1.72	8.61
<i>Glycera capitata</i>	1.56	0.60	1.63	10.24
<i>Onuphis pseudoiridescenes</i>	1.54	0.65	1.62	11.86
<i>Polyeunoa laevis</i>	1.44	0.60	1.51	13.37
<i>Leanira quatrefagesi</i>	1.41	0.65	1.48	14.85
<i>Ninoe falklandica</i>	1.40	0.55	1.47	16.32
<i>Eunice magellanica</i>	1.40	0.53	1.46	17.79
<i>Maldane sarsi</i>	1.39	0.56	1.46	19.24
<i>Nicon maculata</i>	1.37	0.58	1.44	20.68
<i>Aglaophamus praetiosus</i>	1.35	0.59	1.42	22.10
<i>Harmothoe spinosa</i>	1.35	0.63	1.41	23.51
<i>Platynereis australis magalhaensis</i>	1.13	0.47	1.18	24.69
<i>Abyssoninoe abyssorum</i>	1.08	0.53	1.13	25.83
<i>Harmothoe magellanica</i>	1.08	0.51	1.13	26.96
<i>Melinna cristata cristata</i>	1.07	0.51	1.12	28.08
<i>Amphitrite kerquelensis</i>	1.04	0.55	1.09	29.17
<i>Perinereis nuntia vallata</i>	1.03	0.38	1.09	30.26
<i>Gymnonereis hartmannschoederiae</i>	1.00	0.52	1.05	31.31
<i>Eunereis patagonica</i>	0.99	0.51	1.03	32.35
<i>Syllis (Syllis) sclerolaema</i>	0.94	0.44	0.99	33.34
<i>Trypanosyllis gigantea</i>	0.85	0.47	0.89	34.22
<i>Kinbergonuphis dorsalis</i>	0.83	0.44	0.87	35.09
<i>Harmothoe campoglacialis</i>	0.81	0.43	0.85	35.94
<i>Thelepus plagiostoma</i>	0.79	0.43	0.83	36.77
<i>Glycinde armata</i>	0.79	0.42	0.82	37.60
<i>Sternaspis scutata</i>	0.78	0.43	0.82	38.42
<i>Hyalinoecia artifex</i>	0.77	0.33	0.81	39.23
<i>Austrolaenilla antarctica</i>	0.76	0.41	0.80	40.03
<i>Asychis amphiglypta</i>	0.75	0.40	0.78	40.82
<i>Paramphinome australis</i>	0.73	0.41	0.77	41.58
<i>Nereis eugeniae</i>	0.71	0.46	0.74	42.33
<i>Nicolea chilensis</i>	0.70	0.41	0.73	43.06
<i>Nothria anocolata</i>	0.70	0.36	0.73	43.79
<i>Typosyllis armillaris</i>	0.69	0.35	0.73	44.52
<i>Lumbrineris cingulata</i>	0.66	0.49	0.69	45.21
<i>Lumbrineris magalhaensis</i>	0.63	0.43	0.66	45.87
<i>Autolytus charcoti</i>	0.62	0.35	0.65	46.52
<i>Aphelochaeta cincinnata</i>	0.62	0.38	0.65	47.17
<i>Nephtys paradoxa</i>	0.61	0.38	0.64	47.81
<i>Aphrodita magellanica</i>	0.61	0.38	0.64	48.45
<i>Marphysa aenea</i>	0.60	0.29	0.63	49.08
<i>Aphrodita longicornis</i>	0.60	0.29	0.63	49.71
<i>Phylo felix</i>	0.60	0.44	0.63	50.34
<i>Phyllodoce patagonica</i>	0.58	0.46	0.61	50.95

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

8.4 Continued appendix 3: Entities CAHO & HUMB
(Average dissimilarity = 95.97)

Species	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Paraprionospio pinnata</i>	2.22	1.37	2.32	2.32
<i>Ninoe chilensis</i>	2.06	1.35	2.15	4.47
<i>Lumbrineris chilensis</i>	1.73	1.06	1.80	6.27
<i>Cossura chilensis</i>	1.56	0.91	1.63	7.90
<i>Sosanides glandularis</i>	1.50	0.90	1.57	9.47
<i>Tharyx longisetosa</i>	1.44	0.89	1.50	10.97
<i>Spiophanes chilensis</i>	1.44	0.89	1.50	12.46
<i>Nephtys ferruginea</i>	1.34	0.78	1.40	13.87
<i>Levinsenia gracilis</i>	1.27	0.76	1.32	15.18
<i>Laonice cirrata</i>	1.19	0.80	1.24	16.42
<i>Glycera americana</i>	1.18	0.78	1.23	17.66
<i>Prionospio peruana</i>	1.12	0.76	1.17	18.83
<i>Notomastus chilensis</i>	1.08	0.63	1.12	19.95
<i>Maldane sarsi</i>	1.07	0.69	1.11	21.06
<i>Cirratulus cirratus</i>	1.06	0.76	1.11	22.17
<i>Onuphis pseudoiridescens</i>	1.04	0.77	1.09	23.25
<i>Lumbrineris cingulata</i>	1.04	0.84	1.08	24.34
<i>Leanira quatrefagesi</i>	1.02	0.76	1.06	25.40
<i>Sphaerosyllis brandhorsti</i>	1.01	0.81	1.05	26.45
<i>Sigambra bassi</i>	0.96	0.64	1.00	27.45
<i>Typosyllis longisetosa</i>	0.95	0.80	0.99	28.45
<i>Chone rosea</i>	0.83	0.59	0.87	29.31
<i>Ninoe falklandica</i>	0.81	0.61	0.84	30.15
<i>Aglaophamus heteroserratus</i>	0.80	0.68	0.84	30.99
<i>Glycera capitata</i>	0.80	0.64	0.83	31.82
<i>Aglaophamus macroura</i>	0.78	0.69	0.82	32.64
<i>Maldane chilensis</i>	0.78	0.68	0.81	33.45
<i>Gyptis heteroculata</i>	0.75	0.65	0.78	34.23
<i>Sphaerodoropsis parva</i>	0.73	0.71	0.76	34.99
<i>Leitoscoloplos chilensis</i>	0.72	0.63	0.75	35.74
<i>Protula tubularia</i>	0.70	0.48	0.73	36.48
<i>Autolytus gibber</i>	0.68	0.67	0.70	37.18
<i>Harmothoe fimbriata</i>	0.67	0.66	0.70	37.88
<i>Abyssoninoe abyssorum</i>	0.67	0.56	0.70	38.58
<i>Megalomma monoculta</i>	0.67	0.48	0.70	39.28
<i>Nereis dorsolobulata</i>	0.67	0.49	0.70	39.98
<i>Chaetozone curvata</i>	0.67	0.53	0.70	40.68
<i>Magelona annulata</i>	0.67	0.65	0.69	41.37
<i>Harmothoe juvenalis</i>	0.66	0.48	0.69	42.06
<i>Isolda viridis</i>	0.66	0.50	0.69	42.75
<i>Aricidea (Ac) pigmentata</i>	0.65	0.48	0.68	43.43
<i>Magelona phyllisae</i>	0.65	0.48	0.68	44.11
<i>Melinna cristata cristata</i>	0.65	0.55	0.67	44.79
<i>Gymnonereis hartmannschoederiae</i>	0.64	0.56	0.67	45.45
<i>Nicolea lobulata</i>	0.63	0.48	0.66	46.11
<i>Paramphinome australis</i>	0.63	0.55	0.66	46.77
<i>Spiophanes soederstroemi</i>	0.63	0.47	0.66	47.43
<i>Amphitrite kerquelensis</i>	0.61	0.54	0.64	48.06
<i>Terebellides bisetosus</i>	0.60	0.58	0.62	48.69
<i>Aricidea (All.) ramosa</i>	0.55	0.53	0.57	49.26
<i>Perinereis nuntia vallata</i>	0.54	0.43	0.57	49.83
<i>Platynereis australis magalhaensis</i>	0.54	0.48	0.56	50.39
<i>Amphiteis chilensis</i>	0.53	0.53	0.55	50.95

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

8.4 Continued appendix 3: Entities FKLD & HUMB
(Average dissimilarity = 99.21).

Species	Av.Diss	Diss/SD	Contrib%	Cum.%
<i>Paraprionospio pinnata</i>	2.76	1.51	2.78	2.78
<i>Ninoe chilensis</i>	2.55	1.49	2.57	5.35
<i>Lumbrineris chilensis</i>	2.20	1.20	2.22	7.57
<i>Cossura chilensis</i>	1.98	1.00	2.00	9.57
<i>Sosanides glandularis</i>	1.86	0.96	1.88	11.45
<i>Spiophanes chilensis</i>	1.78	0.94	1.79	13.24
<i>Tharyx longisetosa</i>	1.78	0.94	1.79	15.04
<i>Idanthysus armatus</i>	1.75	0.94	1.77	16.80
<i>Nephtys ferruginea</i>	1.68	0.83	1.70	18.50
<i>Serpula narconensis</i>	1.55	0.87	1.56	20.06
<i>Levinsenia gracilis</i>	1.54	0.77	1.55	21.61
<i>Glycera americana</i>	1.46	0.82	1.47	23.08
<i>Laonice cirrata</i>	1.44	0.83	1.45	24.53
<i>Prionospio peruana</i>	1.37	0.79	1.38	25.92
<i>Notomastus chilensis</i>	1.36	0.67	1.37	27.29
<i>Perkensiãna antarctica</i>	1.35	0.80	1.36	28.65
<i>Cirratulus cirratus</i>	1.32	0.80	1.33	29.98
<i>Lumbrineris cingulata</i>	1.19	0.84	1.20	31.18
<i>Sphaerosyllis brandhorsti</i>	1.18	0.84	1.19	32.37
<i>Sigambra bassi</i>	1.18	0.66	1.19	33.57
<i>Typosyllis longisetosa</i>	1.14	0.84	1.15	34.72
<i>Chaetopterus variopedatus</i>	1.12	0.67	1.13	35.85
<i>Chone rosea</i>	1.03	0.61	1.03	36.88
<i>Harmothoe spinosa</i>	0.99	0.68	1.00	37.88
<i>Nicon maculata</i>	0.96	0.64	0.97	38.85
<i>Protula tubularia</i>	0.89	0.51	0.89	39.74
<i>Polyeunoa laevis</i>	0.89	0.63	0.89	40.63
<i>Aglaophamus heteroserratus</i>	0.88	0.67	0.89	41.52
<i>Leitoscoloplos chilensis</i>	0.86	0.66	0.87	42.39
<i>Aglaophamus macroura</i>	0.86	0.66	0.87	43.26
<i>Maldane chilensis</i>	0.86	0.66	0.87	44.13
<i>Gyptis heteroculata</i>	0.86	0.66	0.87	45.01
<i>Aglaophamus praetiosus</i>	0.86	0.58	0.87	45.87
<i>Megalomma monoculta</i>	0.84	0.50	0.85	46.72
<i>Nereis dorsolobulata</i>	0.84	0.51	0.85	47.57
<i>Autolytus gibber</i>	0.83	0.69	0.84	48.41
<i>Aricidea (Ac) pigmentata</i>	0.82	0.50	0.83	49.23
<i>Maldane sarsi</i>	0.82	0.50	0.83	50.06
<i>Magelona phyllisae</i>	0.82	0.50	0.83	50.88

8.5 References

- Antezana, T., Guglielmo, L., Ghirardelli, E. (1992). Microbasins within the Strait of Magellan affecting zooplankton distribution. In: Gallardo V.A., O. Ferretti, H. I. Moyano (eds), *Oceanografías en Antártica*, pp. 453-458. Ediciones Documentadas, Santiago.
- Arntz, W. E., Tarazona, J., Gallardo, V. A., Flores, L. A., Salzwedel, H. (1991). Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño, Modern and ancient continental shelf anoxia (R V Tyson, T H Pearson) *Geol Soc spec publ* 58:131-154.
- Arntz, W.E. (1999). Magellan-Antarctic: Ecosystems that drifted apart. Summary review. In Arntz WE, Ríos C (eds). *Magellan-Antarctic: Ecosystems that drifted apart*. *Sci Mar* 63 (Suppl 1):503-511
- Arntz, W. E., Gili, J., Reise, K. (1999). Unjustifiably ignored: reflections on the role of benthos in marine ecosystems. In Gray J, Ambrose Jr.A, Szaniawska A (eds) *Biogeochemical Cycling and Sediment Ecology*. Kluwer Academic Publishers, Dordrecht: 105-124
- Arntz, W.E., Gorny, M. (1996). Cruise report of the Joint Chilean-German-Italian "Victor Hensen" Campaign in 1994. *Ber. Polarforsch.* 190:1-113.
- Arntz, W.E., Ríos, C. (eds) (1999). *Magellan-Antarctic: Ecosystems that drifted apart*. *Sci Mar* 63 (Suppl 1). 518
- Arntz, W., Brey, T. (2003). The expedition ANTARKTIS XIX/5 (LAMPOS) of RV "Polarstern" in 2002. *Ber. Polarforsch.*, 462: 1-120
- Averince, V.G. (1972). Benthic polychaetes *Errantia* from Antarctic and Subantarctic collected by the Sovietic Antarctic Expedition, 5. *Bio. Res. of Sovietic Antarctic Expedition.*, 5: 88-293.
- Balech, E. (1954). Divisiones zoogeográficas del litoral sudamericano. *Rev. Biol. Mar.*, 4: 184-195.
- Barnes, D., Brockington, S. (2003). Zoobenthic biodiversity, biomass and abundance at Adelaide Island, Antarctica. *Mar Ecol Prog Ser* 249:145-155
- Bastida, R., Urien, C., Lichtschein, V., Ruox, A., Arias, P. (1981). Investigación sobre comunidades bentónicas. Características generales del sustrato (Campañas IV, V, X y XI del B/I "Shinkai Maru"). *Contribuciones del Instituto Nacional de Investigación y Desarrollo Pesquero*, 383: 318-339.
- Bastida, R., Roux, A., Martínez, D. (1992) Benthic communities of the Argentine continental shelf. *Oceanol. Acta* 15(6):687-698
- Benn, D., Clapperton, C. (2000). Glacial sediment – landform associations and paleoclimate during the last glaciation, Strait of Magellan, Chile. *Quaternary Research.*, 54 (1):13-23.
- Bhaud, M. (1998). The spreading potential of polychaete larvae does not predict adult distributions; consequences for conditions of recruitment. *Hydrobiologia.*, 376: 35-47.
- Blake, J. (1983). Polychaetes of the family Spionidae from South America, Antarctica and adjacent seas and islands. *Antarct. Res. Ser.*, 29:205-288.
- Blake, J. (1995). Introduction to the Polychaeta. Chapter 4. In: J. Blake, C. Erséus, B. Hilbig (eds.), *Taxonomic Atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel*, pp. 39-51 Santa Barbara Museum of Natural History. California.

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Böggemann, M. (2002). Revision of the Glyceridae Grube 1850 (Annelida: Polychaeta). *Abh. Senckenb. Naturforsch. Ges.*, 555:1- 249
- Boltovskoy, D., Gibbons, M., Hutching, L., Binet, D. (1999). General biological feature of the South Atlantic. In: Boltovskoy, D. (ed.), *South Atlantic Zooplankton (1)*: 1-42 pp. Backhuys Publishers, Leiden, The Netherlands.
- Bouchet, P. (2000). L'insaisissable inventaire des espèces. *La recherche* 333: 40-44.
- Brambati A, Fontolan, G., Simeoni, U. (1991). Recent sediments and sedimentological process in the Straits of Magellan. *Bol Oce Teor App* 9:261-272
- Brandt, A., K. Linse and U. Mühlenhardt-Siegel. 1999. Biogeography of crustacea and mollusca of the subantarctic and antarctic regions. In Arntz WE, Ríos C (eds). *Magellan-Antarctic: Ecosystems that drifted apart*. *Sci Mar* 63 (Suppl 1):383-389
- Brattström, H., Johanssen, A. (1983). Ecological and regional zoogeography of the marine benthic fauna of Chile. *Sarsia*, 68: 289-339.
- Bremec, C., Elias, R., Gambi, M. (2000). Comparison of the polychaete fauna composition from the Patagonian shelf and Straits of Magellan. Preliminary results from cruise Shinkai Maru IV, V, X and XI (1978-1979) and Second Italian Oceanographic Cruise (1991). *Bull Mar Sci* 67:189-198
- Brémec, C., Elías, C., Gambi, M. (2000). Comparison of the polychaete fauna composition from the Patagonian shelf and Straits of Magellan. Preliminary results from cruise Shinkai Maru IV, V, X and XI (1978-1979) and second Italian Oceanographic Cruise (1991). *Bull. Mar. Sci.*, 67(1): 189-198.
- Brey, T, Gerdes, D. (1999). Benthic community productivity in the Magellan region and in the Weddell Sea. *Sci Mar* 63(Suppl 1):145-148
- Briggs, J.C. (1995). *Global biogeography*. Elsevier, Amsterdam.
- Brown, J.H. and M.V. Lomolino. 1999. *Biogeography*. 2nd Edition. Sinauer Associates, Inc.
- Camarck, E., Foster, T. (1975). Circulation and distribution of oceanographic properties near the Filchner Ice Shelf. *Deep Sea Res* 22:77-90
- Camus, P. (2001). Biogeografía marina de Chile continental. *Rev Chil Hist Nat* 74:587-617
- Cañete, J., Leighton, G., Aguilera, F. (1999). Polychaeta from Aysén Fjord, Chile: Distribution, abundance and biogeographical comparison with the shallow soft-bottom polychaete fauna from Antarctica and the Magellan Province. *Sci Mar* 63 (Suppl 1):243-252
- Carreto, . (1981). Los ecosistemas del Mar argentino. In : "Proyecto el medio ambiente marino en relación a los recursos pesqueros" (MS).
- Chapman, M., Underwood, A. (1999). Ecological patterns in multivariate assemblages: information and interpretation of negative values in Anosim tests. *Mar. Ecol. Prog. Ser.*, 180, pp. 257-265.
- Clapperton, C., Sugden, D., Kaufman, D., McCulloch, R. (1995). The last glaciation in the central Magellan Strait, southernmost Chile. *Quaternary Research*, 44 (2):133-14
- Clarke & Warwick 1994. (1994). Similarity-based testing for community pattern: The two-way layout with no replication. *MAR. BIOL.* 118 (1):167-176

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Clarke, A., Johnston, N. (2003). Antarctic marine benthic diversity. *Oceanogr Mar Biol Ann Rev* 41:47-114
- Conlan, K., Lehnham, H., Kvitek, R., Oliver J (1998) Ice scour disturbance to benthic communities in the Canadian High Arctic. *Mar. Ecol. Prog. Ser.* 166: 1-16
- Cosson-Sarradin, N., Sibuet, M., Paterson, G., Vangriesheim, A. (1998). Polychaete diversity at tropical Atlantic deep-sea sites: environmental effects. *Mar Ecol Prog Ser* 165:173-185
- Cowell, R. (2001). Online User's Guide EstimateS <http://viceroy.eeb.uconn.edu/estimates>
- Cox, C., Moore, P. 2001. *Biogeography: An Ecological and Evolutionary Approach*. 6th Edition. Blackwell, London.
- Crame, J.A. (1992). Trophic structure. In Briggs E, Crowther P. (eds) *Paleobiology: a Synthesis*, pp 385-390. Blackwell Science.
- Chen, G.T., Herman, R.L., Vincx, M. (1999). Meiofauna communities from the Straits of Magellan and the Beagle Channel. *Sci Mar* 63 (Suppl 1):123-132
- Dávila, P., Figueroa, D., Müller, E. (2002). Freshwater input into the coastal ocean and its relation with the salinity distribution off austral Chile (35–55°S). *Con Shelf Res* 22 3:521-534
- Dell, R.K. 1972. Antarctic benthos. *Advances Mar. Biol.*, 10:1-216.
- Draper, N., Smith, H. (1981). *Applied Regression Analysis*. Second edition, Wiley series in Probability and Mathematical Statistics. Wiley J, Sons, New York.
- Earll, R., Farnham, (1997). *Biogeography*. In R. Earll; D. G. Erwin (Eds), *Sublittoral ecology: the ecology of the shallow sublittoral benthos*. Oxford, Clarendon Press
- Eicken, H. (1992). The role of sea ice in structuring Antarctic ecosystems. *Polar Biol* 12:3-13
- Ekman, S. 1935. *Tiergeographie des Meeres*. Leipzig: Akad. Verl.-Ges.
- Ellingsen, K.E. (2001). Biodiversity of a continental shelf soft-sediment macrobenthic community. *Mar Ecol Prog Ser* 218:1-15
- Fahrbach, E., Gerdes, D. (1997). Die Expedition ANTARKTIS XIII/4-5 des Forschungsschiffes "Polarstern" 1996. *Ber. Polarforsch.* 239: 1-126.
- Fauchald, K., Jumars, P. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Ann Rev* 17:193-284
- Fauvel, P. (1941). Annélides polychètes de la Mission du Cap Horn (1882-1883). *Bull. Mus. Hist. Nat. Paris, sér. 2.*, 13 (4): 272-298.
- Fernández, M., Jaramillo, E., Marquet, P., Moreno, C., Navarrete, S., Ojeda, P., Valdovinos, C., Vásquez, J. (2000). Diversidad, dinámica y biogeografía del ecosistema costero bentónico de Chile: revisión y bases para la conservación marina. *Rev. chil. hist. nat.*, 73 (4): 797-830.
- Foggo, A., Martin, J., Matthew, T., Frost, R. (2003). Estimating marine species richness: an evaluation of six extrapolative techniques. *Mar Ecol Prog Ser* 248:15-26
- Forbes, E. (1854). *Map of the distribution of marine life, illustrated chiefly by fishes, Molluscs & Radiata. showing also the limits of the Homiozoic*

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Belts. In Johnston's 'Physical Atlas. Engraved & printed in colours by W. & A.K. Johnston, Edinr. William Blackwood & Sons, Edinburgh & London.
- Frederich, M., Sartoris, F., Pörtner, H-O. (2001). Distribution patterns of decapod crustaceans in polar areas: a result of magnesium regulation?. *Polar. Biol.* 24,(10):719 - 723
- Fütterer, D., Brandt, A., Poore, G. (2003). The expedition ANTARKTIS XIX/3-4 (ANDEEP 1 and II) of the Research Vessel POLARSTERN in 2002. *Ber. Polarforsch.*, 470: 1-174
- Gallardo, C., Penchaszadeh, P. (2001). Hatching mode and latitude in marine gastropods: revisiting Thorson's paradigm in the Southern Hemisphere. *Mar. Biol.* 138(3): 547-552.
- Gallardo, V. (1984). Revisión actualizada a 1983 de la contaminación marina proveniente de fuentes terrestres en la región del Pacífico sudeste (Colombia, Chile, Ecuador, Panamá y Perú). *Rev Com Per Pac* 14:19-173
- Gallardo, V., Medrano, S., Carrasco, F. (1988). Taxonomic composition of the sublittoral soft-bottom Polychaeta of Chile Bay (Greenwich Island, South Shetland Islands, Antarctica). *Ser Cient Inst Antart Chil* 37:49-67
- Gambi, M., Castelli, A., Guizzardi, M. (1997). Polychaete populations of the shallow soft bottoms off Terra Nova Bay (Ross Sea, Antarctica): Distribution, diversity and biomass. *Polar Biol* 17:199-210
- Gambi, M., Mariani, S. (1999). Polychaetes of the soft bottoms of the Straits of Magellan collected during the Italian oceanographic cruise in February-March 1991. In: W.E. Arntz, C. Ríos (eds.), *Magellan-Antarctic: Ecosystems that drifted apart*. *Sci. Mar.*, 63 (suppl. 1): 233-242.
- Gaston, G. (1983). Benthic Polychaeta of the Middle Atlantic Bight: feeding and distribution. PhD Thesis Fac of Marine Science, Virginia.
- Gaston, K. (1996). *Biodiversity: a biology of numbers and difference*. Oxford. Berlin Blackwell Science.
- Gerdes, D. (1990). Antarctic trials of the multi-box corer, a new device for benthos sampling. *Polar Rec* 26:35-38
- Gerdes, D., Hilbig, B., Montiel, A. (2003). Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea. *Polar Biol* 26:295-301
- Gerdes, D., Klages, M., Arntz, W., Herman, R., Galéron, J., Hain, S. (1992). Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. *Polar Biol* 12:291-301
- Gerdes, D., Montiel, A. (1999). Distribution patterns of macrozoobenthos: a comparison between the Magellan region and the Weddell Sea (Antarctic). *Sci Mar* 63 (Suppl 1):149-154
- Gersonde, R., Abelmann, A., Cortese, G., Becquey, S., Bianchi, C., Brathauer, U., Niebler, H.-S., Zielinski, U., Pätzold, J. (2003). The late Pleistocene South Atlantic and Southern Ocean surface waters: a summary of time slice and time series studies, Wefer G, Mulitza S, Ratmeyer V (eds), *The South Atlantic in the Late Quaternary: reconstruction of Material Budget and Current Systems*, pp. 499-529. Springer, Berlin.

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Giangrande, A. 1997. Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanography and Marine Biology. Ann. Rev.* 35:323-386
- Giese, A., Pearse, J (1974). *Reproduction of marine invertebrates*. New York : Academic Press.
- Giribet G. (2003). Molecules, development and fossils in the study of metazoan evolution; Articulata versus Ecdysozoa revisited. *Zoology*, 106 (4): 303-326
- Gilli, J., Coma, R. (1998). Benthic suspension feeders: their paramount role in the littoral marine food webs. *Trends Ecol Evol* 13 (8):316-321
- Glasby, J., Alvarez, B. (1999). Distribution patterns and biogeographic analysis of Austral Polychaeta (Annelida). *J. Biogeograph.*, 26: 507-533.
- Gorny, M. 1999 On the biogeography and ecology of the Southern Ocean decapod fauna. In Arntz WE, Ríos C (eds). *Magellan-Antarctic: Ecosystems that drifted apart*. *Sci Mar* 63 (Suppl 1):367-382
- Gray, J.S. (1981). *The ecology of marine sediments*. Cambridge University Press, Cambridge
- Gray, J.S. (1994). Is deep-sea species diversity really so high? Species diversity of the Norwegian continental shelf. *Mar Ecol Prog Ser* 112: 205-209
- Gray, J.S. (2000). The measurement of species diversity: an example from the continental shelf of Norway. *J Exp Mar Bio Ecol* 250:23-49
- Gray, J.S. (2001a). Antarctic marine benthic biodiversity in a world-wide latitudinal context. *Polar Biol* 24:633-641
- Gray, J.S. (2001b). Marine diversity: the paradigms in patterns of species richness examined. *Sci Mar* 65:41-56
- Gray, J.S. (2002). The species diversity of marine soft sediments. *Mar Ecol Prog Ser* 244:285-297
- Guglielmo, L., Ianora, A. (1997). *Atlas of Marine Zooplankton. Strait of Magellan: amphipods, euphausiids, mysids, ostracods and chaetognaths*. Springer-Verlag, New York.
- Gutt, J. (2000). Some "driving forces" structuring communities of the sublittoral Antarctic macrobenthos. *Ant Sci* 12:297-313
- Gutt, J, Helsen, E., Arntz, W.E., Buschmann, A. (1999). Biodiversity and community structure of the mega-epibenthos in the Magellan region (South America). *Sci Mar* 63(Suppl 1):155-170
- Gutt, J., Starmans, A. (2001). Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). *Polar Biol.* (24):615-619.
- Hartman, O. (1953). Non-pelagic Polychaeta of the Swedish Antarctic expedition 1901-1903. In *Further Zoological Results of the Swedish Antarctic Expedition 1901-1903 under the direction of Dr. Otto Nordenskjöld*. Edited by Odhner N.H. Vol.4: 1-83. P. A. Norstedt & Söner, Stockholm.
- Hartman, O. (1959a). *Catalogue of the polychaetous annelids of the world Part I*. Allan Hancock Found. Publ. Occ. Pap., 23: 1-353.
- Hartman, O. (1959b). *Catalogue of the polychaetous annelids of the world Part II*. Allan Hancock Found. Publ. Occ. Pap., 23: 355-628.

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Hartman, O. (1964). Polychaeta Errantia of Antarctica. *Ant Res Ser* 3:1-131
- Hartman, O. (1966). Polychaeta Myzostomidae and Sedentaria of Antarctica. *Ant Res Ser* 7:1-158
- Hartman, O. (1967). Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic seas. *Allan Hancock Monogr. Mar. Biol.* 2: 1-328.
- Hartman, O. (1978). Polychaeta from the Weddell Sea quadrant, Antarctica. *Antarct. Res. Ser.* 26 (4):125-223
- Hartmann-Schröder, G. (1965). Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. II. Die Polychaeten des Sublitorals. *Mitt. Hamburg. Zool. Mus. Inst.*, 62 (Suppl.): 59-305.
- Hartmann-Schröder, G. (1983). Die Polychaeten der 15., 36. und 76. Reisen von FFS "Walter Herwig" zum patagonischen Shelf (Südwest-Atlantic). *Senckenbergiana mar.* 15 (4): 251-277.
- Hartmann-Schröder, G., Hartmann, G. (1974). Zur Kenntnis des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostküste von Südafrika und Mocambique unter besonderer Berücksichtigung der Polychaeten und Ostracoden. *Mitt. hamburg. Zool. Mus. Inst.*, 69 : 5-94.
- Hartmann-Schröder, O., Rosenfeldt, P. (1988). Die Polychaeten der "Polarstern"- Reise ANT III/2 in die Antarktis 1984. Teil 1; Euphosinidae bis Chaetopteridae. *Mitt hamb zool Mus Inst* 85:25-72
- Hartmann-Schröder, O., Rosenfeldt, P. (1989). Die Polychaeten der "Polarstern"- Reise ANT III/2 in die Antarktis 1984 Teil 2: Cirratulidae bis Serpulidae. *Mitt hamb zool Mus Inst* 86:65-106
- Heiskanen, A., Tallberg (1999). Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. *Hydrobiologia* 393 (1-3):127-140.
- Hilbig, B. (1994). Faunistic and zoogeographical characterization of the benthic infauna on the Carolina continental slope. *Deep-Sea Res. II.*, 41 (4-6): 929-950
- Homziak, J. (1985). Does succession occur in estuarine soft substrates ? Seasonal patterns of colonization and mechanisms of species replacement in experimentally defaunated sediments. Thesis of Ph.D. pp 349
- Hubbell S.P. (2001) The Unified neutral theory of biodiversity and biogeography. Monographs in population biology. Princeton. University Press.
- Hughes, R. (1984). A model of the structure and dynamics of benthic marine invertebrate communities. *Mar Ecol Prog Ser* 15:1-11
- Hutchinson, P. (1998). Biodiversity and functioning of polychaetes in benthic sediments. *Biodiversity conserv.* 7: 1133-1145.
- Jablonski, D., Lutz, R. (1983). Laral ecology of marine benthic invertebrates: Paleobiological implications. *Biol. Rev.* 58:21-89
- Kowalke J. (1998). Energy budgets of benthic suspension feeding animals of the Potter Cove (King George Island, Antarctica). *Ber. Polarforsch.* 286:1-140

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Knox, G. (1957). The distribution of the polychaetes within the Indo-Pacific. *Proc. 8th Pacif. Sci. Congr.*, 3: 403-411.
- Knox, G., Lowry, K. (1977). A comparison between the benthos of the Southern Ocean and the North Polar Ocean with special reference to the Amphipoda and Polychaeta. In: M.J. Dunbar (ed.) *Polar Ocean*, pp 423-462. Arctic Institute of North America, Calgary.
- Knox G, Cameron, D. (1998). The marine fauna of the Ross Sea: Polychaeta. *NIWA Biodiversity Mem* 108:1-125
- Knust, R., Arntz, W.E., Boche, M., Brey, T., Gerdes, D., Mintenbeck, K., Schröder, A., Starbans, A., Teixidó, N. (2003). Iceberg scouring on the eastern Weddell Sea shelf (Antarctica): a benthic system shaped by physical disturbances?. In Huskes, AL, Gieskes WW, Rozema J, Schorno RM, van der Vies SM, Wolff WJ (eds) *Proc SCAR Biol Symp Amsterdam* : Antarctic biology in a global context. Backhuys Publishers, Leiden, p 96-101
- Kudenov, J. (1992). Amphinomidae and Euprosinidae (Annelida: Polychaeta) principally from Antarctica, the Southern Ocean, and Subantarctic regions. *Ant Res Ser* (58):93-150
- Lancellotti, D.A., Vásquez, J. (1999). Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. *J. Biogeography*, 26: 1001-1006.
- Lawrence, G., Keith, W. (1979). Marine benthic diversity: a critique and alternative explanation. *J Biog* 6:115-126
- Levin, L. (1984). Life history and dispersal patterns in a dense infaunal polychaete assemblage: Community structure and response to disturbance. *Ecology*, 65 (4): 1185-1200
- Licher, F. (2002). Revision der Gattung *Typosyllis* Langerhans, 1879 (Polychaeta: Syllidae): Morphologie, Taxonomie and Phylogenie. *Abh senckenb Naturforsch Ges* 551:1-336
- Linse, K. 1999. Abundance and diversity of Mollusca in the Beagle Channel. In Arntz WE, Ríos C (eds). *Magellan-Antarctic: Ecosystems that drifted apart*. *Sci Mar* 63 (Suppl 1):391-397
- Longhurst, A. (1995). Seasonal cycles of pelagic production and consumption. *Prog. Oceanogr.*, 36: 77-167.
- Longhurst, A. (1998). *Ecological Geography of the Sea*. Academic Press. 398pp
- Maurer, D., Williams, S. (1988). Deep-sea polychaetous annelida from Central America to the Antarctic Peninsula and Sandwich Islands. *Int. Revue. Ges. Hydrobiol.*, 73(5): 659-701.
- McCulloch, R., Davies, S. (2001). Late-glacial and Holocene palaeoenvironmental change in the central Strait of Magellan, southern Patagonia. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 173: 143-173.
- McIntosh, W. C. (1885). Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873-1876. En: *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873-1876 under the Command of Captain George S. Nares, R.N., F.R.S. and the*

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Late Captain Frank Tourle Thomson, R.N., *Zoology*, 12 (34): 1-554, pls. 1-55, and 1a-39a.
- Michelato, A., Accerboni, E., Berger, P. (1991). Current meter observations in the eastern and central sectors of the Strait of Magellan. *Mem. Biol. Mar. Ocean.*, 19: 261-272.
- Monro, C. (1936). Polychaeta worms. II. *Discovery Rep.* 12: 59-138.
- Montiel, A., Gerdes, D., Arntz, W.E. (submitted) Distributional patterns of shallow-water polychaetes in the Magellan region: a zoogeographical and ecological synopsis. *Sci Mar*
- Montiel, A., Gerdes, D., Ríos, C. (2001) Distribución y abundancia del macrobentos en una microcuenca marina submareal del estrecho de Magallanes, Chile. *An Inst Patago Ser Cs Nat* 29:117-133
- Montiel, A., Hilbig, B., Rozbaczylo, N. (2002). New records to Chile of the family Paraonidae (Annelida: Polychaeta). *Helgol Mar Res* 56:134-139
- Montiel, A., C. Ríos, E. Mutschke, N. Rozbaczylo. (2004). Poliquetos de fiordos y canales adyacentes al Campo de Hielo Patagónico Sur, Chile (Annelida: Polychaeta). *Cs. Tec. del Mar*.
- Muniz, P., Pires, A. (1999). Trophic structure of polychaetes in the Sao Sebastiao Channel (southeastern Brazil). *Mar Biol* 134 (3):517-528
- Murray, J. (1895). A summary of the scientific results obtained at the sounding, dredging and trawling station of H.M.S. Challenger. *Challenger reports* 2.
- Mutschke, E., Ríos, C., Hromic, T., Gorny, T., Montiel, A., Rauschert, M., Gerdes, D. (1996). Estudios bentónicos en fiordos y canales de los Campos de Hielo sur (45° - 53°S). In: *Comité Oceanográfico Nacional (eds.), Resultados crucero CIMAR - FIORDO 2, 14 de Octubre al 9 de Noviembre 1996, resúmenes ampliados.* pp. 91-98.
- Myers, A., Giller, P. (1988). *Analytical Biogeography: An Integrated Approach to the Study of Animal and Plant Distributions.* Chapman and Hall, London.
- Naruse, R., Aniya, M. (1992). Outline of glacier research project in Patagonia, 1990. *Bull Glac Res* 810:31-38
- Orensanz, J. (1974). Anélidos poliquetos de la provincia biogeográfica magallánica. I. Catálogo de las especies citadas hasta 1974. *Contrib Tec* 1:1-83
- Orensanz, J. M. (1990). The eunicemorph polychaete annelids from Antarctic and Subantarctic seas. With addenda to the Eunicemorpha of Argentina, Chile, New Zealand, Australia, and the southern Indian Ocean. *Biology of the Antarctic Seas XXI. Antarctic Research Series*, 52: 1-183. American Geophysical Union.
- Paiva, P.C. (1993). Trophic structure of a shelf polychaete taxocoenosis in southern Brazil. *Cah Biol Mar* (35):39-55
- Palma, M., Quiroga, E., Gallardo, V.A., Arntz, A., Schneider, W., Gerdes, D., Hebbeln, D. (submitted) Macrobenthic animal assemblages of the continental margin of Chile (23° to 42°). *JMBA*
- Parapar, J., San Martín, G. (1997). "Sedentary" polychaetes of the Livingston Island shelf (South Shetlands, Antarctica), with the description of a new species. *Polar Biol* 17 (6):502-514

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Peck, L., Brockington S., Vanhove, S., Beghyn, M (1999). Community recovery following catastrophic iceberg impact in soft sediment shallow-waters site at Signy Island. *Mar. Ecol. Prog. Ser* 186: 1-8
- Petersen, C.G. (1913). Valuation of the sea. 2. The animal communities of the sea bottom and their importance for marine zoogeography. *Rep Dan Ann Rev* 16:229-311
- Piccolo, M. C. (1998). Oceanography of the western South Atlantic continental shelf from 33 to 5°S coastal segment (5,W). Chapter 9. In: A.R. Robinson, K.H. Brink (eds.), *The Sea*, pp. 253–271. Wiley & Sons, New York.
- Pickard, G., Stantor, B. (1980). Pacific fjords: a review of their water characteristics. In Freeland H, Farne D, Levings (eds). *Fjord Oceanography*. Plenum Press, New York.
- Piepenburg, D., Schmid, M., Gerdes, D. (2002). The benthos off King George Island (South Shetland Islands, Antarctica): further evidence for a lack of a latitudinal biomass cline in the Southern Ocean. *Polar Biol* 25 (2):146-158
- Pinochet, P., Salinas, S. (1998). Estructura térmica y salina de canales y fiordos adyacentes al los Campos de Hielo Sur. In: Comité Oceanográfico Nacional (eds). *Inf. Crucero 1995:15-25*. Litografía Carroza, Valparaíso.
- Pisano, E. (1990). Labilidad de los ecosistemas terrestres fuego-patagónicos. *Ans. Ins. Pat. Ser. Cs. Nts.*, 19 (1): 17-25
- Poulin, E., Palma, A., Féral, J-P. (2002). Evolution versus ecological success in Antarctic benthic invertebrates. *Trends Ecol Evol* 17:218-222
- Reineck, H.E. (1958). Kastengreifer und Lotröhre "Schnepfe". Geräte zur Entnahme ungestörter, orientierter Meeresgrund-Proben. *Senckenb Luthaea* 39:42-48
- Rex, M., Stuart, C., Hessler, R., Allen, J., Sanders, H., Wilson, D. (1993). Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636-637
- Ríos, C., Mutschke, E., Morrison, E. (2003). Biodiversidad bentónica en el estrecho de Magallanes, Chile. *Revista de Biología Marina y Oceanografía* 38(1):1-12
- Snelgrove, P., Grassle, J., Grassle, J., Petrecca, R., Stocks, K. (2001). The role of colonization in establishing patterns of community composition and diversity in shallow-water sedimentary communities. *J. Mar. Res.* 59 (5): 813-831.
- Rosenberg, R. (2001). Marine benthic faunal successional stages and related sedimentary activity. *Sci Mar* 65 (suppl. 2):107-119
- Rouse, G. W., Fauchald, K. (1997). Cladistics and polychaetes. *Zoologica Scripta*, 26 (2): 139-204
- Rouse, G., Pleijel, F. (2001). *Polychaetes*. Oxford University Press, Oxford.
- Rozbaczylo, N. (1985). Los anélidos poliquetos de Chile: índice sinónimo y distribución geográfica de especies. *Monografía Biológica* 3:1-284
- San Martin, G., Parapar, J., Garcia, F., Redondo, M. (2000). Quantitative analysis of soft bottoms infaunal macrobenthic polychaetes from South Shetland Islands (Antarctica). *Bull Mar Sci* 67:83-101
- Sanders, H. (1968). Marine benthic diversity: a comparative study. *Am Nat* 108:243-281

ACKNOWLEDGEMENT, APPENDIX & REFERENCES

- Santos, S., Simon, J. (1980) Marine soft-bottom community establishment following annual defaunation: larval or adult recruitment?. *Mar. Ecol. Prog. Ser.* 2(3): 235-241
- Scheltema, R.S. (1988). Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the East Pacific barrier. *Biol. Bull.*, 174 (2): 145-152.
- Silva, N., Prego, R. (1998). Carbon and Nitrogen spatial segregation and stoichiometry in the surface sediments of Southern Chilean Inlets (41°-56°S). *Est. Coast. Shelf. Sci.*, 55: 763-775.
- Snelgrove, P. (1998). The biodiversity of macrofaunal organisms in marine sediments. *Biodivers Conserv* 7:1123-1132.
- Sousa, W. (2000) Natural disturbance and the dynamics of marine benthic communities. In Bertness, M., Gaines, S. D., Hay M. (eds). *Marine community ecology*, p85-130
- Strelzov, V.E. (1973). Polychaete worms of the family Paraonidae Cerruti, 1909 (Polychaeta, Sedentaria). *Akad Nauk SSSR, Leningrad* (English translation published in 1979 by Smith Inst).
- Strub, P.T., Mesias, J., Montecino, V., Rutllant, J., Salinas, S. (1998). Coastal ocean circulation off western South America coastal segment. In: Robinson AR, Brink KH (eds). *The Sea, Vol 11*. J Wiley, Sons, New York, p 273-313
- Stuardo, J., Valdovinos, C. (1992). Barreras, límites faunísticos y provincias biogeoquímicas en Sudamérica austral. In: V.A. Gallardo, O. Ferretti, H.I. Moyano (eds.), *Oceanografía in Antartide: atti seminario internazionale*, pp. 443-452. ENEA/Centro EULA, Concepción, Chile.
- Syvitski, J.P., Burrell, D.C., Skei, J.M. (1987). *Fjords: Processes, Products*. Springer-Verlag, New York, p 379
- Thatje, S. (2004). Reproductive trade-offs in benthic decapod crustaceans of high southern latitudes: tolerance of cold and food limitation. *Ber. Polarforsch.* 483:1-183
- Thatje, S., Mutschke, E. (1999). Distribution of abundance, biomass, production and productivity of macrozoobenthos in the Sub-Antarctic Magellan Province (South America), *Polar Biol.* 22: 31-37.
- Teixidó, N., Garrabou, J., Arntz, W.E. (2002). Spatial pattern quantification of Antarctic benthic communities using landscape indices. *Mar Ecol Prog Ser* 242:1-14
- Thorson, G. (1957). Bottom communities (sublittoral or shallow shelf). *Geo Soc Am Memoir* 67(1):461-534
- Valdovinos, C., Navarrete, S., Marquet, P. (2003). Mollusk species diversity in the southeastern Pacific: why are there more species towards the pole? *Ecography* 26:139-144
- Viviani, C. (1979). *Ecogeografía del litoral chileno*. *Studies on Neotropical Fauna and Environment* 14: 65-123.
- Wesenberg-Lund, E. (1962). Polychaeta Errantia. Reports of the Lund University Chile Expedition 1948-49. *Lunds Univ. Arsskr. N.F. Avd. 2*, 57 (12): 1-137.
- Wilson, W.H. (1991). Competition and predation in marine soft-sediment communities. *Ann Rev Ecol Syst* 21:221-241