Role of benthic cnidarians in energy transfer processes in the Southern Ocean marine ecosystem (Antarctica)

Rolle der bodenlebenden Nesseltiere im Stofffluß des marinen Ökosystems des Südpolarmeeres (Antarktis)

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To Alex,
who was during many years
beside my work

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Contents

Glossary

d^{-1}	Per day
DOC	Dissolved Organic Carbon
EASIZ	Ecology of the Antarctic Sea Ice Zone
ESW	Eastern Shelf Water
EWD	East Wind Drift
Ind.	Individuals
ISW	Ice Shelf Water
KN	Kapp Norvegia
n	Number of Individuals
POC	Particulate Organic Carbon
ROV	Remote Operated Vehicle
SW	Shelf Water
WW	Winter Water
WDW	Warm Deep Water
WSBW	Weddell Sea Bottom Water
WSC	Weddell Scotia Confluence
WSW	Western Shelf Water
WWD	West Wind Drift
y^{-1}	Per year

1. Summary

Benthic suspension feeder communities are very abundant, diverse and biomass rich in many areas of the Weddell Sea shelf (Antarctica). However, information on the ecology of the organisms forming these dense communities, in particular the cnidarians, is still scarce.

For this reason, the main objective of this thesis was to increase the knowledge on the ecological role of benthic suspension feeders in the Antarctic marine ecosystem. To this aim, three particular objectives were addressed: the distribution patterns, the trophic behaviour, and the reproductive features of selected cnidarian species, and their respective ecological relevance. Sampling was carried out on board the German RV "Polarstern" during three consecutive EASIZ (Ecology of the Antarctic Sea Ice Zone) cruises, two during the austral summer (EASIZ I/1996 and EASIZ II/1998) and one in autumn (EASIZ III/2000).

Distribution patterns are one of the decisive properties defining the ecological role of a species or a community in an ecosystem. In this context, the population density and distribution of one octocoral species, the gorgonian *Ainigmaptilon antarcticum*, were studied. This species is conspicuous and relatively abundant in the eastern Weddell Sea. It presented a clumped distribution pattern with very low densities at the patch level. The possible relationship between distribution and reproductive patterns is discussed.

Trophic aspects were investigated in six cnidarian species, two hydroids (*Tubularia ralphii* and *Oswaldella antarctica*), and 4 anthozoans belonging to different orders: one Alcyonacea (*Anthomastus bathyproctus*), one Stolonifera (*Clavularia* cf. *frankliniana*), and two Gorgonacea (*Primnoisis antarctica* and *Primnoella* sp.).

Two different feeding strategies were found: two of the investigated species, *Tubularia ralphii* and *Anthomastus bathyproctus*, were mainly zooplanktivorous and their diets were composed of copepods and planktonic tunicates, respectively. Other species (*Oswaldella antarctica*, *Primnoisis* *antarctica* and *Primnoella* sp.) were basically "microphagous" and their diets consisted mainly of elements of the fine fraction of seston (i.e. ciliates and dinoflagellates). The last species *Clavularia* cf. *frankliniana* seemed to present a mixed diet. This heterogeneity of diets apparently reflects the adaptation of these species to the environmental variability of the Antarctic ecosystem. Feeding on zooplankton (*Tubularia ralphii*, *Anthomastus bathyproctus*) responds to the highly productive summer season, when the zooplankton concentrations are higher. Feeding on the fine fraction of seston (*Oswaldella antarctica*, *Primnoisis antarctica* and *Primnoella* sp.) may be an adaptation to the Antarctic "flagellate system". This type of diet could allow maintaining the feeding rate all the year round, since the biomass of the fine fraction of the seston is very constant over time.

Reproductive features and trends were investigated in five octocoral species, which presented three different morphotypes: two were bottle-brush shaped (*Dasystenella acanthina* and *Thouarella* sp.), another two presented a dichotomous branching pattern (*Fannyella rossii* and *Fanyella spinosa*), and one was flagelliform (*Ainigmaptilon antarcticum*). Different reproductive strategies were presented among the studied species. Three (*Ainigmaptilon antarcticum, Dasystenella acanthina* and *Thouarella* sp.) showed two generations of oocytes, which suggests a reproductive cycle of more than one year. Conversely, *Fannyella rossii* and *Fannyella spinosa* had only one generation of gonads, indicating a one-year cycle of development. Three of the studied species were brooders (*Thouarella* sp, *Fannyella rossii, Fannyella spinosa).* The incubation mode of *Ainigmaptilon antarcticum* and *Dasystenella acanthina* could not be determined due to the lack of larvae in the observed guts. The reproductive patterns found did not show a different tendency for Antarctic species when compared to species from other latitudes. Factors such as morphology and food availability seem to play a more important role than temperature in determining the reproductive patterns of these species.

The studies showed a high heterogeneity, which evidence the plasticity, adaptability and functional diversity of polar benthic cnidarians. These features enable them to develop rich populations and communities, despite the temporal and spatial unpredictable availability of food. The study of these aspects (distribution, trophic ecology and reproduction) in other suspension feeding populations may permit an acceptance of these conclusions at the community level in the near future.

Zusammenfassung

In vielen Bereichen des Weddellmeerschelfs (Antarktis) existieren reiche Gemeinschaften benthischer Suspensionsfresser. Über die ökologische Rolle der Organismen, die diese Gemeinschaften bilden, ist jedoch noch wenig bekannt.

Das Hauptziel dieser Arbeit war es daher, unsere Kenntnisse über die ökologische Rolle von Suspensionsfressern in der Antarktis zu erweitern. Themenschwerpunkte dieser Arbeit waren: Verbreitung, Ernährungsgewohnheiten und Fortpflanzungsstrategien aus gewählter Cnidarier. Die Probennahmen wurden an Bord des deutschen Forschungsschiffs "Polarstern" während der drei EASIZ (Ecology of the Antarctic Sea Ice Zone) - Expeditionen durchgeführt (EASIZ I/1996 und EASIZ II/1998 im Sommer, EASIZ III/2000 im Herbst).

Das Verteilungsmuster, einer der entscheidenden Faktoren für die ökologische Rolle einer Art oder Gemeinschaft in einem Ökosystem, wurde anhand der Gorgonarie *Ainigmaptilon antarcticum* (Octocorallia) untersucht. Diese großwüchsige Art findet sich im östlichen Weddellmeer häufig. Ihr Verteilungsmuster ist geklumpt, ihre mittlere Abundanz ist jedoch relativ niedrig. Diese Arbeit untersucht Zusammenhänge zwischen Verteilungs- und Fortpflanzungmuster.

Trophische Aspekte wurden bei sechs Cnidariern, zwei Hydrozoen (*Tubularia ralphii* und *Oswaldella antarctica*) und vier Anthozoen aus den Ordnungen Alcyonacea (*Anthomastus bathyproctus*), Stolonifera (*Clavularia* cf. *frankliniana*) und Gorgonacea (*Primnoisis antarctica* und *Primnoella* sp.) untersucht.

Tubularia ralphii und *Anthomastus bathyproctus* ernährten sich ausschließlich von Zooplankton, im wesentlichen von Copepoden und Tunicaten. *Oswaldella antarctica*, *Primnoisis antarctica* und *Primnoella* sp. waren “Mikrophagen”. Ihre Nahrung bestand hauptsächlich aus sestonischen Kleinstpartikeln (0,2 bis 200 µm), z.B. Ciliaten und Dinoflagellaten. Bei *Clavularia* cf. *frankliniana* wurde eine Mischernährung aus Zooplankton und

Mikrophagen gefunden. Diese unterschiedlichen Ernährungsgewohnheiten deuten auf unterschiedliche Strategien in der Anpassung an die spezifischen Nahrungsbedingungen im antarktischen Ökosystem hin. Eine Strategie ist die Konzentration auf große, „wertvolle" Nahrungspartikel, die in hoher Anzahl während einer limitierten Zeitspanne zu Verfügung stehen. Diese Strategie wird durch die Zooplanktonfresser *Tubularia ralphii* und *Anthomastus bathyproctus* repräsentiert. Eine andere Strategie ist die Konzentration auf sestonische Kleinstpartikel mit geringerem Nährwert, die das ganze Jahr über in geringen, aber relativ konstanten Mengen verfügbar sind. Diese Strategie wird durch *Oswaldella antarctica*, *Primnoisis antarctica* und *Primnoella* sp. repräsentiert. *Clavularia* cf. *franklinana* verfolgt eine mittlere Strategie zwischen diesen beiden Extremen.

Bei fünf untersuchten Octocorallia-Arten wurden unterschiedliche Reproduktionstrategien gefunden. Bei *Dasystenella acanthina*, *Thouarella* sp. („flaschen bürsten" artig) und *Ainigmaptilon antarcticum* (flagelliform) weisen zwei Größenklassen von Oocyten auf einen Entwicklungszyklus von mehr als einem Jahr hin. Bei *Fannyella rossii* und *Fannyella spinosa* (dichotom verzweigt) wurde nur eine Größenklasse gefunden, was auf einen einjährigen Zyklus schließen läßt. Drei der untersuchten Arten betrieben Brutpflege (*Thouarella* sp, *Fannyella rossii* und *Fannyella spinosa*). Bei *Ainigmaptilon antarcticum* und *Dasystenella acanthina* wurden keine Larven gefunden, so daß auch keine Aussagen über das Brutverhalten getroffen werden konnten. Die beobachteten reproduktiven Muster unterschieden sich nicht von Arten aus gemäßigten Breiten. Faktoren wie Morphologie und Nahrungsverfügbarkeit scheinen daher eine wichtigere Rolle als geographische Breite oder Wassertemperatur zu spielen.

Verbreitungsmuster, Ernährungsverhalten und Fortpflanzungsstrategie der untersuchten Arten waren sehr heterogen, was auf große ökologische Vielfalt und funktionelle Biodiversität bei polaren benthischen Cnidariern hindeutet. Gerade diese Diversität befähigt diese Organismen zur Entwicklung hoher Populationsdichten und komplexer Gemeinschaften mit anderen Suspensionsfressern, trotz der nichtvorhersagbaren räumlichen und

zeitlichen Schwankungen der Nahrungsverfügbarkeit im polarem Ökosystem. Untersuchungen von anderen Suspensionsfressern unter besonderer Berücksichtigung der Schwerpunkte dieser Arbeit (Verteilung, trophische Ökologie und Reproduktion) könnten in nächster Zeit die Schlussfolgerungen dieser Arbeit auf Gemeinschaften erweitern.

Resumen

La plataforma continental del Mar de Weddell (Antártida), se encuentra poblada en diversos enclaves por comunidades muy abundantes y diversas de suspensívoros bentónicos las cuales presentan además elevados valores de biomasa. Pese a la notable presencia de dichas comunidades, la información acerca del papel ecológico de los organismos que las componen es todavía muy escaso.

El objetivo principal de este trabajo de investigación es avanzar en el conocimiento del papel ecológico que estos organismos juegan en los ecosistemas antárticos. Para lograr este fin, se han definido y elaborado tres objetivos concretos de trabajo en un grupo determinado de especies. Cada objetivo se centra en un aspecto relevante de la ecología de los suspensívoros bentónicos: los patrones de distribución y densidad, el comportamiento trófico y las características reproductoras, focalizando el trabajo en varias especies de cnidarios. El muestreo y trabajo experimental se llevó a cabo a bordo del buque de investigación oceanográfica alemán "Polarstern", a lo largo de tres campañas consecutivas EASIZ (Ecology of the Antarctic Sea Ice Zone, Ecología de la Zona del Margen del Hielo Antártico), dos de ellas durante el verano austral (EASIZ I /1996 y EASIZ II /1998) y una durante el otoño (EASIZ III/2000).

Los patrones de densidad y distribución son uno de los factores decisivos para definir el papel ecológico de especies o comunidades en un ecosistema. En este contexto, se ha estudiado la densidad poblacional de una especie de octocoral, la gorgonia *Ainigmaptilon antarcticum*. Este octocoral es conspicuo y considerablemente abundante en varias zonas de la parte este del Mar de Weddell. La especie presenta una distribución parcheada con bajos valores de densidad en los parches. La posible relación entre distribución y reproducción se discute en este estudio.

Se han investigado así mismo aspectos tróficos en seis especies de cnidarios, dos hidrozoos (*Tubularia ralphii* y *Oswaldella antarctica*), y cuatro antozoos, pertenecientes a diferentes órdenes: un alcyonáceo (*Anthomastus*

bathyproctus), un estolonífero (*Clavularia* cf. *frankliniana*) y dos gorgonáceos (*Primnoisis antarctica* y *Primnoella* sp.).

Dos estrategias de alimentación diferentes han sido encontradas: dos de las especies investigadas (*Tubularia ralphii* y *Anthomastus bathyproctus*) son principalmente zooplanctívoras, estando compuesta su dieta por copépodos y tunicados planctónicos respectivamente. Las otras especies (*Oswaldella antarctica*, *Primnoisis antarctica* y *Primnoella* sp) son básicamnete "micrófagas", y su dieta se basaba fundamentalmente en elementos de la fracción fina del seston (p.e. ciliados y dinoflagelados). La especie restante (*Clavularia* cf. *frankliniana*) parece presentar una dieta mixta entre las dos descritas. Esta heterogeneidad de dietas, refleja la adaptación de estas especies a la variabilidad ambiental del sistema Antártico. La alimentación basada en zooplancton responde a la estación de verano, altamente productiva, siendo durante esta época del año las concentraciones de zooplancton más elevadas, permitiendo así a los predadores aprovechar las misma. Alimentarse en la fracción fina del seston es una adaptación al "sistema de flagelados" antártico, muy constante en su composición en términos de biomasa, permitiendo así a las especies alimentarse durante todo el año.

Las características de la reproduccción y tendencias de la misma han sido investigadas en cinco especies de octocorales, pertenecientes a tres morfotipos diferentes. Dos de ellas eran de tipo "bottle-brush" (*Dasystenella acanthina* y *Thouarella* sp.), otras dos presentaban un patrón de ramificación dicótomo (*Fannyella rossii* y *Fanyella spinosa*) y una era flageliforme (*Ainigmaptilon antarcticum*). Diferentes estrategias reproductivas han sido encontradas entre las especies. Tres de ellas (*Ainigmaptilon antarcticum, Dasystenella acanthina* y *Thouarella* sp.) presentan dos generaciones de oocitos, lo que indica un ciclo reproductor de más de un año de duración. Por otro lado, *Fannyella rossii* y *Fannyella spinosa* tenían tan solo una generación, indicando un ciclo de desarrollo gonadal de un año. Tres de las especies estudiadas son incubadoras o "brooders" (*Thouarella* sp, *Fannyella rossii, Fannyella spinosa).* El modo de incubación de *Ainigmaptilon antarcticum* y *Dasystenella acanthina* no pudo determinarse debido a la

ausencia de larvas en las cavidades gastrovasculares examinadas. Los patrones reproductores hallados no parecen mostrar tendencias diferentes para las especies antárticas comparadas con las descritas para especies de otras latitudes, mientras que otros factores como la morfología y la disponibilidad de alimento parecen jugar un papel más importante en determinar los patrones reproductivos que otros factores como la temperatura o la latitud.

En general, los estudios llevados a cabo muestran una gran heterogeneidad, que evidencia la plasticidad, adaptablidad y diversidad funcional de los cnidarios bentónicos polares. Estas características ecológicas permiten a estos organismos, a pesar de la estocástica distribución espacial y temporal del alimento disponible típicas de los ecosistemas polares, formar densas poblaciones y comunidades junto con otros grupos de suspensívoros bentónicos. El estudio de estos aspectos (distribución, ecología trófica y reproducción) en otras poblaciones de suspensívoros dará lugar a ampliar las conclusiones de este trabajo al nivel de comunidad.

2. Introduction

2.1 Benthic suspension feeding communities on the Antarctic shelf, with particular emphasis on the cnidarians

Most benthic assemblages in Antarctica are dense and taxonomically diverse. Traditionally densities and biomasses of macrobenthos have been described to be high in the Antarctic on both hard and soft bottoms (e.g. Knox & Lowry 1977, Mühlenhardt-Siegel 1988, among others), particularly in comparison to related Arctic communities (Dayton 1990). Although a fully developed epifaunal assemblage in Antarctica may not be comparable, in terms of biodiversity, to a tropical reef, it is nevertheless rich in species. Average benthic biomass in the Antarctic is higher than in temperate and subtropical communities (Brey & Clarke 1993, Arntz 1997). However, productivity/biomass (P/B) values of Antarctic benthic invertebrates are, in general, significantly lower than those of their temperate counterparts (Brey & Clarke 1993, Arntz et al. 1994).

The major component of the Antarctic benthic communities are sessile suspension feeders, e.g. sponges, bryozoans, ascidians, and certain echinoderms (Dayton et al. 1974, Arnaud 1977) (Fig. 1). These communities are spatially highly structured, as has also been observed in temperate (Gili & Coma 1998) and tropical (Karlson 1999) waters, with a high functional diversity and a considerable degree of patchiness in species

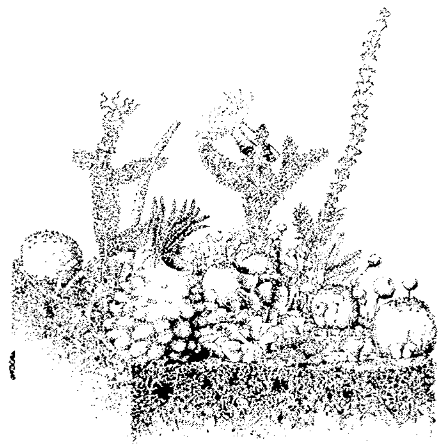

Fig. 1 Ideal representation of a benthic community on the Weddell Sea shelf. (Drawing by Jordi Corbera).

composition at small or intermediate spatial scales (Piepenburg et al. 1997, Gutt & Starmans 1998). Bryozoans, sponges and ascidians dominate many of the Antarctic benthic communities on the shelf (Voß 1988, Galerón et al. 1992), however cnidarians are also a notable component of the suspension feeding communities. According to Starmans et al. (1999), anthozoans are the third dominant taxon in the shelf communities of the Weddell Sea accounting for 10% of the individuals. It is likely that they are the group that contributes most to the tridimensional structure of benthic Antarctic communities (pers. obs. from ROV images).

Therefore, knowledge of the ecological role of benthic cnidarians in the Antarctic system is more relevant than previously assumed. Despite their importance, basic ecological information on their distribution and their trophic and reproductive ecology is scarce in polar regions (e.g. Arntz et al. 1994). Recently, ecological studies of Antarctic suspension feeders have notably increased, e.g., on bivalves (e.g. Davenport 1997, Albertelli et al. 1998), sponges (e.g. Starmans et al. 1999, Kowalke 2000), ascidians (e.g. Sahade et al. 1998, Kowalke 1999), bryozoans (e.g. Sanderson et al. 1994, Barnes & Clarke 1994) and some boreal sponges (e.g. Pile et al. 1996, Riisgård et al. 1998). However, studies in polar regions on passive suspension feeders, such as cnidarians, are still scarce.

The first step to elucidate the ecological role of a given group of organisms in an ecosystem is the determination of its abundance and distribution patterns. Some studies in this field are available (e.g. Gutt & Koltun 1995, Piepenburg et al. 1997, Starmans et al. 1999), however the species level is still very poorly documented. The second main aspect is the behaviour as predators and prey, which implies investigation of the diet, a topic almost unknown in Antarctic assemblages. From an ecological point of view, the energy contribution (Coma et al. 1998) offers the most rigorous and complete information about the ecological role of the organisms. First of all are evaluations of the inputs (feeding) and outputs (investment of the ingested energy) required. The outputs are basically the basal metabolism, growth and reproduction. Growth studies require a detailed temporary monitoring, which is very difficult to achieve on board an oceanographic ship during cruises of 1-2 months. However, the quantification of reproductive parameters is feasible.

In the following paragraphs, three aspects of the ecology of the Antarctic benthic cnidarians will be explained in more detail: distribution, feeding and reproduction.

2.2 Density and distribution of benthic organisms

The spatial pattern exhibited by soft bottom macrobenthic organisms is the first clear evidence of their response to environmental factors and determines their ecological role (Thrush 1991). In nature, organisms are generally aggregated in patches, or form gradients or other spatially related structures. Large-scale (both spatial and temporal) abiotic factors cause broad patterns of distribution (Barry & Dayton 1991). Other processes operate continuously at smaller temporal and spatial scales modifying distributions and abundances. These smaller-scale factors may be biotic, abiotic or involve interactions between both (Thrush 1991).

The distribution patterns of invertebrate benthic megafauna species are usually patchy (e.g., Picken 1980, Miller 1998). Ecological analyses of Antarctic assemblages on a spatial scale from metres to a few hundred kilometres showed a patchy distribution (e.g. Voß 1988, Gutt 1991, Gutt & Piepenburg 1991, Barthel & Gutt 1992, Gutt & Koltun 1995). This patchiness seems to be mainly affected by variation in sediment type and benthic food supply, which depends on primary production, sedimentation, hydrographic factors and seasonal ice cover (Grebmeier & Barry 1991). Studies from the Weddell Sea shelf did not show any correlation between environmental variables (water depth, longitude, latitude and distance between stations and ice edge) and faunal distribution (Starmans et al. 1999). An interpretation of this phenomenon may be found in the fact that communities do not exhibit a depth zonation gradient in the Weddell Sea, where the same authors found a geographical zonation and distinct assemblages despite pronounced meso-scale patchiness.

Anthozoans exhibit contagious patterns of distribution (Williams 1976) and several octocoral species also show a patchy distribution (e.g. Chia & Crawford 1973, Langton et al. 1990, Rice et al. 1992). Most of the literature available corresponds to tropical and temperate regions (Gili et al. 1999). In these areas, high density at the patch level is a common phenomenon (e.g Kinzie 1973, Grigg 1977, Gili & Ros 1985), contrasting with the patterns found in the Antarctic (Gili et al. 1999).

Taking into account the information on distribution patterns and features of benthic megafauna in the Weddell Sea, as well as the knowledge on octocoral distribution patterns from other latitudes, we focused on the distribution of the Antarctic octocoral: *Ainigmaptilon antarcticum*, a conspicuous species in many areas of the Eastern Weddell Sea shelf.

2.3 Trophic ecology of the cnidarians

The Southern Ocean is in general an oligotrophic environment dominated by flagellates and other small organisms of the pelagic retention system, with short overlying outbursts of microalgae (bloom system) in spring and summer (Sakshaug & Holm-Hansen 1984, Scharek & Nöthig 1995) which are essential for larger zooplankton. The benthic suspension feeders must adapt their feeding strategies to the features of the Southern Ocean: high primary productivity in summer, reduced to almost zero in winter, and to the vertical flux characteristics. The apparently discontinuous pattern of food availability may determine their activity rhythms, metabolic rates, and reproductive

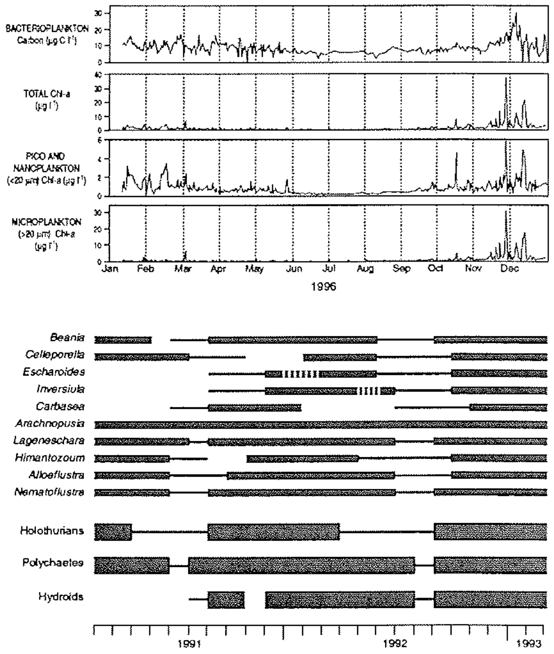

Fig. 2 The upper part of the figure shows the variation of pico-, nano- and microplankton as well as of chlorophyll throughout the year. The diagram below shows the activity rhythms of different suspension feeders. (Sources: Kang et al. 1997, Barnes & Clarke 1995, respectively).

patterns. For some time the summer blooms were suspected to determine the feeding strategies and diet composition of the benthic communities in Antarctica. These organisms were thought to feed heavily during a few weeks in summer, and sustain long periods of starvation the rest of the year. This would resemble overwintering as resting stages or hibernation periods that have been described for other latitudes (Gili & Hughes 1995, Garrabou 1999). However, Barnes & Clarke (1995) have demonstrated that certain species of Antarctic shallow-water benthic suspension feeders are able to feed throughout the year with only short periods of starvation (Fig. 2).

Microplankton (20-200 µm) dominates the phytoplankton assemblages in the Antarctic water column and the sediment only during short periods, while pico- and nanoplankton (between 0.2 and 20 µm) dominate during most of the year (Cripps & Clarke 1998). This ambivalent planktonic system may potentially supply food to suspension feeders throughout the year. Planktonic communities are actively exploited by benthic suspension feeders (e.g. Graf 1992), as these animals partially return the organic matter captured from the water column, in detritic and dissolved form or through meroplanktonic larvae. All these findings come, however, from shallow waters. The question arises whether the shallow water situation is also applicable to shelf communities.

Like other suspension feeders, cnidarians depend on the available food suspended in the water column and on the near bottom currents. In the Southern Ocean not only vertical fluxes (Bodungen

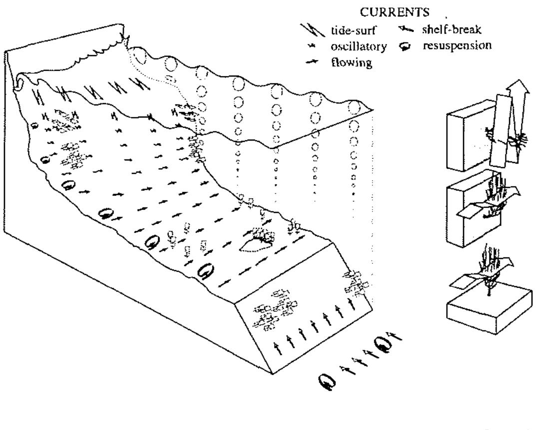

Fig. 3 Bottom water currents along the continental shelf and slope, composed of oscillatory, longitudinal and lateral coast currents including resuspension processes (black circular arrows in the general view, and white arrows in the detailed view) (modified from Riedl 1971). Diagrams show the orientation of suspension feeder colonies and where development of dense suspension feeder communities is likely.

et al. 1986, Nöthig & Bodungen 1989), but zooplankton, seston, elements of the microbial food web and resuspension processes contribute to the potentially available food for benthic suspension feeders. Horizontal advection processes (Dunbar et al. 1989, Grebmeier & Barry 1991) and meso- and small- scale hydrodynamic mechanisms (Gili et al. in press) enable continuous water renewal close to the bottom, which probably explains the dense benthic suspension feeder communities on the shelf and slope (Fig. 3).

Although cnidarians have traditionally been considered mainly carnivorous (Hyman 1940), recent findings from Antarctica (Gili et al. 1996) and other latitudes (e.g. Fabricius et al. 1995 a,b, Elyakova et al. 1981) give evidences of herbivory.

The diet of gorgonians as well as that of other suspension feeders varies between dissolved organic matter (via plankton) and other benthic organisms (Fig. 4). It is very well coupled to the dynamics of their potential prey, making this group a good example of bentho-pelagic coupling (Ribes et al. 1998, 1999). The ability of suspension feeders to capture important amounts of planktonic prey implies that the grazing pressure on the water column planktonic communities by benthic macro-invertebrates must be much greater than previously thought (e.g. Coma et al. 1995a, Pile et al. 1996, Gili et al. 1999, Riisgård in press, Orejas et al. in press).

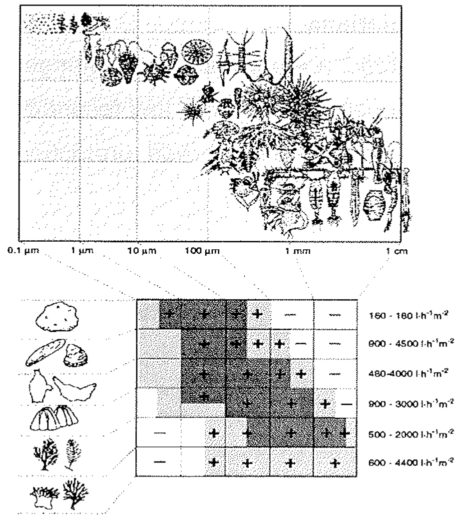

Fig. 4 Prey type and size in different benthic suspension feeders, considering the recent findings on their natural diet which increased the range of quality and quantity of prey both at small size (pico and nanoplankton, continuous prey) and at big size (zooplankton and microplankton, occasional prey). Light shaded areas and bold crosses refer to information that has been added to Riedl's original figure. Potential of filtering water (right hand) of each group is also shown. (Gili et al. 2000 after Riedl 1966).

Information on the trophic ecology of cnidarian species in Antarctic communities is very scarce

(Gili et al. 1996, Slattery et al. 1997, Gili et al. 1999). Preliminary studies analysing gut contents of several gorgonians from Antarctic waters (Alvà et al. 1997) showed a very low number of zooplankton prey in the polyps, despite high zooplankton densities in the water column. Another paradoxial fact is the high reproduction rates of octocorals in Antarctic waters (Gili et al. 1999), comparable to those from other latitudes (Orejas et al. submitted).

This indicates that these organisms must take other planktonic components in order to cover their energetic demands. Recent literature shows that the fine fraction of seston (mainly phytoplankton, pico- and nano-plankton) plays an important role in the diet of various benthic suspension feeders from temperate and boreal latitudes (e.g Ribes et al. 1998, 1999, Riisgård et al. 1998), tropical areas (Fabricius et al 1995, Yahel et al. 1998), and also in the Antarctic (Kowalke 2000, Orejas et al. in press).

The present work tries to evaluate the trophic behaviour and diet composition of some selected species of this taxonomic group in Antarctica.

2.4 Reproductive ecology of the cnidarians

Reproductive patterns in the Antarctic are defined by prolonged gametogenesis, delayed maturation, seasonal reproduction, low fecundity, large yolky eggs, non-pelagic development, brooding, brood protection, viviparity, slow embryonic development, and advanced newly-hatched juvenile stages (Thorson 1950, Pearse et al. 1991). Although some factors seem to define general features of reproduction in Antarctic organisms (e.g. Arnaud 1974, White 1977) (Fig. 5), there are large differences among groups and even species (Arntz et al. 1994). The general trend suggested by

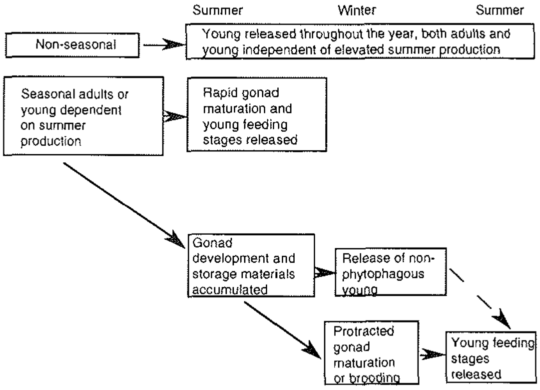

Fig. 5 Model of Antarctic poikilotherm breeding cycles (from White 1977).

Thorson (1950) towards non-pelagic development and brood protection in polar waters was corroborated for some groups such as echinoderms (e.g. David & Mooi 1990, Pearse et al. 1991) and bivalves (Pearse 1986). Pearse et al (1991) and Berkman et al. (1991) discussed the validity of "Thorson's rule" as several benthic species with pelagic development mode were found. Among the types of pelagic development, lecitotrophic larvae seem to be the most frequent. This mode of development requires less energy than the planktotrophic one (Picken 1979), which may explain the preponderance of lecitotrophic patterns of development in Antarctic prosobranch gastropods where trophic resources are thought to be particularly limiting (Picken 1979). However, despite the prevalence of lecitotrophic development, some of the most common and widespread shallow-water Antarctic marine invertebrates have pelagic planktotrophic larvae (see Pearse et al. 1991 for a review), and even planulae of octocorals have been found throughout the year in Signy Island (Stanwell-Smith et al. 1999).

Studies on reproduction patterns of anthozoans have been conducted in the last two decades in temperate and tropical regions (e.g. Hughes & Jackson 1980, Martin 1982, Brazeau & Lasker 1990, Coma et al. 1995b). Quantification of the reproduction of octocorals is carried out using a combination of parameters such as oocyte number and size as well as environmental and biological factors (e.g. food availability and morphology). These factors have been identified as elements which govern reproduction processes. Some general patterns have been found for octocorals at different latitudes (e.g. Grigg 1977, Martin 1982, Coma et al. 1995b), for instance, separate sexes and a sex ratio of 1:1. Seasonality in gamete development and size at first reproduction (Sebens 1982, Hughes & Cancino 1985) seem to define reproduction features and timing. Some reproductive patterns of deep-sea cnidarians are known (e.g. Van Praet et al. 1990, Tyler et al. 1995, Eckelbarger et al. 1998), but information on polar species is scarce. The descriptive studies of Wright & Studer (1889) and Versluys (1906) argued that separate sex and brooding seem to be also common features of Antarctic and deep-sea octocorals. However, there are so far only two studies on the reproductive ecology of Antarctic cnidarians: the work of Brito et al. (1997) on the gorgonian *Thouarella variabilis* and the study of Slattery & McClintock (1997) on *Clavularia* cf. *frankliniana*.

In this study the features and trends of reproduction of five Antarctic octocoral species were studied and compared with those of other Antarctic invertebrates and those of octocorals from other latitudes.

2.5 Aims of the present study

The objectives of this thesis are:

(a) To determine the density and distribution patterns of an Antarctic gorgonian (*Ainigmaptilon antarcticum*), using video material (first approach to underwater visual studies of Antarctic cnidarians).

(b) To determine the diet of six species of Antarctic cnidarians: *Oswaldella antarctica* (Hydrozoa), *Tubularia ralphii* (Hydrozoa), *Clavularia* cf. *frankliniana* (Anthozoa), *Anthomastus bathyproctus* (Anthozoa), *Primnoisis antarctica* (Anthozoa) and *Primnoella sp.2* (Anthozoa), considering the physical and biological features of the Antarctic environment, the factors which regulate the availability of food at the sea floor, and the various potential food sources for benthic suspension feeders. The main objective of the trophic studies was to ascertain the cnidarian diet spectrum, and to find out the relevance of the fine fraction of seston is in the diet of Antarctic cnidarians.

(c) To define the reproductive patterns of five species of Antarctic octocorals from the Weddell Sea shelf (*Dasystenella acanthina*, *Thouarella* sp., *Fannyella rossii*, *Fannyella spinosa* and *Ainigmaptilon antarcticum*) and to compare them with those of other related Antarctic invertebrates and octocorals from other latitudes.

(d) To find out the factors which might be responsible for the timing in the reproductive processes of the studied species.

(e) To investigate the role of the benthic cnidarians in the Antarctic ecosystem discussing the similarities and differences to other latitudes.

3 Study Area

The studies presented here were carried out in the eastern Weddell Sea (Antarctica). The main sampling area was the continental shelf in front of Kapp Norvegia (Fig. 6).

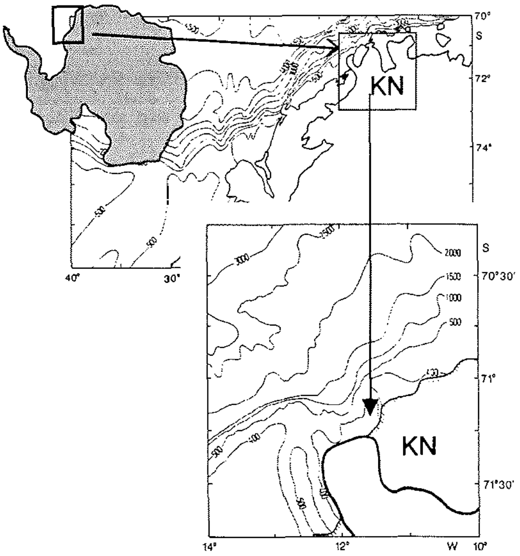

Fig. 6 Study area. Continental shelf of the Eastern Weddell Sea in front of Kapp Norvegia. (Source: Fahrbach et al. 1992).

3.1 Geographical location and physical characterisation of the eastern Weddell Sea

The Weddell Sea is surrounded by the Antarctic Peninsula to the west, the Scotia Arc to the north, East Antarctica to the southeast, and West Antarctica to the southwest (Fig. 7).

Due to this particular geographical emplacement between the High Antarctic and the Scotia Subregions the Weddell Sea may be regarded as a transition zone, a "bridge" with elements belonging to the neighbouring areas.

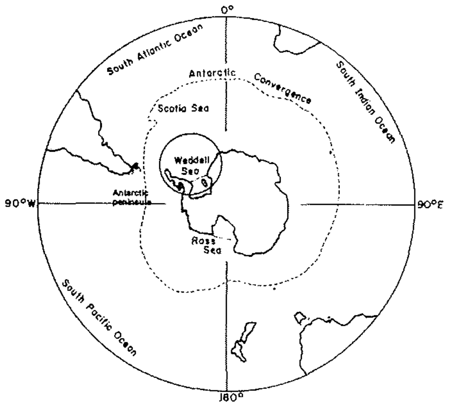

Fig. 7 Location of the Weddell Sea in the Antarctic. (Source: Nicol 1994)

The environmental factors characterising the Weddell Sea are (like in other oceans in the world): depth, temperature, salinity, substrate features, hydrography, water currents etc. The marked seasonality of biotic factors are not exclusive of this system either, however, the duration of the ice cover is a specific polar feature that needs to be taken into account.

In the last years knowledge on the physical and biotic features of the Weddell Sea has much improved. In this chapter, a brief description will be given derived from the available literature.

3.1.1 Bathymetry, topography and sediment characteristics

The bathymetry of the continental margin and the coastal regions of Antarctica is still only partly known. Due to its remote character and presence of ice-cover, the Weddell Sea is a region of difficult access and there are little available data on the bathymetry of the area, which supply information of different type, source and quality. Few original data are available for the central and southern part of the Weddell Sea and the sea bottom below the Filchner-Rønne ice shelf. Bathymetric features of the Weddell Sea are the very deep shelf, reaching ca. 600m, and a narrow extension (30 km in the Kapp Norvegia area). Fig. 8 shows a perspective of the southern part of the trench off Kapp Norvegia.

The particular topographic features in the eastern Weddell Sea influence the hydrographic patterns in the area. For example, the topographic rise at the shelf edge off Kapp Norvegia reduces horizontal advection and retains cold Winter Water (WW) during summers (Fahrbach et al. 1992). In contrast Warm Deep Water (WDW) can be found on the shelf off Halley Bay. This

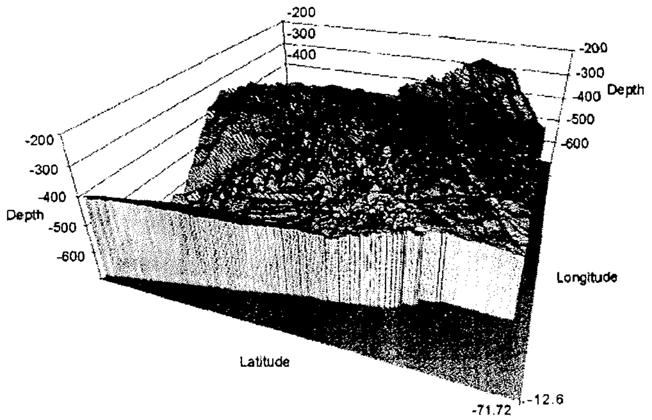

Fig. 8 Perspective view of the southern part of the trench off Kapp Norvegia (Source: Niederjasper et al. 1997).

illustrates rather heterogeneous conditions in the near bottom water layers due to differences in the exchange rates with the open ocean and with the near surface layers (Fahrbach et al. 1992). The first topographic characterisations of the Weddell Sea were presented by Kvinge (1968), Carmack & Foster (1977), Kohnen (1981) and Grobe (1986). Among the most recent papers are those of Bell & Brozena (1990), Hinze (1994), and the bathymetric charts of Schenke et al. (1998).

Current directions in the area are strongly directed by the bottom topography and tidal currents are very important for sediment transport (Fahrbach et al. 1992). According to Grobe (1986) the sedimentation rate on the Weddell Sea shelf in front of Kapp Norvegia is 0-3 cm/1000 years. Voß (1988) described the different sediment types in this area. Sediment characteristics as well as sedimentation processes are widely described in the literature (e.g. Anderson et al. 1980, Orheim & Elverhoi 1981, Elverhøi & Roaldset 1983, Haase 1986, Grobe 1986). Recently the sediment was characterized also using new acoustic methods (Kuhn & Weber 1993).

A general feature for the eastern part of the Weddell Sea are the biogenic sediments, composed mainly of sponge spicules. These spicules are also abundant in deeper sediment cores as spicule mats (Grobe 1986). In some places fragments of Bryozoa are another component forming biogenic sediment beds. In the eastern part, a variety of channels and sediment ridges have been detected, indicating intensive sediment redeposition by bottom currents (Weber 1992).

3.1.2 Hydrography

General oceanographic circulation of the Weddell Sea is characterised by an elongated cyclonic movement of all water masses, denominated the Weddell Gyre (Fig. 9). Early pioneers (e.g., Brennecke 1918, Sverdrup 1954) recognized the Weddell Sea as the major source for the formation of bottom water: 70-80% of the bottom water produced world wide originates from the Weddell Sea (Carmack 1977, Foldvik & Gammelsrød 1988). Together with deep convection of cool and low-salinity in the area of Maud Rise (Gordon 1982), the formation of Weddell Sea Bottom Water (WSBW) on the southern and south western Weddell Sea shelf (Filchner-Rønne Ice Shelf) plays a key role in bottom water formation. Two water masses contribute to the bottom water formation: the high-salinity Western Shelf Water (WSW) and the super cooled Ice Shelf Water (ISW). In Fig. 10 a schematic representation of the water masses in the Weddell Sea is given.

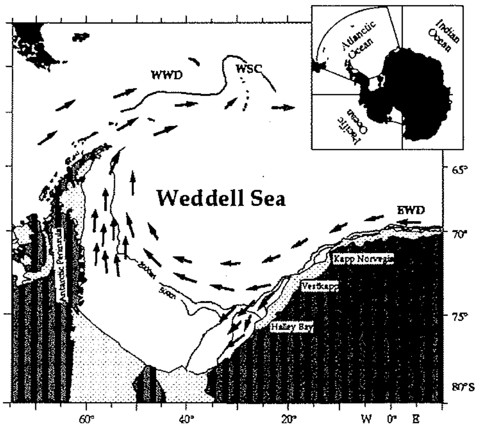

Fig. 9 The mean oceanic surface currents which form the Weddel Sea gyre (after Hubold 1992). (For abbreviations see Glossary).

On the shelf of the Weddell Sea there is a conjunction of different water masses. The largest water mass in the eastern Weddell Sea is located of the "Filchner Cavity" and is named Eastern Shelf Water (ESW). Features of this water mass are salinity values ranging from 34.28 to 34.44%o and temperatures between -2.0°C and -1.6°C. In the Kapp Norvegia area the warm and highly saline core reaches potential temperatures of 0.8°C and salinities of 34.69%o. The salinity maximum is found about 100m deeper than the temperature maximum. The depth of the surface mixed layers is 50 to 100m in the open ocean and increases to more than 500m near the continental shelf edge (Fahrbach et al. 1992).

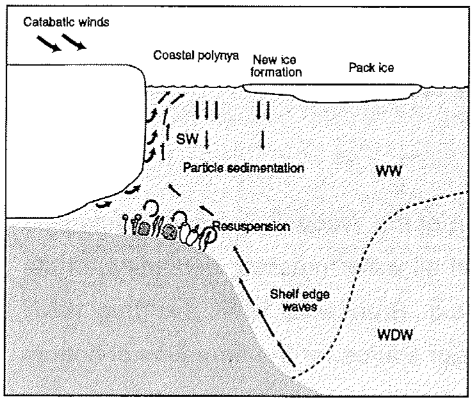

Fig. 10 Schema of the water masses and thermohaline circulation under an open polynya. Resuspension processes and their influence on the benthic communities on the Weddell Sea shelf. (Source: Scharek 1991). (For abbreviations see Glossary).

Current directions vary strongly during the year in the Kapp Norvegia area, between 197° to 257° at different locations and depths. Current speed ranges on average from 10 to 20 cm/s, and reaches maximal values of 54 to 68 cm/s on the shelf of Kapp Norvegia at 400-680m depth (Fahrbach et al. 1992). Thiel et al. (1960) estimated tidal currents ranging between 10 and 15 cm/s on the Weddell Sea shelf. In the eastern Weddell Sea, the current associated with the Antarctic Slope Front splits into two cores, centered above the continental slope in water depths of 1000m and 300m. Surface currents in the southern core are close to 50cm s^{-1}. In addition, a shallow, fast current just inshore of the southern core may indicate the merging with the Antarctic Coastal Current often observed on the continental shelf, near the front of ice shelves. A northeast undercurrent at 800m depth on the flank of the continental slope has a transport of approximately 0.1 Sv (1 Sv= 10^6 m^3 s^{-1}) (Heywood et al. 1998).

The correlation between the seasonal cycle of wind and current speeds points to the wind as an important driving force of the coastal current. Seasonal variations of the current decrease towards the bottom and offshore (Fahrbach et al. 1992). Catabatic winds and/or pronounced tidal currents lead to the formation of coastal polynyas in front of the ice shelves (Gill 1973, Gamelsrød & Slotsvik 1981). Within the polynyas the extent of thermohaline convection is reduced in summer due to melting of sea-ice. There is an intensified sea ice formation in winter resulting in enhanced thermohaline convection (Foster 1972, Foldvik 1986).

3.1.3 Ice conditions

A large part of the Weddell Sea is covered during the whole year by ice, which is renewed every year. During August this ice cover reaches its largest extension: 4.36 x 10^6 km^2, whereas in February, there is a marked reduction to values close to 1.14 x 10^6 km^2 (Ropelewski 1983). In winter, the ice may reach 60° S in northern direction (Foster 1981). During the austral summer there is, however, a wide ice-free area (Fig. 11). The ice cover varies notably between the same season in different years, mainly in the eastern part of the Weddell Sea. In the last years, knowledge on the ice conditions in the Weddell Sea has increased considerably, for example on ice formation rates (Eicken 1998), regional and temporal variation of the sea ice draft (Strass & Fahrbach 1998) and sea ice seasonality (Parkinson 1998).

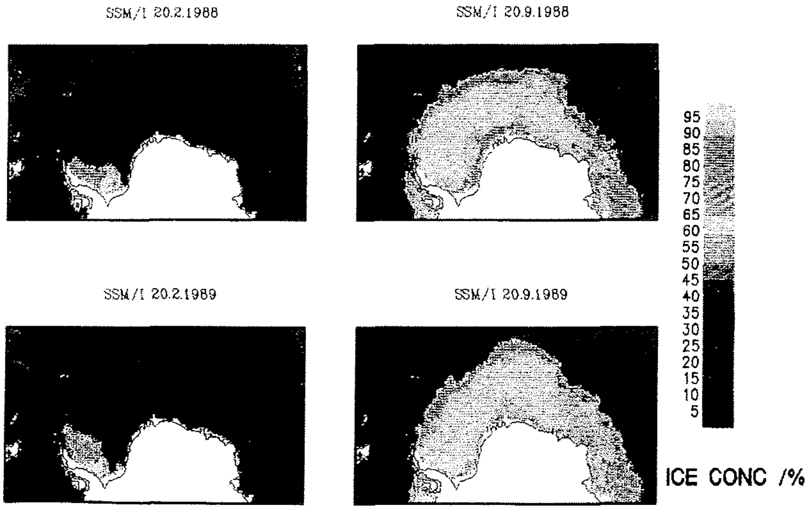

Fig. 11 Sea ice-cover in summer (left) and winter (right) in two consecutive years, obtained from satellite images. (Source: Lemke & Viehoff 1991).

3.1.4 Disturbance by iceberg scouring

The most important agent of disturbance in the Antarctic is the ice (Dayton 1990, Clarke 1996). Periodicity and seasonality of disturbance by ice in the Antarctic depends on many factors, such as depth substratum profile and latitude (Barnes 1999).

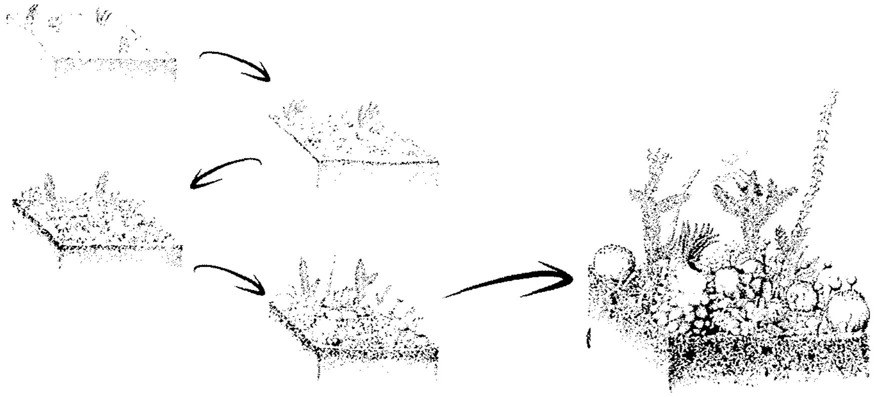

Fig. 12 Idealised diagram of succession in Antarctic shelf suspension feeder communities. The development of dense, three-dimensional communities involves continuous patch spreading and aggregation during succession which is believed to be a slow process (Drawing by Jordi Corbera).

Ice scour is caused by floating icebergs and is the most evident disturbance on benthic communities because the bergs ground and scrape on the sea floor. The physical process occurring during this scraping, at the level of the seabed, has been described in a recent review of Woodworth-Lynas et al. (1991).

In the eastern Weddell Sea, the use of imaging methods showed for the first time that iceberg scouring destroys benthic life on the Antarctic continental shelf and originates recolonisation processes in disturbed areas by mobile invaders and sessile pioneer species (Gutt 2000) (Fig. 12). The rate of disturbance in the Weddell, Amundsen and Bellinghausen Seas was calculated at 4.4% of the affected area. From these data a first approximation has been derived as to the possible periodicity of this kind of disturbance, which was suggested to occur on average once every 230 years (Gutt et al. 1996).

The influence of iceberg scouring on the structure and biodiversity of a benthic community in the southeastern Weddell Sea has also been evaluated (Gutt et al. 1998). The result was that despite the devastation at small scale, biodiversity increases at larger scales due to the multitude of successional stages present. However, knowledge of the influence of icebergs in the pelagic and benthic ecosystems is still scarce. For example, modification of currents due to the presence of icebergs should be very important, mainly in places where icebergs are accumulated such as the iceberg cemetery of Auståsen, in front of Kapp Norvegia. Change of current direction and speed should also influence the plankton dynamics. Furthermore, scraping of the seabed and stirring up sediment may have an important influence on the dynamics of the benthic communities.

3.2 Biological characterisation of the study area

3.2.1 Brief introduction to the benthic system

Around the entire Antarctic continent, similar species assemblages seem to occur. This is a unique phenomenon in marine biogeography as a consequence of the circumpolar current. On the Weddell Sea shelf, most of the coastal regions exhibit differences in community composition on small spatial scales, usually in response to differences in wave exposure, topography or substrata. Voß (1988) published the first characterisation of the Kapp Norvegia area in the eastern Weddell Sea. As main features of the area he described the presence not only of sandy bottoms, but also of sponge spicules mats, bryozoan debris, stones, he also found a large number of taxa, and high species diversity and evenness. A first description of the benthic associations in the Weddell Sea was also included in this work and extended by Galéron et al. (1992) and Gerdes et al. (1992) who in particular referred to their species richness mainly in sponges and bryozoans (see Fig. 1). Furthermore, Gutt (1991), Gutt & Piepenburg (1991), Gutt & Koltun (1995) and Starmans (1997) contributed to the description and characterisation of the eastern Weddell Sea shelf communities. Gutt & Starmans (1998) and Starmans et al. (1999) identified assemblages of taxa as well as key species, described the biodiversity of the assemblages and tried to determine environmental and biological factors that influence faunal composition. Weddell Sea communities did not appear to be correlated with depth, geographical situation or locality on the shelf or shelf edge (Starmans et al. 1999). The different assemblages identified by Gutt & Starmans (1998) in the eastern Weddell Sea and their relations with different substrate types can be seen in Fig. 13.

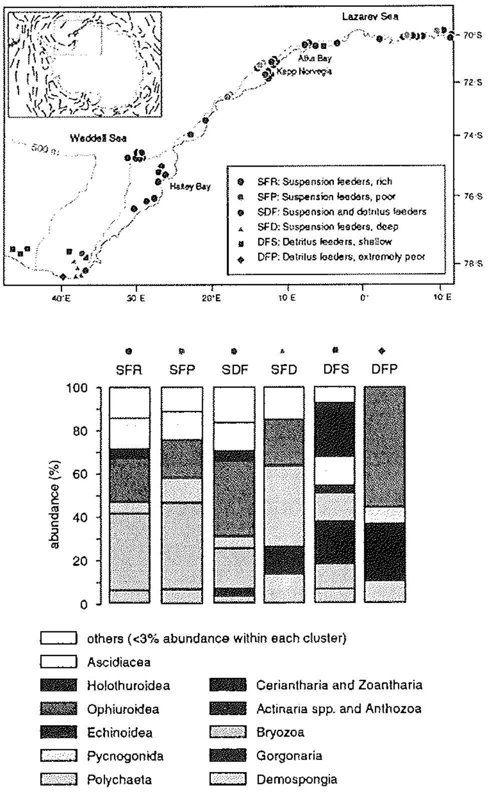

Fig. 13 Upper part: Assemblages of benthic suspension and deposit feeders in the study area. Below: Relative abundance of the different benthic groups in each assemblage. (Source: Gili et al. 2000, redrawn from Gutt & Starmans 1998).

3.2.2 Brief introduction to the planktonic system

Due to the special character of the present work, where the benthopelagic coupling is relevant to an understanding of the ecological role of the benthic suspension feeders, it was considered necessary to present a short paragraph on the phyto- and zooplankton system in the eastern Weddell Sea.

Antarctic shallow waters are characterised by dense but brief summer blooms of diatoms (8-10 weeks y^{-1}) and high productivity associated with low productivity during other periods of the year (Clarke 1988). Near the Weddell Front, low values of primary production ranging from 100 to 350 mg C m^{-2} d^{-1} were obtained in October-November, and from 50 to 250 mg C m^{-2} d^{-1} in May

(Mathot et al. 1994). A peculiarity of the planktonic system in the Weddell Sea, and other areas in the Southern Ocean, is that the organisms living in the sea ice contribute up to 30% of the total biomass production of the South Polar Sea (Spindler & Dieckmann 1991).

The meso- and macrozooplankton epipelagic communities have been described in detail in the Weddell Sea by Boysen-Ennen & Piatkowski (1988). Based on topography and water mass features three distinct epipelagic communities were defined in the Weddell Sea: the oceanic, the southern shelf and the north-eastern community (Boysen-Ennen & Piatkowski, 1988). The last mentioned, which corresponds to our sampling area, was characterised by the highest zooplankton abundances (ca. 31,000 ind/1000m^3). The fauna was composed of oceanic and neritic species, and fine filter feeders prevailed, mainly (65%) copepods and tunicates (Boysen-Ennen & Piatkowski 1988). However, most of the research on planktonic communities was done in the first 200-300m of the water column (e.g. Montu & Oliveira 1986, Boysen-Ennen & Piatkowski 1988, Hosie 1994). Very little literature is available for deeper waters and most of it deals only with the most abundant species (e.g. Atkinson 1991, Schnack-Schiel & Hagen 1995). Recent results from winter show a higher spatial and temporal variability of the Weddell Sea ecosystem than previously thought (Spiridonov et al. 1996), which may influence the seasonal pattern of organic carbon transport from the pelagic zone to deeper waters and to the sea floor. The observed pattern for various zooplanktonic organisms of maximal biomass concentration in surface layers during summer and in deep layers in winter (Smith & Schnack-Schiel 1990) could also be very relevant for the benthic communities.

4. Material and Methods

4.1 Sampling

Sampling was performed on board the German RV "Polarstern" during the EASIZ cruises I (ANT XIII/3, January-March 1996), II (ANT XV/3, January-March 1998) and III (ANT XVII/3; March-May 2000). For more details on the expeditions see Arntz & Gutt (1997, 1999) and Arntz & Brey (in press). Specimens were sampled between 200 and 400 m depth with Agassiz and bottom trawls, a small dredge and a TV Grab of 1.82 m^2 area. Images were taken with a Remotely Operated Vehicle (ROV).

As comprehensive descriptions of the methods used are included in the separated publications, they will only be shortly outlined here with references to the appropriate publications. Fig. 14 presents an overview of the used methods.

4.2 Sample treatment

Five different methods have been employed for the treatment of the samples:

a) Density and distribution studies. Transects were conducted with a ROV (for a detailed description of the ROV see Starmans et al. 1999) and recorded using a video camera, at depths ranging between 142 and 363 m. Images have been processed following the methodology described in publication III.

b) Feeding experiments. To conduct the feeding experiments, the specimens were immediately transferred to sea-water aquaria, and placed in a container equipped for operation at low temperature (-1°C to 0,5°C). For details see "material and methods" chapter of publications I and II.

c) Determination of gut contents and reproduction studies. Samples were preserved on board "Polarstern" in 10% formalin (in the case of feeding studies) and 4% formalin (in the case of the reproduction studies). See the "material and methods" of publication I and II for the feeding aspects and of publication III and IV for the reproductives patterns.

d) Histological reproduction studies. To study the reproductive stage of the gorgonian *Ainigmaptilon antarcticum*, histological sections were prepared. Technical aspects and details are in publication III.

e) SEM observations. In order to see the structure of the gonads of *Ainigmaptilon antarcticum* samples were prepared for SEM (scanning electron microscopy). Detailed information is available in publication III.

The species used for the different studies were selected in function of their abundance in the study area and in the case of the feeding experiments also in function of their survival in aquaria. For the reproduction studies the selected species should be representative of the different morphotypes present in the area. Originally it was planned to do a comprehensive study of distribution, feeding and reproductive ecology of the gorgonian *Ainigmaptilon antarcticum*. The difficulties to keep this species in aquaria did not allow to perform the feeding experiments.

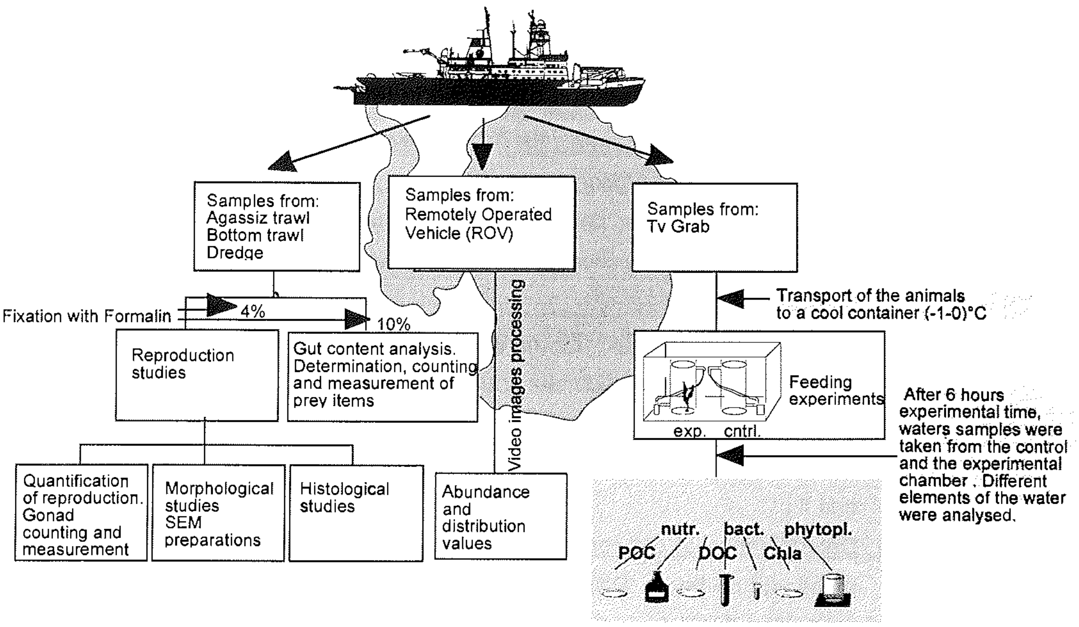

Fig. 14 Summary of the sampling procedure and sample treatment for the different studies. Details are given in the "Material and Methods" section of each publication.

5. Conclusions and discussion

In this section an overview of the main results obtained in the four papers will be presented. Specific topics are discussed in more detail in the separate publications. Ecological observations of the species and populations studied are analysed and discussed in relation to environmental and biological conditions of the Antarctic ecosystem and compared with patterns observed in species inhabiting at other latitudes.

5.1 Density and distribution patterns of the cnidarian *Ainigmaptilon antarcticum* in the Weddell Sea

The distribution pattern of *Ainigmaptilon antarcticum* was very clumped, and showed low densities at the patch level (Fig. 15). The average density for all transects was 12 ind $100m^{-2}$ and in the patches 17 ind $100m^{-2}$. The dispersion index used (Morisita's Index) pointed to an aggregated distribution pattern, even at small scale (dozens of meters). This distribution seems to be similar to the patterns observed in other Antarctic gorgonians (Gili et al. 1999) and, in general, in Antarctic shelf communities (e.g. Gutt 1991, Gutt & Piepenburg 1991, Gutt & Koltun 1995). These low densities contrast with the density of gorgonians in temperate and tropical areas (e.g. Gili & Ros 1985). The reasons for this kind of distribution are unclear, but it is known that feeding modes contribute to spatial configurations, influencing large-scale distribution patterns with changes in biomass, production and diversity along a gradient of food availability (Thrush 1991). Environmental factors, such as water depth and movement, sediment type, and the sea bed are believed to determine large-scale patterns of distribution (e.g.

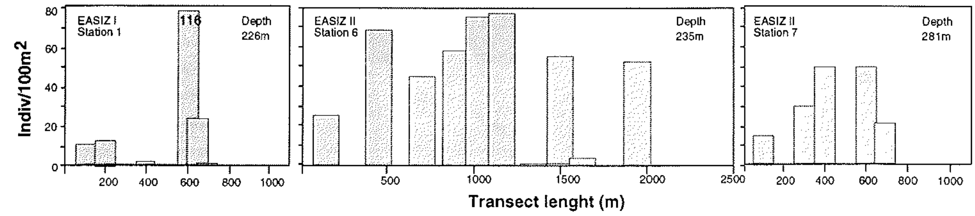

Fig. 15 Density of *A. antarcticum* in some transects in the area of Kapp Norvegia (Weddell Sea).

Thorson 1957, Gray 1974, Warwick & Davies 1977, Barry & Dayton 1991, Piepenburg et al. 1997). In addition to these abiotic factors, biological interactions influence species diversity and spatial dispersion patterns (e.g. Dayton & Hessler 1971, Grassle & Sanders 1973, Sanders 1979).

***Ainigmaptilon antarcticum* shows an aggregated distribution pattern with low abundances. Distribution and density are likely to be determined by food availability and dispersion mode.**

5.2 Trophic behaviour of cnidarian species on the Weddell Sea shelf

The six Antarctic species investigated have developed different feeding strategies and are thus able to profit from the different trophic niches offered

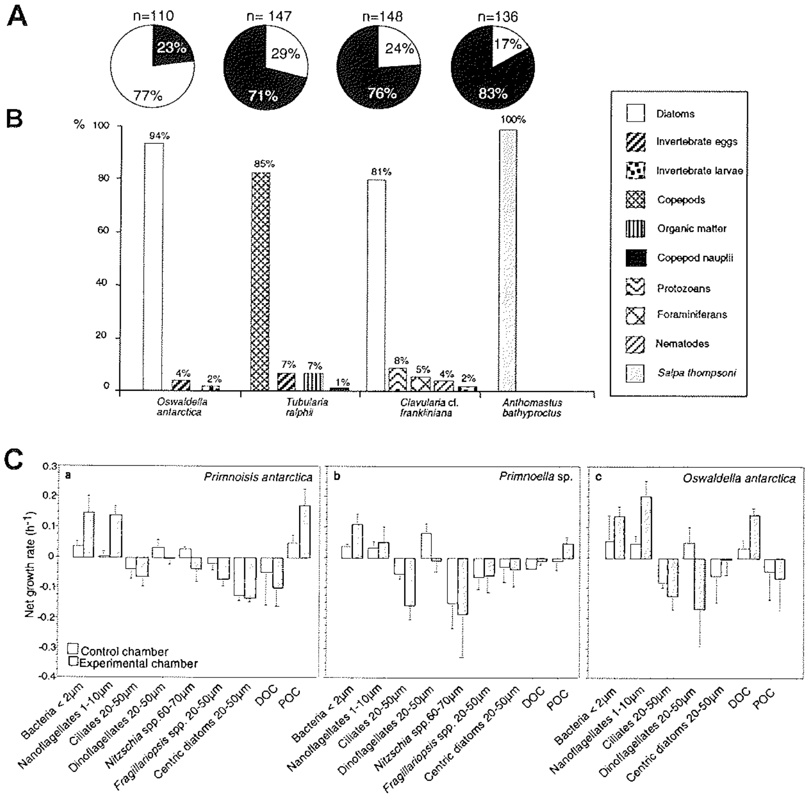

Fig. 16 A) Percentage (by number) of full and empty gastrovascular cavities in the four studied species. Black colour shows coelenteron with prey items , white colour without. B) Percentage (by number) of prey items of different groups found in the dissected polyps. C) Net growth rates (h^{-1}) (mean±SD) in the control (white bars) and experimental (dotted bars) chamber for *Primnoisis antarctica* (a), *Primnoella* sp. (b) and *Oswaldella antarctica* (c), for each prey group, POC and DOC. Size range of each plankton group is indicated.

by the ecosystem.

Two main strategies were identified: (1) "macrophagy", corresponding to benthic zooplanktivorous species, which feed either on substratum-associated organisms and larvae or on few holoplanktonic animals such as calanoid copepods (Sebens & Koehl 1984), and (2) "microphagy", corresponding to benthic organisms which feed on the fine fraction of seston (Orejas et al. in press). *Tubularia ralphii* and *Anthomastus bathyproctus* clearly belonged to the first category whereas *Oswaldella antarctica*, *Primnoisis antarctica*, and *Primnoella* sp. showed microphagous feeding behaviour. *Clavularia* cf. *frankliniana* presented a mixed diet. The different diets encountered are summarised in Fig. 16.

Apparently, feeding strategies and diets in the Antarctic cnidarians are similar to those of other latitudes. The wide variety of diets found in the Antarctic benthic cnidarians coincides with findings for gorgonian species in the Caribbean (Lasker et al. 1983, Ribes et al. 1998) and in the Mediterranean Sea (Ribes et al. 1999). The prey items were quite different, comprising from bacteria to zooplankton. Similarly the capture rates obtained in our studies on hydroids are comparable to those of related species in temperate waters (Gili et al. 1998).

The studied octocoral species do not seem to make much use of large zooplankters and feed primarily on the fine fraction of seston, mainly on particles > 5 µm. The presence of benthic diatoms in the gastrovascular cavity of *Primnoella* sp. and *Primnoisis antarctica*, both in field and experimental specimens, leads to the conclusion that resuspension (see Fig. 10) may be an important food source for these organisms.

Different trophic strategies have been developed among Antarctic benthic cnidarians enabling them to feed on a wide food spectrum. These differences are reflected in resource partitioning in the community.

An apparent difference with regard other oceans is the quantity of food ingested, which is significantly lower than in octocorals from other latitudes. However, the Antarctic octocorals might be able to feed during the whole year, due to the relatively constant concentration of the Antarctic microplankton system, whereas octocorals from temperate seas show a more seasonal feeding behaviour. The consumption rate should be related to the metabolism of the organisms and their productivity. Consumption in Antarctic cnidarians is lower than in other latitudes in absolute values, in relative values it is comparable.

The studied Antarctic octocorals do not seem to present a different diet spectrum compared with octocorals from other latitudes. However, their consumption rates are lower.

Passive suspension feeders in the Antarctic may be able to overcome the winter trophic constraints due to their ability to:

(1) Reduce their activity and lower their consumption rates (Coma et al. 2000).

(2) Predate on the fine fraction of seston, which remains very constant during the year as demonstrated by Clarke & Leakey (1996). Resuspension and advection processes seem to supply food to the Antarctic benthic suspension feeders in the winter season, when ice covers the water surface and vertical flux is low. In these periods, both the lateral inputs due to the advection processes and the "reversed vertical" input due to resuspension may be key phenomena governing their trophic dynamics. The so called "Antarctic paradox" (Hedgpeth 1977) may need to be reformulated considering these facts.

Cnidarians exploit both food particles available all year and larger food items seasonally available. This reinforces the idea that the activity and production of Antarctic benthos does not stop during winter.

5.3 Reproductive behaviour of cnidarian species on the Weddell Sea shelf

The five studied species have separate sexes and a sex ratio of 1:1. At least three (*Thoaurella* sp., *Fannyella rossii* and *Fannyella spinosa*) are clearly brooders, as indicated by the presence of larvae in their gastrovascular cavities (Fig. 17). In the case of *Ainigmaptilon antarcticum* and *Dasystenella acanthina* the lack of larvae in the polyps and colonies precluded any clear definition of the development mode of the species. However the large size of the oocytes and the large duration of the oogenesis (probably two years) would indicate a brooding incubation mode.

The number and size of oocytes vary among species and along the colony zones of the octocorals investigated. These results agree with patterns found in other latitudes (Hughes 1989), and suggest that reproductive effort varies along the colonies regardless of latitude. The diversification of biological functions in the colony, some parts being devoted to prey capture, defense against predators, etc. and others to reproduction, might explain this different reproductive effort, as has been pointed out by other authors (e.g. Hughes 1989, Brito et al. 1997).

Fig. 17 Polyp of *Fannyella spinosa* brooding a larva (indicated by the arrow) in the gastrovascular cavity.

The evidence of brooding in three of the investigated octocorals, the large size of the oocytes of the two other species, and the references in the literature (Brito et al. 1997 and references in this work) indicate that brooding seems to be the tendency for Antarctic octocorals. However it is also important to take into account that lecitotrophic larvae of octocorals were found recently in Antarctic shallow waters (Stanwell-Smith et al. 1999), and that the traditional idea that large oocytes are correlated with brooding is actually under discussion (e.g. Fadlallah 1983, Kruger et al. 1998).

Gonochorism and sex ratio 1:1 seem to be the trend for Antarctic octocorals. Only a few species have been investigated, but these suggest brooding to be the principal incubation mode.

Two different timings in gametogenesis were identified:

1) The bottle-brush species *Dasystenella acanthina* and *Thouarella* sp. and the flagelliform *Ainigmaptilon antarcticum* have two generations of oocytes (Fig. 18, 19). This pattern suggests a two-year reproductive cycle as observed in several octocoral species in other regions (e.g. Benayahu & Loya 1986, Van Praet et al. 1990). Autumn samples of *A. antarcticum* also support the two-year cycle (Fig.19) and does not show a clear pattern as occurs in other latitudes (see Benayahu et al. 1990, Dahan & Benayahu 1997).

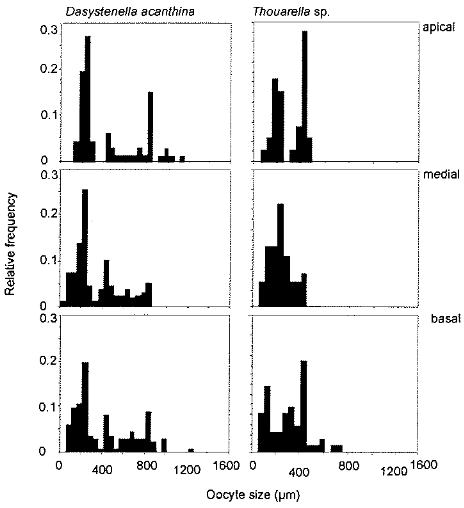

Fig. 18 Frequency distribution of oocyte size for *Dasystenella acanthina* and *Thouarella* sp.

The oocyte development patterns of these species agree with the slow rates of embryonic development observed in Antarctic marine invertebrates which may be related with their large egg sizes (Clarke 1982).

2) The dichotomous species *F. rossii* and *F. spinosa* present only one generation of oocytes, which suggests a one-year reproductive cycle (Fig. 20). This mode has also been observed in species from other latitudes (e.g. Benayahu & Loya 1983).

These two different gametogenesis duration periods

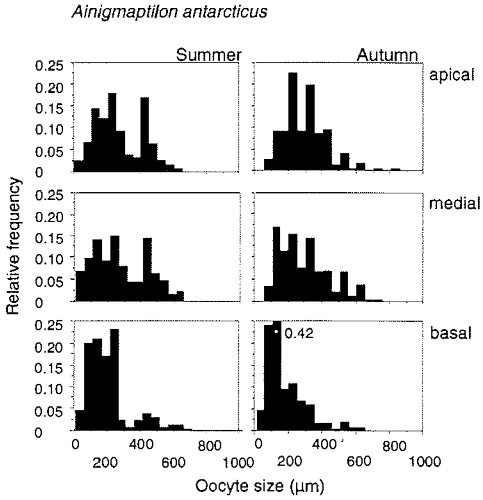

Fig. 19 Frequency distribution of oocyte size for *Ainigmaptilon antarcticum*

do not seem to be clearly related to factors such as temperature, whereas the morphology of the colonies seems to play a role in the definition of the gametogenesis processes. Food availability should also be taken into account in further research in reproduction, since this aspect has a strong influence on the reproductive modes and rhythms in other latitudes (e.g. Hughes 1989, Coma et al. 1998).

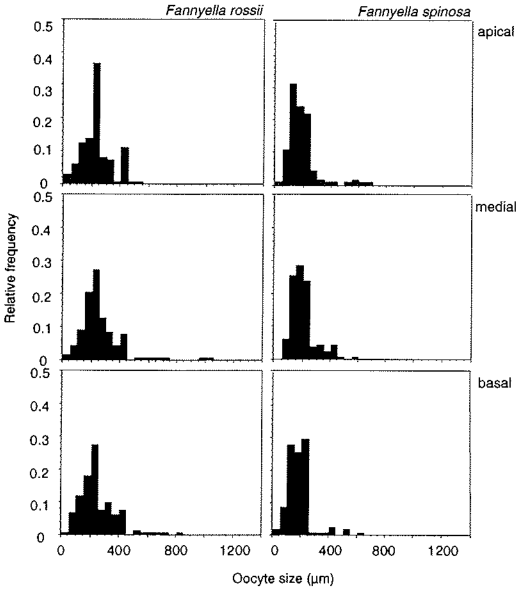

Fig. 20 Size frequency of oocytes of *Fannyella rossii* and *Fannyella spinosa*.

Antarctic octocorals present reproduction features and trends which do not seem to be different from those of octocorals at other latitudes. Oocyte numbers and sizes fit into the pattern observed in other regions, as so does the duration of gametogenic cycles. The presence of one or more oocyte size classes points to cycles of one or several years duration, respectively, as also occurs in octocorals from tropical seas. Different octocoral morphologies revealed different reproductive patterns, which also coincides with reports from other latitudes. "Architectural" parameters must be considered to identify possible trends.

CONCLUDING REMARKS

The distribution, feeding and reproduction patterns observed in the studied species demonstrate the high ecological plasticity and functional diversity presented by Antarctic benthic cnidarians. These ecological characteristics enable these benthic organisms of Antarctica to develop dense populations and communities together with other groups of suspension feeders, despite the uncertain spatial and temporal food availability. The extrapolation of the "cnidarian model" to other sessile groups may allow us to extend the conclusions of this work to the community level in the future.

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Publications

This thesis is composed of the publications mentioned in the list below. The contribution from each author in the different publications is also outlined.

Publication I

Feeding strategies and diet composition of four Antarctic cnidarian species
Covadonga Orejas, Josep Maria Gili, Pablo José López-González, Wolf E Arntz
Polar Biol (in press)

The first and second author discussed the conceptual frame of this paper. The first author developed the experimental design and carried out the laboratory work in collaboration with the third one. Data processing, analysis and interpretation was conducted by the first author. The first version of the manuscript was written by the first author and it was improved with the cooperation of the other co-authors.

Publication II

The role of the fine fraction of seston in the diet of two Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.): ecological implications
Covadonga Orejas, Josep Maria Gili, Wolf E Arntz

The original idea for this publication was developed by the first two authors. The first author developed the experimental design and carried out the practical work. The data analysis was also conducted by the first author. The concept of the manuscript and first version was developed by the first author, the last version was achieved with the joint work of first author and co-authors.

Publication III

Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea
Covadonga Orejas, Pablo José López-González, Josep Maria Gili, Nuria Teixidó,
Julian Gutt, Wolf Arntz

The concept and initial idea for this paper was elaborated by the first and third authors. Practical work was conducted by the first author, in collaboration with the second one for the histological work, and with the fourth one for the video image analysis. The fifth author provided the video material. The data processing was conducted by the first author, as well as the writing of the first draft of the manuscript. The revision of the first version was made in cooperation with the second, third, fourth and sixth author.

Publication IV

Reproductive patterns of four Antarctic octocorals in the Weddell Sea: comparisons across different species, morphologies and latitudes
Covadonga Orejas, Josep Maria Gili, Pablo José López-González, Christiane Hasemann, Wolf Arntz

The original concept was elaborated by the first, second and third authors. The first author conducted the practical work, the data analysis and wrote the first version of the manuscript. The last version was the result of the comments of the rest of the co-authors on that first draft.

Publication I

Feeding strategies and diet composition of four Antarctic cnidarian species

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Abstract

The diet of four species of Antarctic cnidarians, two hydroids and two anthozoans has been investigated. One hydroid, *Tubularia ralphii*, and one anthozoan, *Anthomastus bathyproctus* seem to basically consume zooplankton whereas the other hydroid species, *Oswaldella antarctica*, has a diet mainly based on the fine fraction of seston. The last cnidarian investigated, the stoloniferan alcyonacean *Clavularia* cf. *frankliniana* feeds mainly on resuspended material. The wide range of diets of these Antarctic cnidarians indicates opportunistic behaviour by feeding on different sources taking advantage of the available food sources. Data related with low C/N ratio in the sediment and high NO_2 concentrations in areas with dense communities of benthic suspension feeders, along with data on capture rates, lead us to hypothesize that these organisms play an important role in the recycling processes of organic matter in Antarctic benthic ecosystems.

Introduction

Cnidarians are one of the most conspicuous taxonomic groups on the Antarctic continental shelf, being part of the rich epibenthic communities which have been described from several locations around Antarctica (e.g. Arntz et al. 1994; Gutt and Starmans 1998; Starmans et al. 1999). Like other suspension feeders, cnidarians depend on the available food suspended in the water column and on the near bottom currents for its renewal.

The Southern Ocean is principally an oligotrophic environment dominated by flagellates and other small organisms of the pelagic retention system, with short overlying outbursts of microalgae (bloom system) in spring and summer (Scharek and Nöthig 1995) which are, however, essential for larger zooplankton. For quite some time these blooms were suspected to determine the feeding strategies of the benthic suspension feeders in Antarctica and the composition of their diet. These organisms were thought to feed heavily during a few weeks in summer and to be able to sustain large periods of starvation during most of the year. This would resemble overwintering as resting stages or the hibernation periods that have been described for other latitudes (Gili and Hughes 1995; Garrabou 1999). However, Barnes and Clarke (1995) have demonstrated recently that certain species of Antarctic shallow-water benthic suspension feeders are able to feed throughout the year with only short periods of starvation. Phytoplankton (mainly microplankton) in these areas, too, is dominant in the water column and the sediment only during short periods of the year, but pico- and nanoplankton (between 0.2 and 20 µm) dominate the water column and the sediment during most of the year, and the suspension feeders take advantage of them (Cripps and Clarke 1998). From these findings the question arose whether this situation might apply to deeper shelf communities as well.

In the Southern Ocean not only vertical fluxes (Nöthig and von Bodungen 1989) are the source of food for the benthic suspension feeders, but zooplankton, seston, elements of the microbial food web and resuspension processes could also contribute to the potential available food for this group. Although cnidarians have traditionally been considered mainly carnivorous (Hyman 1940), more recent studies have found evidence of herbivory (Elyakova et al. 1981; Fabricius et al. 1995 a,b) which is supported by a study on an Antarctic hydroid, *Silicularia rosea*, which consumes mainly diatoms (Gili et al. 1996b). On the other hand gorgonian diet varies from dissolved organic matter via plankton to benthic organisms, and is very well coupled with the dynamics of their potential prey (Ribes et al. 1998, 1999).

Considering the various potential food sources for benthic suspension feeders, the goal of the present study was to determine the diet of four species of Antarctic cnidarians: *Oswaldella antarctica* (Hydrozoa), *Tubularia ralphii* (Hydrozoa), *Clavularia* cf. *frankliniana* (Anthozoa) and *Anthomastus bathyproctus* (Anthozoa). We also consider the relation between their feeding strategies, the Antarctic environment and the factors which regulate the availability of food at the sea floor. We present new insights into the significance of plankton production, resuspension processes and nekton migration for the feeding strategies of these organisms, and on the role of the group in the trophic food web of the Southern Ocean.

Materials and methods

Four benthic cnidarian species were studied (Fig. 1). *Oswaldella antarctica* (Jäderholm 1904) is a benthic hydroid found on hard substrates in a depth range between 50 to 200 m approximately, forming arborescent colonies and presenting very small polyps (200-375 µm diameter). *Tubularia ralphii* Bale 1884 is a common Antarctic hydroid, which forms creeping colonies on stones and is mainly distributed in shallow areas (Stepanjants 1979). *T. ralphii* presents large hydranths with long aboral tentacles, and the hydrocaulus is usually more than 2 cm above the substratum. The stoloniferan alcyonacean *Clavularia* cf. *frankliniana* Roule, 1902 was one of the most common species collected in shallow waters during the second EASIZ (Ecology of the Antarctic Sea Ice Zone) cruise. This species forms encrusting colonies covering, in some cases, great part of the stones. *Anthomastus bathyproctus* Bayer, 1993 is a common alcyonacean in the waters of the Antarctic Peninsula area. Their colonies live mainly on sandy substrates. They were caught between 400 and 450m depth, however off the South Shetland Islands specimens have been found at 1153 m depth (Bayer 1993).

Sampling, experimental design and analysis of gastrovascular contents

Sampling on board RV "Polarstern" was carried out during the second EASIZ cruise between January and March 1998, at two sites: for *O. antarctica*, *T. ralphii* and *C.* cf. *frankliniana* in the eastern Weddell Sea, for *A. bathyproctus* off the Antarctic Peninsula (Table 1). Sampling was conducted with an Agassiz trawl, a bottom trawl and a large TV grab of 1.82 m^2 sampled area.

In order to know the trophic role of the seston (also of its fine fraction) for suspension feeders, data are derived from analyses of cnidarian gastrovascular contents and from feeding experiments. Polyps of all four species were dissected to analyze the gastrovascular contents under a binocular and a light microscope. The number of dissected polyps was between 110 and 148 depending on the species because of their varying abundance in the samples and in the studied area.

Feeding experiments were done only with the hydrozoan species *O. antarctica*. A modified prototype of incubator developed by the Instituto de Ciencias del Mar (Ribes et al. 1998) was used to study the diet of benthic suspension feeders. The incubator consists of a chamber in which the colony is placed, and an empty control chamber. Each closed chamber was connected to a pump that recirculated sea water at a renewal rate of 3.3 l min^{-1}. Water was collected as close to the seafloor as possible by means of a CTD equipped with a rosette. Simultaneously temperature and salinity were measured using a CTD. The chambers and all necessary material and instrumentation were placed in a cool room container equipped for operation at Southern Ocean ambient temperature (-1°C to +0.5°C). Colonies were kept in sea water within the cool room until the incubation experiments. Animals were placed in the experimental chamber and were allowed to fully expand before the experiment started. After the acclimation time (which was from 3-4 hours for some colonies to one day for others), the incubation chambers were closed and initial water samples of 2000 ml were taken from both chambers. After 6 hours another set of water samples was collected. Capture rates were calculated using the decreasing concentration levels of bacteria, flagellates, ciliates, and phytoplankton in the water samples, considering their growth rates during the experiment. To quantify heterotrophic bacteria, water samples were storaged for flow cytometry by standard methods (Gasol and del Giorgio 2000). Quantification and measurement of picoplankton was done using epifluorescence microscopy. To quantify, measure and identify phytoplankton and ciliates, water samples were stored in acid Lugol. Nutrients (NO_2, NO_3, Si, and PO_4) for the water samples were also measured using a Technikon Autoanalyzer II System von Bran and Lübbe and following standard methods. Carbon and nitrogen were measured using a Leco CN 2000 analyzer.

In the sampling areas a visual check of benthic fauna was made just when the gear arrived on board to find possible relations between nutrient concentrations, C/N ratio and densities of benthic suspension feeders. At all sampling sites, a sample of 2 cm^3 of surface sediments was collected and frozen in liquid nitrogen and carbon and nitrogen content was measured using a Leco CN 2000 analyzer.

To know the abundance of zooplankton near the bottom complementary data collected during the second EASIZ cruise by means of a epibenthic sledge were revised and compared with the zooplankton abundance and distribution in the water column (Brandt et al. 1999, Schiel pers. comm.).

Statistical and numerical treatment

Results are noted as means ± standard deviation and the differences between the samples are tested using ANOVA model 2 at different significance levels. The Wilcoxon test has been used to test possible differences between initial and final values of prey net growth rate, POC (Particulate Organic Carbon), DOC (Dissolved Organic Carbon) and nutrient values (NO_2, NO_3, Si and PO_4) in the experimental and control chambers. Depletion rates of the plankton were calculated assuming exponential growth and clearance of prey as described in Ribes et al. (1998).

Results

Gastrovascular contents

O. antarctica contained three different types of prey: diatoms (94%), invertebrate eggs (4%) and invertebrate larvae (2%) (Fig. 2). Sizes of the prey were from 20 µm (smallest) to 235 µm (biggest), however 81% of prey belonged to the size range 20-42µm (Fig. 3). 25 of the dissected polyps (23%) contained some prey in the stomachs whereas 85 were empty (77%) (Fig. 4). Statistically significant differences were found in prey size among different polyps (ANOVA, F= 5.35, N= 110; $p<0.05$).

104 (71%) polyps of *T. ralphii* contained prey and 43 (29%) were empty (Fig 5). The diet was composed mainly of copepods (85%), followed by invertebrate eggs (7%), organic matter (7%) and copepod nauplii (~1%) (Fig. 2). Prey number and prey size showed significant differences between polyps

(ANOVA, F= 74.876, N= 147; $p<0.0001$; ANOVA, F= 11.165, N= 147; $p<0.005$, respectively). The size range of prey items was very wide (45-1145 µm) (Fig. 3).

Of a total of 148 polyps of *C.* cf. *frankliniana* (belonging to different colonies), 36 (24%) were empty and 112 (76%) showed prey items in the gastric cavity (Fig. 4) The diet was diatoms (81%), protozoans (8%), foraminiferans (5%), nematodes (4%) and invertebrate larvae (2%) (Fig. 2). Size range of prey varied between 48 and 1920 µm, with 92% of prey being in the range 48-235 µm (Fig. 3). Prey number varied significantly between polyps of different diameter (ANOVA, F= 5.928, N=148; $p<0.05$), but not between different prey size.

The 8 studied colonies of *A. bathyproctus* had a total of 136 polyps. Salps belonging to the species *Salpa thompsoni* were found in 113 (83%) of them whereas 23 (17%) were empty (Fig 5). The size of the salps was between 10 and 50 mm (Fig. 3). Many polyps contained other items (mainly diatoms of the genus *Corethron*, and also centric diatoms and fecal pellets of small size). It seems, however, that these items came from prey gut contents, which was confirmed by dissecting the prey guts. No statistically significant differences were found between number and size of prey items and polyp diameter, neither between number of prey items and capitulum diameter. However, there were significant differences between number of prey items and height of the capitulum (ANOVA, F=10.649, N= 8; $p<0.01$), and between prey size and height of the capitulum (ANOVA, F=6.087; N= 8; $p<0.05$). The number of polyps/capitulum in relation with height of the capitulum and also with capitulum diameter showed significant differences (ANOVA, F=61.898, N= 8; $p<0.001$; ANOVA, F= 139.033, N=8; $p<0.001$, respectively).

Feeding experiments

Net prey growth rates were calculated for the potential prey items of *O. antarctica* working at the level of taxonomic group: bacteria, nanoflagellates, dinoflagellates, ciliates and diatoms; POC and DOC values were also calculated. Sizes of the prey items have also been taken into account (excluding in this case values of bacteria). Statistically significant differences ($p<0.01$) were found for nanoflagellates (Wilcoxon test). Results are shown in

Fig. 5. However, a pattern could be observed also for the other groups: dinoflagellates showed a clear decrease in the experimental chamber, as did *Chaetoceros* species and other phytoplankton groups. Different types of diatoms were lumped because of the low number of specimens found in the samples.

Nutrients and C/N ratio

The concentration of nutrients NO_2, NO_3, and PO_4 varied between 0.02 and 0.20 µmol/l, 15.94 and 40.35 µmol/l and 0.77 and 1.49 µmol/l, respectively. C/N values in the sediment varied between 6 and 293, showing a clear pattern in relation with the distribution of benthic suspension feeder communities: areas which showed high presence of benthic suspension feeders presented the highest values (Fig. 6). Conversely, the areas with higher nitrogen values correspond to areas with a low density of benthic suspension feeders. The same pattern was observed for nutrient values, with higher values in areas where benthic suspension feeder communities were abundant.

Zooplankton abundance

Data of zooplankton densities (focusing on copepod data because of their abundance) have been extracted from preliminary results of the second EASIZ cruise. Near bottom copepod abundances, obtained by epibenthic sledge, were registered by Brandt et al. (1999) on the Weddell Sea shelf reaching summer values between 232 and 702 individuals/1000m^2 at 400 m depth. Copepod abundance (Calanoids) has also been measured by Schiel (pers. comm.) in the upper 200 m of the water column in the same area. The values ranged between 1000 and 4500 ind/1000 m^3 during the Antarctic summer.

Discussion

Anthozoans and hydrozoans are groups which have received great attention in tropical and temperate waters, and substantial data on their natural diet are available (anthozoans e.g: Coma et al. 1994; Ribes et al. 1998; hydrozoans e.g: Gili et al. 1998). Scarce information exists, however, about Antarctic and Arctic species (Gili et al. 1996b; Slattery et al. 1997). Benthic zooplanktivorous species, which feed on substratum-associated organisms or larvae also consume a few holoplanktonic animals such as calanoid copepods (Sebens and Koehl 1984). We name these species "macrophagous" but introduce a new food item: the fine fraction of seston, calling the species, which feed on this fraction, "microphagous". The four studied species reflect this whole spectrum of prey items (Fig. 2).

It has been hypothesized that benthic organisms just feed during favourable periods, remaining in hibernation or in resting stages during cold seasons and under unfavourable environmental conditions (see for review Gili and Hughes 1995). This is true for the "macrophytoplankton system" (Smetacek et al 1990; Scharek and Nöthig 1995) which occurs in summer and most zooplanktonic (hence macrophagous) species profit from these summer blooms to grow and reproduce. However, the "flagellate system" (Smetacek et al. 1990; Scharek and Nöthig 1995), consisting mainly of nanoplankton and members of the microbial food web, is also active during winter (Clarke 1988; Ahn 1993). This system might be capable to sustain communities of benthic suspension feeders during the whole year, as has been observed by Barnes and Clarke (1995) at Signy Island.

Diet: macrophagous and microphagous suspension feeders

Macrophagous species: *T. ralphii*, *C.* cf. *frankliniana*, *A. bathyproctus*

T. ralphii showed a diet highly dependent on the water column. 85% of their diet were copepods, some of which have been identified as pelagic harpacticoids, indicating a dependence on the planktonic community. The lack of relation between polyp size and prey size suggests an opportunistic strategy contrasting with that observed in a congeneric species from the North Atlantic, *T. larynx* (Gili et al. 1996a).

The feeding strategy of the stoloniferan *C.* cf. *frankliniana* could be linked with resuspension processes at the seafloor. Its polyps are located very close to the substrate and they capture prey moving around their tentacle crown. This kind of feeding is quite frequent in massive and encrusting anthozoans such as alcyonaceans and actiniarians (Sebens and Koehl 1984). Sediment might be continually resuspended by the effect of currents, but also by various animals such as bivalves (e.g. Stockton 1984; Alexander and DeLaca 1987), echinoderms (McClintock 1994) and demersal fish.

The diet of *A. bathyproctus* is probably related to the patchiness of plankton. They might profit from episodes of high availability of food, as occur during the salps' downward migration. The occurrence of gelatinous zooplankton close to the seafloor has been shown in some cases (Gili et al. in press). Vertical migration of Antarctic zooplankton to the sea bed has been documented for salps (Weibe et al. 1979; Casareto and Nemoto 1986) and krill (Gutt and Siegel 1994). In gorgonians (Coma et al. 1994), plankton patches can cause events of high prey capture rates. The presence of big, although occasional, prey in the stomachs of the studied species may be quite significant for their energetic balance (Coma et al. 1998). In the guts of the *A. bathyproctus* specimens we also found diatoms (mainly *Corethron* spp), which seem, however, to come from prey gut contents, as has been described for other prey items in other cases (Sebens and Koehl 1984).

Two possible strategies might be applied by *A. bathyproctus*: 1) they might feed on zooplankton, i.e. prey that occasionally passes by, in an opportunistic way, but feed on the fine fraction of seston, too, using a "sieving" mechanism; 2) they might feed episodically only on big prey items. This last possibility does not appear to be realistic because they would depend completely on the Antarctic summer production to survive. A more realistic scenario is that they use, in different proportions, both resources. In any case, *A. bathyproctus* is neither a deposit nor a sediment feeder. Its anatomical characteristics show the animal to be capable to double its size by way of hydrostatic mechanisms. Thus it can take better advantage of the water column, the food composition of which can vary highly from the bottom to some centimetres above it (Schloss et al. 1999).

Microphagous species: *O. antarctica*

Little information exists on the role of types of prey other than zooplankton in hydroid feeding (Gili and Hughes 1995). Several studies reported that dinoflagellates, diatoms, tintinnids, and bacteria are sparse in hydroid gut contents (Gili et al. 1996a). On the other hand, nanoplankton, mainly of plant origin, is the most abundant food source in the Southern Ocean, and Coma et al. (1995) demonstrated that detritus from plant matter or particles of unspecified origin represents more than 90% of prey captured in a Mediterranean hydroid. Diatoms have been also reported to be an important food source for the Antarctic hydroid *Silicularia rosea* (Gili et al. 1996b).

Recently it has been observed that the fine fraction of seston (pico- and nanoplankton) may represent an important part of the diet of benthic suspension feeders (Pile et al. 1996; Ribes et al. 1999). The studies by Bröckel (1981) showed that nanoplankton cells are also a very important component of the planktonic community in nearshore Antarctic waters. The case of *O. antarctica* is the first where the importance of this fraction has been shown for hydroids. Our feeding experiments show that components from the fine fraction of seston contribute to the diet of the hydroid (Fig. 5). This is not surprising taking into account that particles smaller than 2 µm and between 2 and 20 µm diameter dominate the pelagic planktonic community in terms of biomass and production (Platt et al. 1983). It has also been demonstrated that suspension feeders can remove very effectively particles of these sizes, and that active filtration is not the only method by which suspension feeders extract efficiently small particles from the water (Rubinstein and Koehl 1977; Okamura 1990). The importance of small prey in the diet of hydroids indicates that other mechanisms of capture may also occur, e.g. inertial impact or gravitational deposition, and creation of currents (Koehl 1977a,b; LaBarbera 1984, Harris 1990).

A wide variety of diets in benthic cnidarians has recently been shown also for two gorgonian species: *Plexaura flexuosa* (Ribes et al. 1998) in the Caribbean and *Paramuricea clavata* (Ribes et al. 1999) in the Mediterranean Sea, with prey items comprise from bacteria to zooplankton. Apparently, feeding strategies and diets in this group are not very different in Antarctica compared with other latitudes. An example is the capture rates of *T. ralphii*, which are in the same order of magnitude as for related species in temperate waters (Gili et al. 1998).

Role of the suspension feeder communities in the Antarctic benthic communities

Particle composition in the water column in Antarctica may be very different along the year (Clarke and Leakey 1996). In the Southern Ocean, a strong vertical flux of organic matter occurs during a short time, but due to the low decomposition rate of the sediments, they keep their nutritional value longer (Bathmann et al. 1991). The data of Palanques et al. (in press) show high values of nitrogen even in winter. Benthic communities may respond to sedimentation events increasing their activity and production (e.g. Grémare et al. 1997).

The low values of C/N ratio observed (Fig. 6) in places where the benthic suspension feeders are very abundant might reflect their feeding activity consuming the sediment organic component (POC or small organisms). Benthic cnidarians might be able to use sediment material due to resuspension processes. A similar set of sediment C/N values has been observed in the Bransfield Street (Palanques et al. in press) and the authors hypothesize that this organic sediment decomposition could be related with the activity of benthic organisms, not to the different organic composition of material sedimenting from the water column. Parallel to these near-bottom feeding processes high nutrient values such as the observed nitrite values may be expected (Fig. 6). Below the depth limit of photosynthetic activity nitrite cycling is controlled by microbial nitrification as well as denitrification in the water layer close to the bottom, but benthic filter feeders can increase nitrite cycling by ammonium from their excretion processes. The role of nitrite as an obligatory intermediate in nitrification processes and the high values found during our experimental work point to the possible role of benthic suspension feeders in the recycling and remineralization of the organic matter and their role as very active organisms in the dynamics of benthic boundary layers.

In summary, cnidarians exploit both patch food and seasonally available food. This information on the natural diet of Antarctic benthic cnidarians supports the hypothesis that they are adapted to perform a wide spectrum of prey capture, which enhances their survival in a stochastic environment. Furthermore it indicates that the activity and production of Antarctic benthos does not stop during winter. The role of benthic suspension feeders in such communities is still far from being clear, but they must play a principal role both in the benthic pelagic coupling processes and in organic matter recycling.

Acknowledgements

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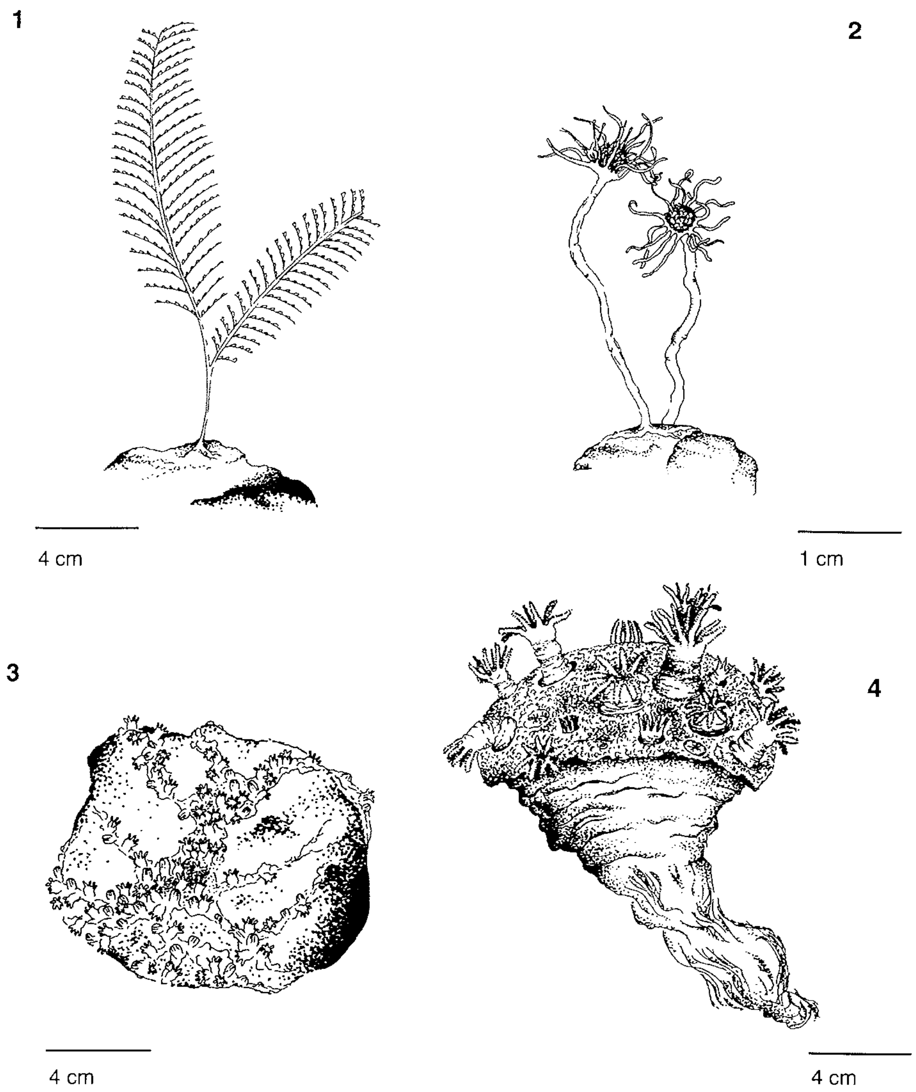

Fig .1 Studied species: 1. *Oswaldella antarctica*. 2. *Tubularia ralphii*. 3. *Clavularia* cf. *frankliniana*. 4. *Anthomastus bathyproctus*.

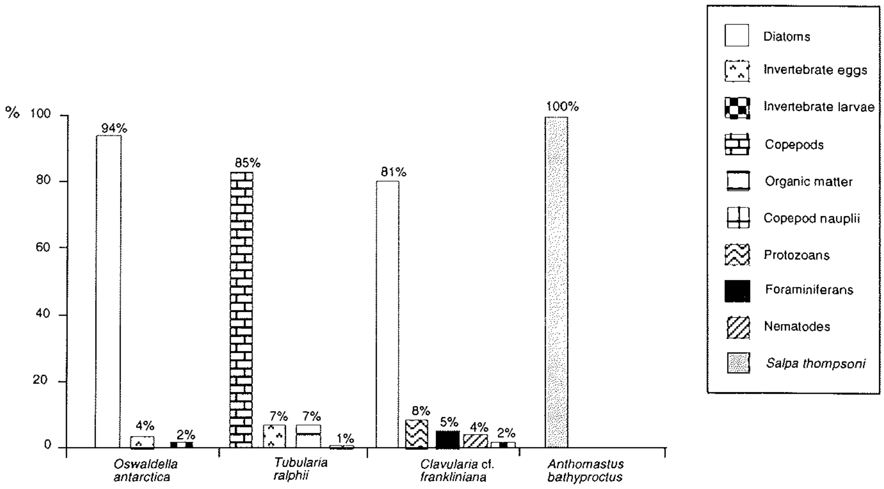

Fig. 2 Percentage (by number) of prey items in the dissected polyps for each studied species.

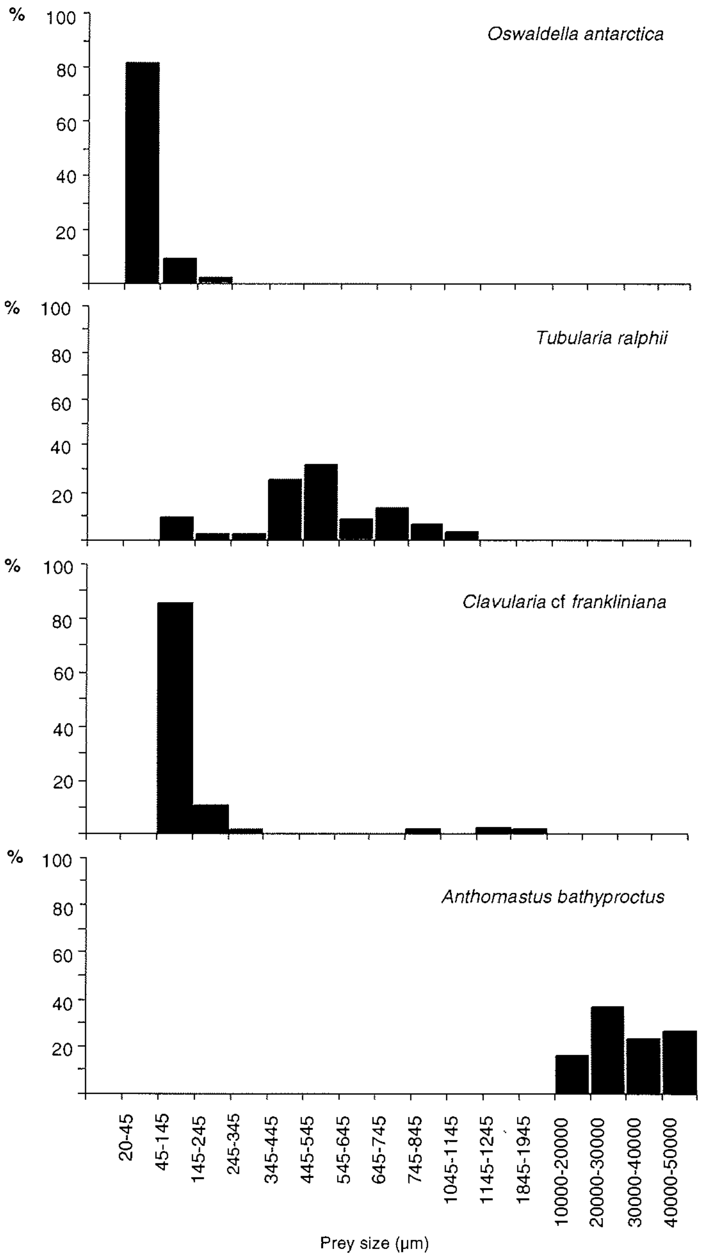

Fig. 3 Percentage (by number) of prey items of different size range found in the dissected polyps for the four studied species.

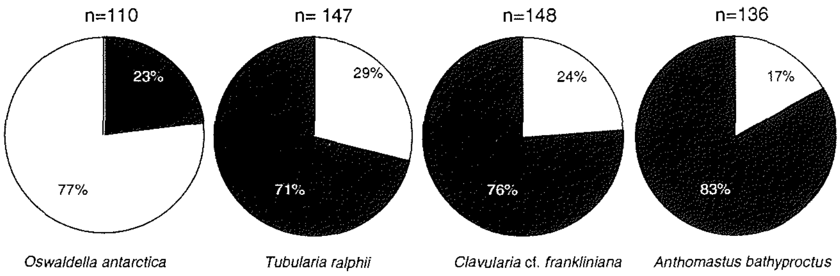

Fig. 4 Percentage (by number) of full and empty gastrovascular cavities for the four studied species. Black colour shows coelenteron with prey items, white colour without prey items.

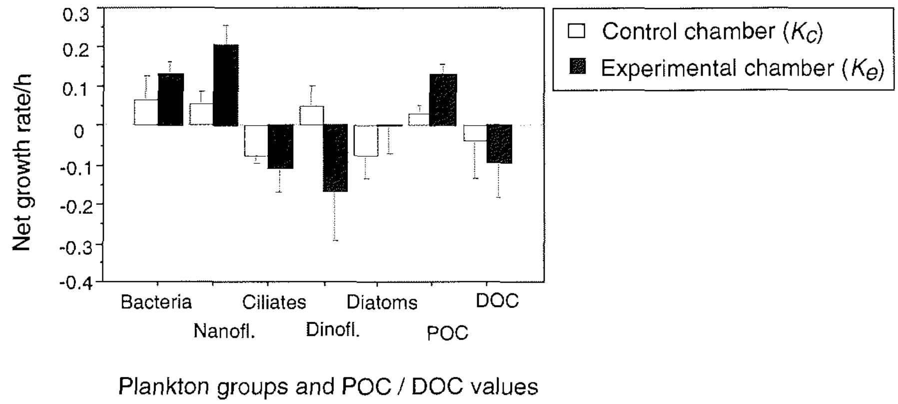

Fig. 5 Net growth rate in control (*K*c) and experimental (*K*e) chamber of the different groups of plankton and POC, DOC.

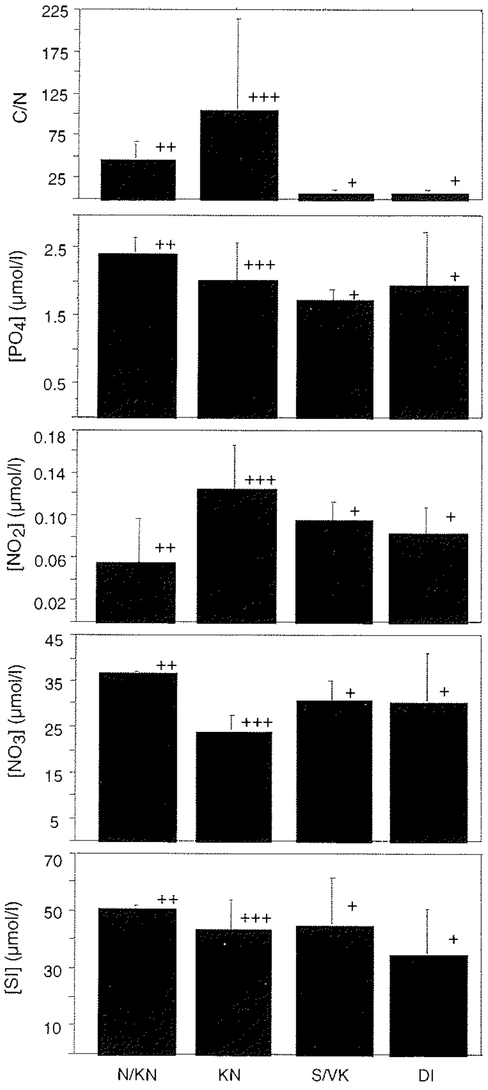

Fig. 6 Values of C/N rate and nutrients for the areas North of Kapp Norvegia (N/KN), Kapp Norvegia (KN), South of Vestkapp (S/VK), and Drescher Inlet (DI). +++ High dominance of benthic suspension feeders; ++ Regular abundance of benthic suspension feeders; Occasional presence of benthic suspension feeders.

Table 1. Sampling stations for the 4 studied species. KG= King George Island; KN= Kapp Norvegia; N/KN= North of Kapp Norvegia; AGT= Agassiz trawl; BT= bottom trawl; TV grab= bottom grab 1.82 m^2 with video camera.

	Area	Station	Gear	Latitude (S)	Longitude (W)	Depth (m)
Oswaldella antarctica	N/KN	71	BT	70°49.3'	10°28.6'	281
	KN	210	TVgrab	71°07.2'	11°28.4'	67
Tubularia ralphii	KN	210	TVgrab	71°07.2'	11°28.4'	67
Clavularia cf *frankliniana*	KN	210	TVgrab	71°07.2'	11°28.4'	67
Anthomastus bathyproctus	KG	303	AGT	62°16.5'	58°43.1'	430
	KG	304	AGT	62°16.4'	58°43.9'	447

Publication II

The role of the fine fraction of seston in the diet of two Antarctic octocorals (*Primnoisis antarctica* and *Primnoella* sp.)

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Abstract

The diet composition of two Antarctic octocorals, *Primnoisis antarctica* and *Primnoella* sp. from the shelf of the eastern Weddell Sea (Antarctica) has been studied for the first time. Although meso-zooplankton is very scarce in the diet of these organisms, it seems to be important because of its high carbon content. Feeding experiments showed that components of the seston including the finer fraction of suspended organic matter (ciliates, dinoflagellates and phytoplankton) are an important part of the octocoral diet. It was estimated that in *Primnoisis antarctica,* the diatom *Fragillariopsis* spp. accounted for 77% of the total numbers of cells captured, followed by dinoflagellates (20%), *Nitzschia* spp. (2%) and ciliates (1%). In *Primnoella* sp., dinoflagellates were consumed preferentially (92%), followed by ciliates (6%) and centric diatoms (2%). However, the consumption rates in carbon terms, were low (1.11×10^{-5} mg C polyp^{-1} d^{-1} for *Primnoisis antarctica* and 1.34×10^{-4} mg C polyp^{-1} d^{-1} for *Primnoella* sp.). The ability of these suspension feeders to take small cells at lower concentrations may allow these organisms to remain seasonally active for considerably longer periods than previously thought.

Introduction

It has long been assumed that Antarctic ecosystems experience an extended period of biological inactivity because of the extended periods of ice cover (Gruzov 1977). However, recent studies on Antarctic shallow waters suggested only a brief period of feeding inactivity in some Antarctic benthic suspension feeders (Barnes & Clarke 1995). This is related to the finding at littoral sites that in winter nanoplankton chlorophyll exceeds that of the microplankton during approximately three months (Clarke & Leakey 1996).

Pico - (cells <2 µm) and nanoplankton (cells 2-20 µm) dominate many planktonic communities in terms of production (e.g. Platt et al. 1983, Stoeckner & Antia 1986, Burkill et al. 1993). The plankton of the Southern

Ocean is however characterised by a dominant phytoplankton community represented by nanoflagellates and small pennate diatoms (e.g. Sakshaug & Holm-Hansen 1984, Nöthig et al. 1991, Scharek & Nöthig 1995). These organisms are present at low abundance during the winter but exhibit blooms during spring. In contrast, large populations of heterotrophic nanoflagellates, dinoflagellates and ciliates are present practically all year round (Hewes et al. 1985). This "split" planktonic system might provide a key to the understanding of the ecology of benthic suspension feeding organisms.

In recent years, ecological work on Antarctic suspension feeders has increased notably, for instance, on bivalves (e.g. Davenport 1997, Albertelli et al. 1998), sponges (e.g. Starmans et al. 1999, Kowalke 2000), ascidians (e.g. Sahade et al. 1998, Kowalke 1999), and bryozoans (e.g. Sanderson et al. 1994, Barnes & Clarke 1994). Some studies from boreal sponges are also available (e.g. Pile et al. 1996, Riisgård et al 1998). However, studies on passive suspension feeders in polar regions are still scarce.

Suspension feeders are able to capture important amounts of planktonic prey, and the grazing pressure on the water column planktonic communities by benthic macro-invertebrates appears to be much greater than previously thought (e.g. Coma et al. 1995, Pile et al. 1996, Riisgard et al. in press, Orejas et al. in press).

Many anthozoans such as corals, zoantharians, alcyonaceans and actinians from different latitudes capture zooplankton (for a review see Coma et al. 1994). However the study of gastrovascular contents of gorgonians in Antarctic waters (Alvà et al. 1997) revealed a very low number of zooplankton prey items. This would seem to be a paradox taking into account that summer is the period in the Antarctic when higher primary production rates and higher zooplankton densities occur. Additionally, the high reproduction rates of octocorals in Antarctic waters are comparable to those from other latitudes (Orejas et al. submitted), indicating that other planktonic components must be taken by these organisms in order to meet their energetic demands. Recent studies have suggested that the fine fraction of seston (mainly phytoplankton) plays an important role in the diet of various benthic suspension feeders from temperate and boreal latitudes (e.g Ribes et al. 1998a,b; 1999a,b; Riisgard et al. 1998), tropical areas (Fabricius et al

1995, Yahel et al. 1998), and also in the Antarctic (Kowalke 2000, Orejas et al. in press).

Previous studies on Mediterranean (Ribes et al. 1999a) and Caribbean (Ribes et al. 1998a) species have revealed the importance of the fine fraction of seston. Furthermore, cnidarians represent a conspicuous group in benthic Antarctic shelf communities at many locations (e.g. Arntz et al. 1994, Gutt & Starmans 1998). According to Starmans et al. (1999), anthozoans are the third dominant taxon in the shelf communities of the Weddell Sea accounting for 10% of the individuals. Therefore, the ecological role of these animals in the Antarctic system is of considerable interest.

The aim of this study is to determine the role of the fine fraction of seston in the diet of two Antarctic gorgonians.

Material and Methods

Description of the species

Primnoisis antarctica (Studer, 1879) (Isididae, Octocorallia) has a branched shape with arborescent growth form (Fig. 1a). Specimens were collected from soft substrata in a depth range between 200 and 500 m. The second species, *Primnoella* sp. (Primnoidae, Octocorallia) (Fig. 1b), was also common but is yet to be determined because of the extreme variability of the genus (P. López-González, pers. comm.). It has a flagelliform, unbranched shape, with polyps arranged in whorls. This species lives attached to stony substrata and occurs mainly in shallow areas (60 to 100 m depth approximately).

Sampling

Sampling was carried out on board RV "Polarstern" during the EASIZ II cruise (ANT XV/3, January-March 1998) in the Kapp Norvegia area (eastern Weddell Sea, approximately 71°5S, 13°E, and at depths of 60 to 500 meters) (Fig. 2). Details on the expedition are given in Arntz & Gutt (1999). Specimens were sampled with a large TV grab of 1.82 m^2 area and immediately transferred to sea-water aquaria maintained at Southern Ocean temperature (-1°C to 0.5°C). The sampled area was characterised by Voß

(1988), who described the presence of sandy bottoms but also sponge spicule mats, bryozoan debris and a few stones. High species richness, diversity and evenness are also characteristic of the Kapp Norvegia area (Galéron et al. 1992).

Gastrovascular contents

To determine the role of zooplankton prey in the diet of both species, polyp gastrovascular contents were analysed. 195 polyps from 13 colonies of *P. antarctica* and 200 polyps from 8 colonies of *Primnoella* sp. were dissected under a binocular and a light microscope. The prey items were identified to groups and, where feasible, to taxa, and their sizes measured. Calculation of biomass values for the various groups was done using literature conversion values (Edler 1979, Coma et al. 1995) and unpublished data of S. Schiel.

Feeding experiments

The role of the fine fraction of seston in the diet of *P. antarctica* and *Primnoella* sp. was also evaluated from feeding experiments. A modified form of the incubator developed by the Institut de Ciències del Mar (Ribes et al. 1998a) was used to study the diet of benthic suspension feeders. The incubator (Fig. 3) consists of a chamber in which the colony is placed, and an empty control chamber. Each closed chamber was connected to a pump that re-circulated sea-water at a renewal rate of 3.3 l min^{-1}. Water was collected as close to the seafloor as possible by means of a CTD equipped with a rosette. Temperature and salinity were simultaneously measured. The chambers and all required material and instrumentation were held in a refrigerated experimental room to maintain environmental temperature. Colonies were held in the cooled aquarium until the incubation experiments were carried out. Immediately prior to the experiments (6 replicates for each species), animals were placed in the experimental chamber and were allowed to fully expand. After this period of acclimation (3-4 hours), the incubation chambers were closed and initial water samples of 2000 ml were taken from both chambers. A second set of water samples was collected 6 hours later.

Capture rates were calculated using the variation in the concentration levels of bacteria, nanoflagellates, ciliates, dinoflagellates, diatoms, total Particulate Organic Carbon (POC), and Dissolved Organic Carbon (DOC) in the water samples, correcting for their net growth rate (for bacteria, nanoflagellates, ciliates, dinoflagellates and diatoms) and the net increasing rates for POC and DOC during the experiment as revealed by the control chamber.

To quantify heterotrophic bacteria, water samples were stored for flow cytometry by standard methods (Gasol & del Giorgio 2000). For quantification and measurement of nanoplankton (nanoflagellates) water samples were stained with DAPI, counted and measured by epifluorescence microscopy (Porter & Feig 1980). To quantify, measure and identify ciliates, dinoflagellates, and diatoms, water samples were stored in acid Lugol (Utermöhl 1931, 1958) for subsequent microscopy.

Cell biovolume was calculated from length and width by approximation to the nearest regular geometric volume. Carbon content of heterotrophic bacteria was estimated from literature conversion factors (Fry 1988). For pico- and nanoplankton and for the different diatom groups, the method described in Edler (1979) was followed. Nutrients (NO_2, NO_3, Si, and PO_4) in the water samples were measured using a Technikon Autoanalyzer II System following standard methods (Grasshoff 1976). Carbon content was measured using a Leco CN 2000 analyzer. Water samples for these analyses were taken close to the bottom, between 200 and 400 metres depth, in the same areas where the specimens for the experiments were collected. Initial concentrations of plankton groups as well as POC and DOC in the experiments were taken as environmental concentrations too.

To calculate the biomass of the *P. antarctica* and *Primnoella* sp. colonies used in the experiments, specimens were rinsed with water to remove salt and associated macrofauna, and dry mass was determined after drying at 90° C for 24 hours. In order to determine ash free dry mass, the tissue and axis of the colonies were separated, and combusted separately at 450°C for 5 hours.

Depletion rates for the different potential prey items were calculated by assuming exponential growth and clearance of prey as described in Ribes et al. (1998a). Because the data were not normally distributed, a non-parametric test (Wilcoxon test) (Sokal & Rohlf 1995) was used to identify possible differences between prey net growth rate, and POC, DOC and nutrients net increment rate in the experimental and control chamber.

Ingestion rates were estimated from the clearance rates calculated from the feeding experiments and the mean prey concentration value for each prey type during the experiment (Ribes et al. 1999b). Ingestion was expressed in terms of number of cells colony^{-1} time^{-1}, and in terms of carbon as a proportion of organic carbon weight of tissue time^{-1}. All results are expressed as mean ± standard deviation (SD).

Results

Feeding on zooplankton

A small number of zooplankton prey was found in the 195 analysed polyps of *Primnoisis antarctica* (Table 1). The maximal number of prey items per colony was 4; 3 copepod nauplii and a tintinnid. *Primnoella* sp. did not contain any zooplankton prey in the dissected polyps. These results agree with the observations of Alvà et al. (1997) who also dissected polyps of different Antarctic gorgonian species, finding scarce zooplankton prey in the gastrovascular cavities of them.

It is difficult to estimate the contribution of zooplankton in the diet of *P. antarctica* without additional information about diel zooplankton capture rate. However, looking at the high carbon content of zooplankton prey items (Table 1) it is clear that they play a more important role by mass in the diet of this species than is indicated by their low number.

Feeding on the fine fraction of seston

Net growth rates were calculated for each plankton taxon (excluding zooplankton bigger than 100µm) and for POC and DOC in both the control and experimental chambers (Fig. 4). Net growth rates of ciliates and dinoflagellates, followed by *Nitzschia* spp., *Fragillariopsis* spp. and centric diatoms were generally lower in the experimental than in the control chamber. The concentrations of some groups (bacteria, nanoflagellates and

POC) increased in both chambers, but to a greater extent in the experimental one. DOC showed, in contrast, a general decrease in concentration, being higher in the experimental chamber for *P. antarctica* and in the control chamber for *Primnoella* sp. Average prey concentrations (cells l^{-1}) of ciliates, dinoflagellates, and diatoms in the environment and during the experiments are shown in Table 2.

The Wilcoxon test applied to the results for *P. antarctica* detected statistically significant differences in the net growth rate ($p<0.05$) for *Fragillariopsis* spp. and for nanoflagellates. For *Primnoella* sp. statistically significant differences in the net growth rate ($p<0.05$) were detected for ciliates, dinoflagellates, and for DOC.

In our experiments, neither species appeared to graze on organisms <5 µm. Ingestion rates for both species are summarised in Table 4. The highest ingestion rate (cells $polyp^{-1}$ d^{-1}) in *P. antarctica* was for *Fragillariopsis* spp. followed by dinoflagellates, *Nitzschia* spp. and ciliates. For *Primnoella* sp., the highest ingestion rate was for dinoflagellates followed by ciliates and centric diatoms.

Total ingestion rates, taking into account all seston groups and food items, of *P. antarctica* and *Primnoella* sp. were the same order of magnitude (Table 4). However, *Primnoella* sp. generally exhibited higher ingestion rates than *P. antarctica*. Ingestion rates did not vary clearly with concentrations for *P. antarctica* (Fig. 5 a) suggesting that the grazing on all groups was close to the maximum. In *Primnoella* sp. (Fig. 5 b), there was a general tendency to increase predation when the cell concentration increased. A significant positive correlation between grazing rate and concentration in the environment was observed in two groups: ciliates ($r^2=0.832$; $p<0.05$) and centric diatoms ($r^2=0.891$; $p<0.05$). On average, *P. antarctica* and *Primnoella* sp. ingested 1.11×10^{-5} (SD$\pm$0.01) mg C^{-1} $polyp^{-1}$ d^{-1} and 1.34×10^{-4} (SD$\pm$0.12) mg C^{-1} $polyp^{-1}$ d^{-1}, respectively, from these prey items (Table 4).

The available prey in the environment for both studied species is shown in Fig. 6. The composition of the plankton groups was quite similar in both cases as would be expected because both samples were taken approximately from the same area and depth. The differences in the carbon content are caused by the cell size dependency of the carbon content (different cell sizes were found at the sampling stations).

The percentage contribution of each group to the diet of both species was also calculated (Fig. 7). For *P. antarctica*, *Fragillariopsis* spp. was the main contributor in % of ingested cells (77%), followed by dinoflagellates (20%), *Nitzschia* spp. (2%) and ciliates (1%), whereas the higher contribution in mg C was supplied by *Fragillariopsis* spp. and dinoflagellates followed by ciliates and *Nitzschia* spp. For *Primnoella* sp., dinoflagellates accounted for 92% of ingested cells in the diet, followed by ciliates (6%) and centric diatoms (2%). The highest contribution in terms of mg C was made by dinoflagellates (85%), followed by ciliates (13%) and centric diatoms (2%).

Nutrient concentrations were not significantly different at the beginning and at the end of the experiment. However, in some of the replicates the nitrite and nitrate concentrations were slightly higher at the end.

Discussion

Recently it has become evident that Antarctic diatom blooms occur primarily in restricted embayments such as the inner Ross and Weddell Seas and the continental shelf of western Antarctic Peninsula, and are associated with seasonally receding ice edges (e.g., Comiso et al. 1993). In contrast, in the vast open areas of the Southern Ocean, pico- and nanoplankton are the dominant contributors to both planktonic biomass and primary production (e.g. Weber and El-Sayed 1987, Jochem et al. 1995). The idea that autotrophic nanoflagellates constitute an important group in the pelagic food web has only recently become accepted (e.g. Becquevort et al. 1992, Kopczynska 1992). The spring diatom bloom may be superimposed on a phytoplankton assemblage consisting mainly of autotrophic nanoplankton (Smetacek et al. 1990). The cycles of alternation between a diatom-dominated system and a flagellate-dominated system are not sufficiently known, partly because of the difficulty in obtaining consistent time series data in polar areas (Socal et al. 1997). The proportions of the different components of the plankton community in the Weddell Sea (Fig 5) are comparable to values from other geographical areas (Table 6).

Concentrations of the groups predated on by both Antarctic species studied here are generally lower compared with other latitudes. Nevertheless, the two gorgonians are able to feed on them. Antarctic bryozoans are also adapted to feed at very low cell concentrations, indicating that the polar winter may be shorter and less harsh for shallow water benthic suspension feeders than previously thought (Barnes & Clarke 1994). One of these bryozoan species, *Arachnopusia inchoata*, continued feeding all year around, and three others showed only relatively short periods of winter cessation of feeding activity.

The feeding behaviour of the bryozoans studied by Barnes & Clarke (1994) could explain the absence of over-wintering energy reserves in these benthic suspension feeders (Peck et al. 1986, 1987), related to reduced metabolic costs in benthos compared with plankton (Clarke & Peck 1991). The work of Barnes & Clarke (1994) was one of the first studies which challenged the concept of the long winter period as a "hibernation" time in polar sessile suspension feeders (Gruzov 1977), i.e. the idea of a long winter period of starvation, which was a dominant concept in Antarctic marine ecology for many years (Clarke 1988).

Predation on the fine fraction of seston by suspension feeders has recently been described in the literature. Studies of sponges in the Arctic (Pile et al. 1996), gorgonians in the Caribbean (Ribes et al. 1998a) as well as several Mediterranean species (Ribes et al. 1999a, b) have shown high grazing efficiency by these benthic invertebrates on the small-plankton communities in near-bottom waters. The Antarctic hydrozoan *Oswaldella antarctica* also feeds on the fine fraction of seston (Orejas et al. in press), although hydroids have traditionally been considered as carnivorous (Gili & Hughes 1995). This corroborates some previous observations which reported that bacteria, phytoplankton, and suspended organic matter may play an extremely important role in the feeding of non-molluscan suspension feeders (e.g. Riisgård 1991, Pile et al. 1997). In studies carried out on coral reefs in the Gulf of Aqaba (Red Sea) Yahel et al. (1998) showed that the taxa responsible for the depletion of phytoplankton at the reef were most likely species of sponges and ascidians. Another study by Yahel et al. (unpubl. data in: Yahel et al. 1998) on feeding by individual specimens of bivalves, sponges and ascidians showed an efficiency of more than 60% for grazing rates on eukaryotic phytoplankton.

The Antarctic gorgonians studied here are able to predate on the fraction of seston > 5 µm. The results of this study (Fig. 4) support the results from other latitudes (Pile et al. 1996, Ribes et al. 1998b, 1999b). For some Antarctic ascidians the diet is composed mainly of particles ranging from 1.2 µm to 6.5 µm (Kowalke 1999). These examples together with the available literature lead to the conclusion that resource partitioning is present among passive benthic suspension feeders, due to the wide range of potential prey they have, corresponding to different trophic strategies in a community (Orejas et al. in press, see also Stuart & Klump 1984). Furthermore, Antarctic active suspension feeders, such as the bivalve *Laternula elliptica* (Ahn 1993), behave similarly to species from other latitudes (Jørgensen 1990), thus supporting these results.

The predation of suspension feeders on ciliates and dinoflagellates leads to increase of the growth rates in bacteria and nanoflagellates as observed during the experiment (see Fig. 4). The important role of ciliates and dinoflagellates as predators of bacteria (e.g. Caron et al. 1999, Gast et al. 1999) and nanoflagellates (Banse 1982) has been confirmed by many authors. Because of their potential for rapid growth, ciliates play an important role in the microbial food webs as predators of microflagellates and as predators and grazers of both heterotrophic and autotrophic picoplankton, respectively. According to Gast (1985) and Porter et al. (1985), in eutrophic coastal regions such as estuaries and fjords, bacterivory is likely to be of greater importance for ciliates and other microzooplankton. However, the majority of ciliates in the open ocean are not bacterivorous, as they feed largely on heterotrophic and phototrophic nanoplankton (Fenchel 1984). Their larger size makes some picoplankton more suitable for ingestion by ciliates than the smaller (0.4-0.6 µm) free-living bacteria (Banse 1982). Tsuda & Kawaguchi (1997) indicated that microzooplankton, including flagellates, ciliates, heterotrophic dinoflagellates and microcrustaceans, may be regarded as major consumers of pico- and nanophytoplankton. Accordingly, microflagellates are probably the most important grazers of algal picoplankton in aquatic ecosystems. As predators with a high assimilation efficiency and rapid growth potential, they serve to keep heterotrophic and autotrophic picoplankton in an active growth phase by their cropping and subsequent release of dissolved organic matter and inorganic nutrients (Goldman et al. 1985, Goldman & Caron 1985). As in the case of flagellate predation on picoplankton, grazing by ciliates and other microzooplankton contributes to the dissolved organic matter pool for utilisation by bacteria, and to the release and recycling of inorganic nutrients for bacteria and phytoplankton (Caron et al. 1985, 1988).

Feeding studies on gorgonians have only rarely reported the capture of zooplankton prey items (e.g. Lasker 1981, Lasker et al. 1983). For this reason, alternative food sources such as suspended particulate matter (Lasker 1981), mucus produced by corals (Coffroth 1984, Herndl & Velimirov 1986), dissolved organic matter (Murdock 1978), and microplankton (Pile et al 1996, Ribes et al. 1998a,b 1999a,b) have been proposed. In fact, significant capture of naturally occurring zooplankton prey in situ has only been documented in the Mediterranean species *Paramuricea clavata* (Coma et al. 1994) and the Caribbean gorgonians *Plexaura flexuosa* and *Pseudoplexaura porosa* (Ribes et al 1998a). In our cases, *Primnoisis antarctica* had a very small amount of zooplankton prey items in their gastrovascular cavities. However, as in *P. clavata* (Coma et al. 1994), the small contribution of zooplankton prey might be very important to cover the energetic requirements of the species, since the carbon content of a zooplankton prey item is much higher than that of micro-, nano- and picoplankton items. This has been recently pointed out for benthic sessile organisms (Gili et al. in press). The combination of low metabolism (Clarke 1998) and individual nutritive prey could make up for a long period of starvation. *Primnoella* sp. did not show any zooplankton prey items in their gastrovascular cavities. We observed, however, that all dissected polyps were filled by well developed gonads (up to 13 oocytes in one gastrovascular cavity) which might explain the absence of large prey in the polyps. This same phenomenon has been mentioned by Brito et al. (1997) for the Antarctic gorgonian *Thouarella variabilis*.

In summary, the Antarctic octocorals studied here seem to show the same trophic behaviour as do octocorals studied in other latitudes. They do not seem to make much use of large zooplankters but feed primarily on the fine fraction of seston, i.e. on particles not smaller than 5 µm. The presence of benthic diatoms in the gastrovascular cavities of both studied gorgonians and their grazing observed in the feeding experiments lead to the conclusion that resuspension may play an important role in the food available for these organisms. Sediment resuspension is a common phenomenon already documented in shallow near shore environments surrounding Antarctica (e.g. Klöser et al. 1994). This phenomenon may be particularly relevant during the austral winter. In shallow areas detritus resuspended by wind-generated waves, anchor ice and currents may be a viable food source for benthic invertebrates during this season. This phenomenon was called "utilisation of redistributed accumulated energy" by Gruzov (1977).

The apparent difference with regard to species studied in other oceans does not refer to the quality but to the quantity of food they ingested, which is significantly lower than in octocorals from other latitudes. Antarctic organisms have low metabolic rates (Clarke 1991), which suggests higher growth efficiencies and reduced cost of maintenance. In addition, low resting metabolic rates provide energetic advantages (overwintering reserves can be reduced) but limit the rate at which food can be processed, being an energetic constraint. However, the Antarctic octocorals might be able to feed during the whole year, whereas octocorals from temperate seas show a seasonal feeding behaviour. Feeding the year round, although at lower rates, would reduce the difference in their impact on the ecosystem as compared to other areas.

The ability of suspension feeders to feed on the fine fraction of seston all year round (Clarke & Leakey 1996), the resuspension processes, which supply food to the suspension feeders in the winter season in form of "reversed vertical" inputs, and the lateral advection processes, may be key factors in the trophic dynamics of Antarctic benthic suspension feeders. What Hedgpeth (1977) called "Antarctic paradox" may need to be reformulated in the light of these new studies.

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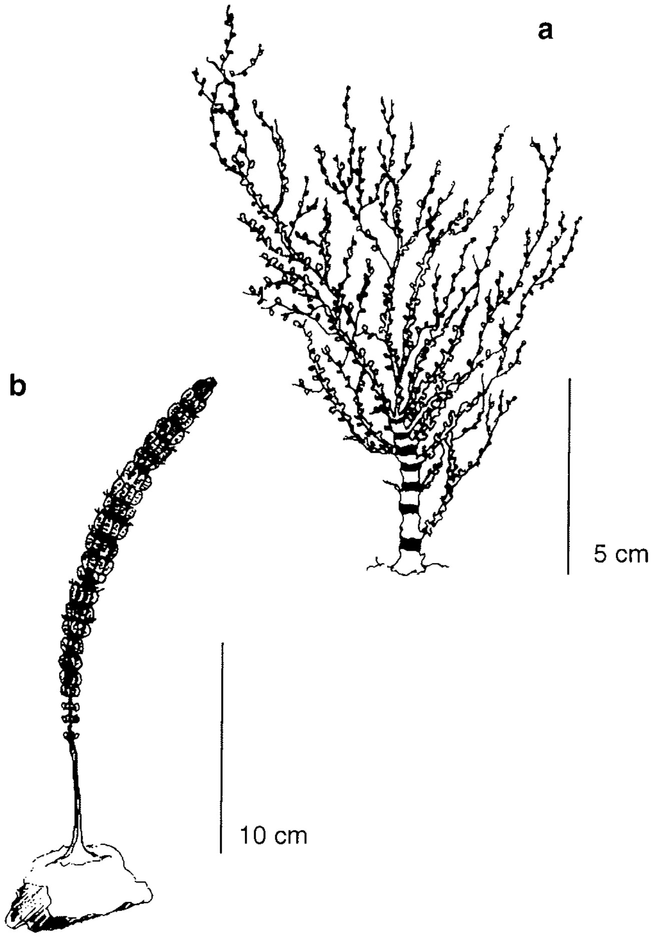

Fig. 1 Studied species. a *Primnoisis antarctica*, b *Primnoella* sp.

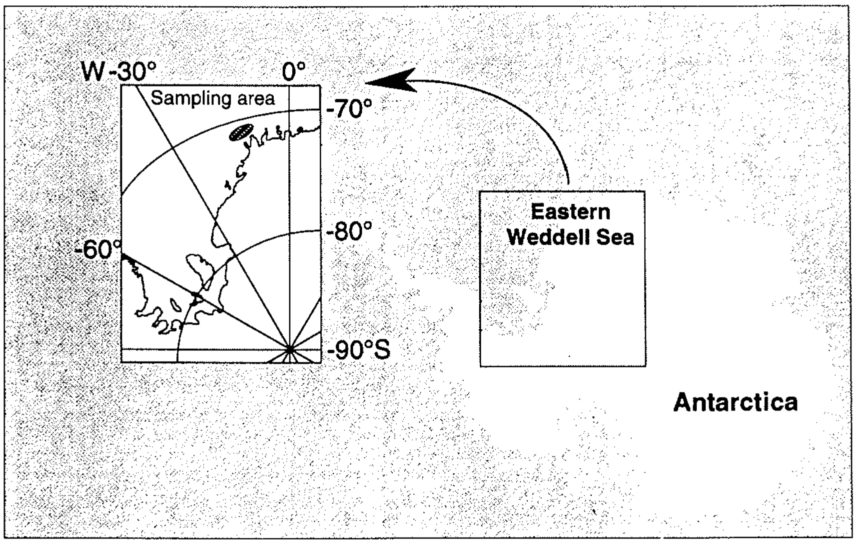

Fig. 2 Sampling area in the High Antarctic Weddell Sea.

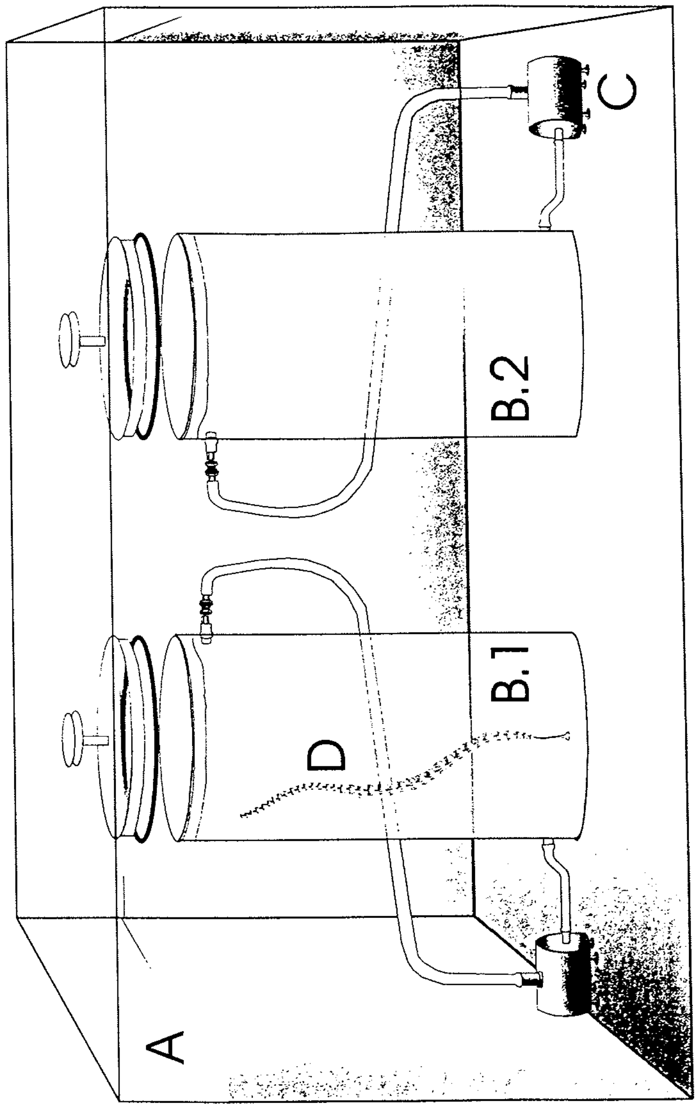

Fig. 3 Experimental device for the feeding experiments. A: Aquarium container, B.1.: Experimental chamber, B.2.: Control chamber, C: Pump, D: Specimen.

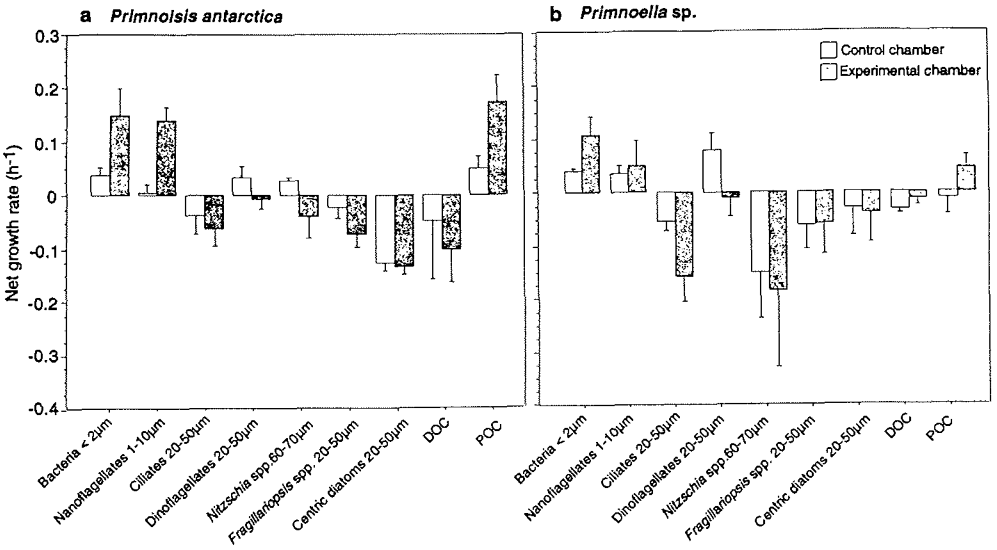

Fig. 4 Net growth rates (h^{-1}) (mean±SE) in the control (white bars) and experimental (dotted bars) chamber for *Primnoisis antarctica* (a) and *Primnoella* sp. (b) for each plankton group, POC and DOC. Size range of each plankton group is indicated. Bars indicated standard error.

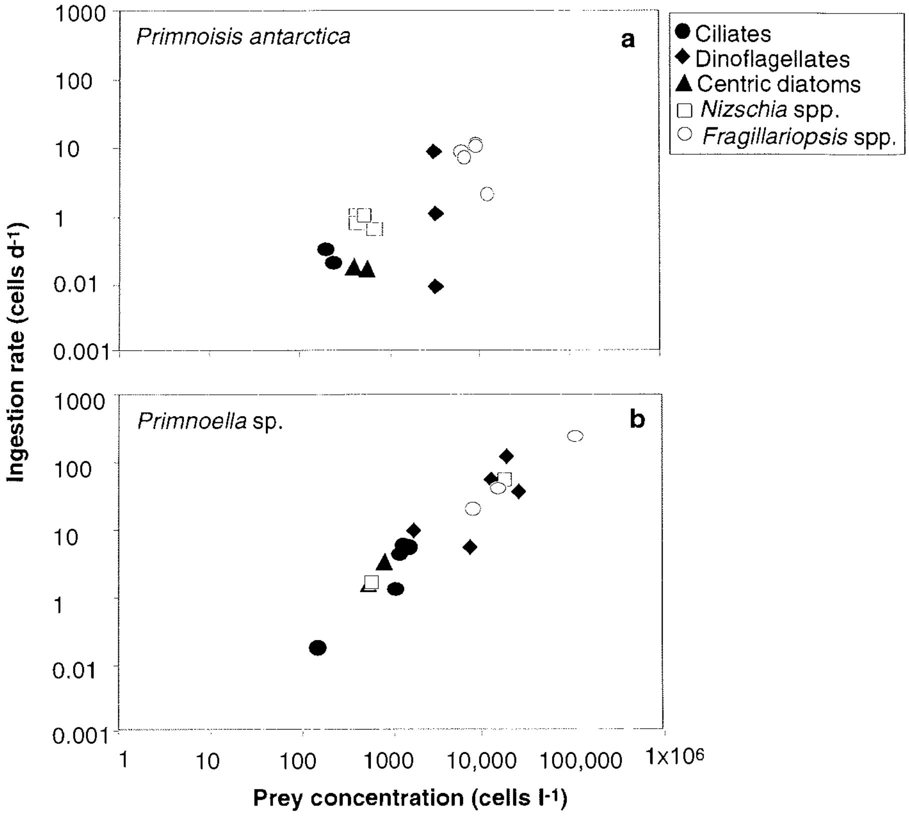

Fig. 5 Ingestion rate (cells d^{-1}) vs. prey concentration (cells l^{-1}) of *Primnoisis antarctica* (a) and *Primnoella* sp. (b) for each prey group. Logarithmic scale for both variables.

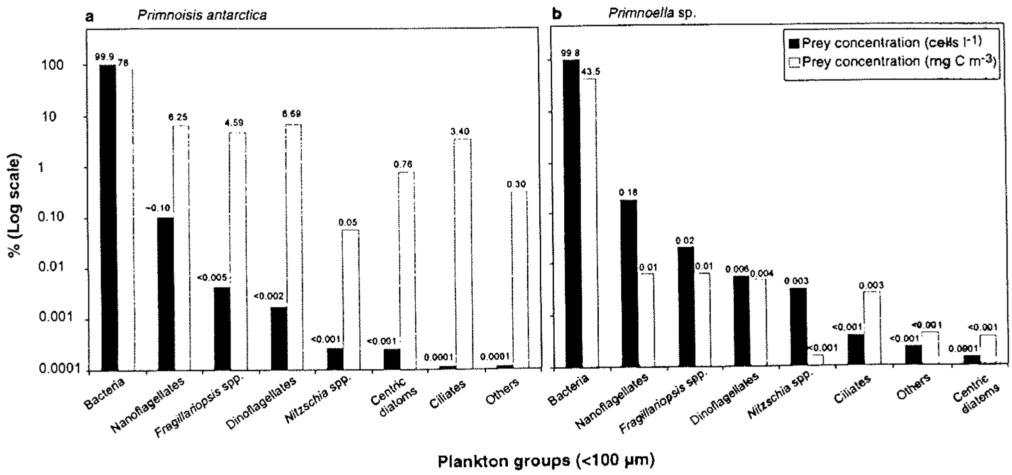

Fig. 6 Prey concentration split by each group in the respective environment where the gorgonians were sampled for a): *Primnoisis antarctica* and b): *Primnoella* sp. Black bars show prey concentration in % of cells and white bars in % of mg C.

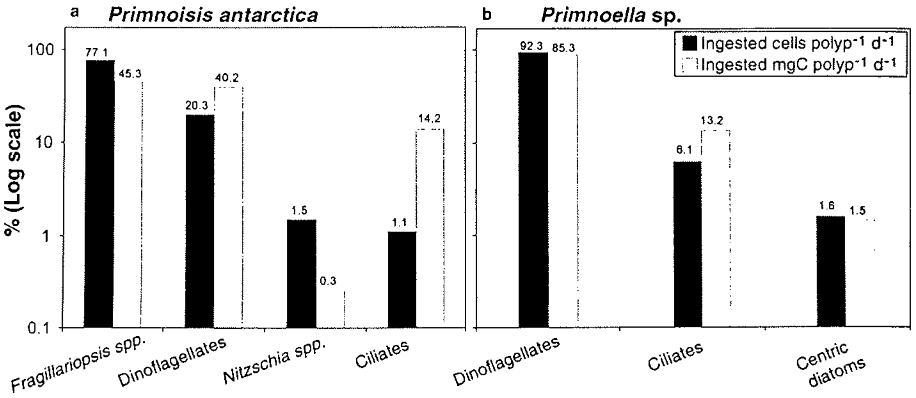

Fig. 7 Ingested prey of each plankton group in % for a): *Primnoisis antarctica* and b): *Primnoella* sp. Black bars show ingested prey in % of cells and white bars in % of mg C.

Table 1 Number and type of zooplankton prey items found in the gastrovascular cavities of *Primnoisis antarctica*, and content in carbon of each prey item (expressed in mg C). (Source for conversion in mg C: Edler (1979) and S. Schiel (pers. Comm.)).

Colony	N° of dissected polyps	Prey number	Prey type	mg C/prey item
1	15	0	-	-
2	15	0	-	-
3	15	1	Tinntinid	~ 3.2×10^{-3}
4	15	0	-	-
5	15	2	Nauplii Tinntinid	~7.5×10^{-3} ~ 3.2×10^{-3}
6	15	0	-	-
7	15	0	-	-
8	15	1	Inv. larva	~7.2×10^{-5}
9	15	0	-	-
10	15	0	-	-
11	15	4	Nauplii (3) Tintinnid	~7.5×10^{-3}- 18.0×10^{-3} ~ 3.2×10^{-3}
12	15	1	Nauplius	~11.0×10^{-3}
13	15	0	-	-

Table 2 Initial values (control) and mean values of experimental chambers. Control concentration used as environmental concentrations for the different groups and components of the fine fraction of seston.

	Primnoisis antarctica		*Primnoella* sp	
	$C_{control}$ (cells ml^{-1})	$C_{experiment}$ (cells ml^{-1})	$C_{control}$ (cells ml^{-1})	$C_{experiment}$ (cells ml^{-1})
Bacteria	$1.25x10^{5}\pm0.31$	$0.53x10^{6}\pm6.57$	$2.28x10^{6}\pm0.61$	$4.49x10^{6}\pm2.15$
Nanoflagellates	202.48±103.79	614.38±388.96	265.16±79.77	341.41±144.83
Ciliates	0.24±0.06	0.18±0.05	0.94±0.52	0.42±0.20
Dinoflagellates	3.12±0.10	2.86±0.76	13.22±9.33	9.83±7.89
Nitzschia spp.	0.54±0.10	0.48±0.39	13.22±9.33	5.39±7.80
Fragillariopsis spp.	8.77±2.46	6.19±2.60	37.82±39.81	31.16±24.95
Centric diatoms	0.45±0.09	0.31±0.06	0.43±0.31	0.30±0.17
	(mg C ml^{-1})	(mg C ml^{-1})	(mg C ml^{-1})	(mg C ml^{-1})
POC	0.06±0.04	0.17±0.05	0.14±0.05	0.24±0.18
DOC	$2.01x10^{-6}\pm1.55$	$2.14x10^{-6}\pm1.28$	0.24±0.22	0.24±0.23

Table 3 Ingestion rates of Primnoisis antarctica and Primnoella sp. For each prey plankton group. Values are expressed as mean (± SD), in cells polyp^{-1}, mg C polyp^{-1} d^{-1}, mg C mg DW h^{-1}, mg C mg AFDW h^{-1}.

P. antarctica

	Ciliates	Dinoflagellates	*Nitzschia* spp.	*Fragillariopsis* spp.	Total
Ingestion (cells polyp^{-1} d^{-1})	0.12 ± 1.66	$2.20x10 \pm 4.64$	$1.63x10^{-1} \pm 1.64$	$8.38x10 \pm 3.87$	$5.20x10 \pm 0.45$
Ingestion (mgC polyp^{-1} d^{-1})	$3.53x10^{-7} \pm 4.93$	$9.99x10^{-7} \pm 2.02$	$6.22x10^{-9} \pm 38$	$1.13x10^{-6} \pm 0.69$	$1.11x10^{-5} \pm 0.01$
Ingestion (mgC mg DW d^{-1})	$3.97x10^{-7} \pm 5.55$	$1.12x10^{-6} \pm 2.27$	$6.99x10^{-9} \pm 43$	$1.27x10^{-6} \pm 0.78$	$1.25x10^{-5} \pm 0.12$
Ingestion (mgC mg AFDW d^{-1})	$4.21x10^{-7} \pm 5.88$	$1.19x10^{-6} \pm 2.41$	$7.41x10^{-9} \pm 44.98$	$1.34x10^{-6} \pm 0.83$	$1.32x10^{-5} \pm 0.13$

Primnoalla sp.	Ciliates	Dinoflagellates	Centric diatoms	Total
Ingestion (cells polyp^{-1} d^{-1})	$3.22x10 \pm 3.11$	$4.87x10^{1} \pm 5.18$	$8.84x10^{-1} \pm 1.80$	$26.67x10^{1} \pm 3.59$
Ingestion (mgC polyp^{-1} d^{-1})	$9.00x10^{-8} \pm 0.10$	$1.58x10^{-5} \pm 1.51$	$1.92x10^{-7} \pm 7.02$	$1.34x10^{-4} \pm 0.12$
Ingestion (mgC mg DW d^{-1})	$1.41x10^{-5} \pm 1.58$	$2.47x10^{-5} \pm 2.36$	$2.22x10^{-7} \pm 12$	$2.09x10^{-4} \pm 0.19$
Ingestion (mgC mg AFDW d^{-1})	$2.37x10^{-5} \pm 2.66$	$4.16x10^{-5} \pm 3.97$	$3.74x10^{-7} \pm 19$	$3.52x10^{-4} \pm 0.31$

Table 4 Comparative concentration values (x10^3 cells ml^{-1}) of the different groups which constitute the fine fraction of seston in different seas at different latitudes. The sign (-) means no data are available.

Location	Depth (m)	Picoplankton	Picoeucaryotes	Autotrophic nanoeucaryotes	Heterotrophic nanoeucaryotes	Source
Baltic Sea	10-20	30-80	-	-	-	Larsson & Hangström 1982
Celtic Sea	0-50	200-600	-	-	<1 – 7	Joint & Pomroy 1983
Gulf Stream (Slope Water/North)	-	±1	-	-	-	Waterbury et al. 1979
Woods Hole Harbour	-	2-360	-	-	-	Waterbury et al. 1979
Nova Scotia, coastal slope and eddy	~200	4-50	-	-	-	Douglas 1984
Rhode Island shelf	50-100	495	-	-	-	Johnson & Sieburth 1979
Narragansett Bay	50-100	1,800	-	-	-	Johnson & Sieburth 1979
Japan, coastal waters	0-70	<1-100	-	-	-	Takahashi et al. 1985
Mediterranean Sea	15	516	1.64	<1	<1	Ribes et al. 1998
Azores	65-89	4-17	-	-	-	Platt et al. 1983
Red Sea (Aqaba Gulf)	1-50	-	<1-8	-	-	Yahel et al. 1998
Costa Rica Dome	0-80	500-1500	-	-	-	Li et al. 1983
Peru and Arabian Sea	200-400	<0.01-0.3	-	-	-	Waterbury et al. 1979
Hawaii	0-30	690	-	<1	±1	Laws et al. 1984
Signy Island (Antarctica)	20-25	304	-	-	-	Clarke & Leakey 1996
Weddell Sea	250-300	117-252	<1	-	<1	This study

Publication III

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Distribution and reproductive ecology of the Antarctic octocoral *Ainigmaptilon antarcticum* in the Weddell Sea

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Abstract

Ainigmaptilon antarcticum (Molander, 1929) is one of the most common octocoral species of the family Primnoidae in Antarctic benthic communities of the Weddell Sea. Little is known about the ecology of this and other primnoid species, despite that this group is one of the dominant components of the benthos. We studied the spatial distribution, density and reproductive ecology of *A. antarcticum* using samples (colonies) collected during the EASIZ (Ecology of the Antarctic Sea Ice Zone) cruises I, II, and III, (1996, 1998 and 2000). Samples were taken using Agassiz and bottom trawls between 150 and 600 m depth and using a Remotely Operated Vehicle (ROV, video recording transects). *A. antarcticum* showed a very patchy distribution with a mean density of 12.0 ind.100m^{-2} (SD$\underline{+}$ 22.6) in the study area. This gorgonian species is gonochoric with a sex ratio of 1:1. Two size classes of oocytes in different developmental stages were observed in summer and autumn, ranging from 25 to 700 µm in summer, and from 20 to 900 µm in autumn. Differences in developmental stages among different zones of the colony were observed. The apical and medial part showed the highest fecundity. The distribution of gonad-size differed between summer and autumn; our results suggest that this species has a continuous gametogenesis of nearly two years duration with a seasonal spawning period in autumn. The relative frequency of the largest oocyte size class decreased in the autumn samples. No larvae were found. The results are discussed in the context of the relationship between reproductive strategies of marine invertebrates and environmental factors.

Introduction

Antarctic shelf communities are dominated by sessile invertebrates (Dayton et al. 1974, White 1984, Voß 1988). Anthozoans (mainly gorgonians) are the second most dominant macrobenthic taxon in abundance in the

Weddell Sea (Starmans et al. 1999). Moreover, anthozoans, and especially gorgonians, are also common organisms in sublittoral benthic communities in temperate (e.g. Weinberg 1979, 1980, Gili et al. 1989) and tropical areas (e.g. Kinzie 1973, Grigg 1977, Muzik 1982, Lasker et al. 1983, Yoshioka & Yoshioka 1989). Despite the importance of gorgonians in polar regions, studies of their basic ecology have been very few in polar regions (e.g. Arntz et al. 1994).

The distributional patterns of many invertebrate benthic megafauna species has been shown to be patchy (e.g. Picken 1980, Miller 1998). Contagious patterns of distribution have been found for anthozoans (Williams 1976), and several octocoral species also show a patchy and clumped distribution (e.g. Chia & Crawford 1973, Langton et al. 1990, Rice et al. 1992). However, most of these studies have been undertaken in tropical and temperate regions (but see Gili et al. 1999).

Similarly, patterns of reproduction of anthozoans have been well studied in temperate and tropical regions (e.g. Weinberg & Weinberg 1979, Hughes & Jackson 1980, Martin 1982, Brazeau & Lasker 1990, Coma et al. 1995a). Gonochorism and a sex ratio of 1:1 have been considered the general pattern for this group in the Caribbean Sea (Kinzie 1970, 1974, Goldberg & Hamilton 1974, Behety-González & Guardiola 1979, Martin 1982), the Pacific Ocean (Grigg 1977) and the Mediterranean Sea (Coma et al. 1995a). Other important reproductive features are seasonality in gamete production and size at first reproduction (Sebens 1982, Hughes & Cancino 1985). Some work has been done on reproductive patterns of deep-sea cnidarians, mainly actinians (e.g. Van Praet 1990, Van Praet et al. 1990), zoantharians (Muirhead et al. 1986) and sea pens (e.g. Rice et al. 1992, Tyler et al. 1995, Eckelbarger et al. 1998), however, information on polar species is scarce (e.g. Arntz et al. 1992, Barthel & Gutt 1992, Poulin & Féral 1996, Brito et al. 1997, Barnes & Clarke 1998). To our knowledge, the study of the gorgonian *Thouarella variabilis* (Brito et al. 1997) provides the only data on reproductive ecology available for Antarctic gorgonians so far, although descriptive information on reproductive modes of some Antarctic octocorals was first obtained a long time ago (in Brito et al. 1997: e.g. Wright & Studer 1889, Versluys 1906). These papers suggest that gonochorism and brooding seem to be common features of Antarctic and deep-sea octocorals.

The objectives of this study were to: (1) determine patterns of density and spatial distribution of the Antarctic gorgonian *Ainigmaptilon antarcticum*, and (2) describe the reproduction of this species (distribution of gonads within a colony, number of oocytes produced, seasonality in gonad production and spawning). We discuss the relationship between distribution and reproductive output, and compare our results with the patterns described for species of octocorals from other latitudes, as well as with other Antarctic benthic organisms.

Material and methods

This study was carried out in the eastern Weddell Sea (Antarctica; Fig. 1). Sampling was carried out on board of the German RV "Polarstern" (for details on the expeditions see Arntz & Gutt 1997, 1999 and Arntz & Brey, in press), during the EASIZ cruises I (ANT XIII/3, January-March 1996), II (ANT XV/3, January-March 1998) and III (ANT XVII/3; March-May 2000). The sampled area was characterised by Voß (1988), who described the presence of sandy bottoms but also sponge spicules matts, bryozoan debris and a few stones. A high number of taxa, species diversity and evenness are also characteristics of the Kapp Norvegia area.

Spatial patterns of density

Transects were conducted with a Remotely Operated Vehicle (ROV) (for detailed description see Starmans et al. 1999) and recorded using a video camera, at depths ranging between 142 and 363 m. Five transects from EASIZ I and 12 from EASIZ II, each covering areas between 377.6 m^2 and 1695.9 m^2 and corresponding to a total of 13,921.2 m^2, were studied (Table 1). Each transect was split into adjacent areas (sampling units) of approximately 100 m^2 and 4 of those sampling units of each transect were randomly selected to obtain density values, in order to avoid statistically dependent samples. The degree of contagious of the population was determined using the variance to mean ratio ($S^2/\overline{X}$) and Morisita's index of dispersion (I_d) (Morisita 1962). Random spatial distribution is indicated when the value of this index equals 1, while the distribution tends to be contagious as the value becomes greater than 1. Randomness of the null hypothesis was tested by a χ^2-test at 5% significance level.

Reproduction

Samples were collected with Agassiz, bottom, and benthopelagic trawls, and with a small dredge at depths ranging between 250 and 600 m. All specimens were preserved in 4% formalin prior to further work in the laboratory. A total of 136 colonies (indicated by the presence of the holdfast) were examined for sex ratio. A χ^2-test was done in order to test for statistically significant differences in the frequency of individuals of both sexes.

Studies on the anatomy of the genus *Ainigmaptilon* (Dean 1926, Molander 1929, Carlgren 1943, Bayer 1954) showed that the polyps tend to fuse at different levels, forming distinct polyp leaves (Fig. 2). The selected "working unit" for all the reproductive studies was the polyp leaf because of the difficulty of isolating the gonadal products from each gastrovascular cavity during dissection (Dean 1926). The selection of the polyp leaf as the working unit was based on preliminary morphological and histological studies which confirmed the discontinuity of the gastrovascular cavities in *A. antarcticum*. Selected polyp-leaves previously fixed in formalin were washed in distilled water, dehydrated in acetone, and subsequently dried with CO_2 in a Balzer CPD 030 Critical Point Dryer for scanning electron microscopy (SEM) morphological studies. Samples were mounted on stubs by a carbon impregnated film, coated with 20 nm gold in a Edwards & Kniese Vakuum Coating System E 306 A, and observed with a Philipps scanning electron microscope SEM 515 at an acceleration voltage of 10.2 kv. For the histological observations we selected portions of fixed colonies, dehydrated them in butanol (Johansen 1940), and embedded in paraffin wax. 6-10 µm thick histological sections were mounted, and stained with Ramón y Cajal's Triple Stain (Gabe 1968). The sections were also used to confirm and identify the developmental stages of the gonads.

The rest of the reproductive studies were done using a binocular. After dissection gonads were measured using an eyepiece calibrated against a stage micrometer. The number of polyps per polyp leaf and the number of polyp leaves per colony were counted in 6 colonies collected during EASIZ I (3 females and 3males). The length of sixty polyps per leaf were measured. To determine fecundity (according to the definition given by Lincoln et al. 1998), the number of gonads per polyp in 5 colonies from EASIZ I (3 females and 2 males) and 5 colonies from EASIZ II (2 males and 3 females) were examined. Total numbers of oocytes and spermatic cysts per polyp leaf were counted in three zones (apical, medial and basal) of the colony (Fig. 2). Two leaves per zone were analysed for each zone of each colony. Oocytes and spermatic cysts counts were done in the summer samples only, in order to avoid the possible error of overlooking gametes released during the autumn season.

In order to determine developmental stages, 11 colonies from EASIZ I (8 females and 3 males), 10 colonies from EASIZ II (5 females and 5 males), and 20 colonies from EASIZ III (10 females and 10 males) were selected. The relatively low number of specimens available for examination was caused by the fragility and the consequent difficulty of obtaining complete colonies. The developmental stage of the gonads was studied in each colony in the apical, medial and basal zones (Fig. 2), following the methodology described by Brazeau & Lasker (1990), Coma et al. (1995b), and Brito et al. (1997). In all the colonies (41), 200 gonads per colony zone were randomly selected and measured.

Our data set for number and size of gonads was not distributed normally, despite different transformations. Since a 3-way ANOVA was necessary to test both individual effects and interactions of the factors cruise, sex and colony zone on gonads size and number, parametric tests were used. In order to achieve a distribution as near as possible to a normal distribution and to meet the homocedasticity assumption, data were subjected to BoxCox transformations (Sokal & Rohlf 1995). In case of significant differences, a Bonferroni/Dunn post-hoc analysis of means was performed. For data transformation and further statistical analyses we used the statistical package Statview (SAS Institute 1998).

Results

Density and distribution

The mean density for all transects was 11.95 ind. 100 m^{-2} (SD± 22.61) (Table 1). The high variance (much higher than the mean value) indicated a very patchy distribution for *A. antarcticum*. The average patch size was 33.97 m^2 (SD± 29.68) (patch area ranged from 3 to 98 m^2), and the average number of individuals per patch (excluding zeros) was 16.7 ind. 100 m^{-2} (SD±30.8).

In all transects except one (transect 3, EASIZ II), values of Morisita's Index of dispersion exceeded unity (Table 1) (in 3 other transects density was zero), suggesting that *A. antarcticum* has a contagious distribution. Ananlysis of χ^2 statistic showed that the values of Morisita's Index differed significantly from a random distribution for most of the analysed transects ($p<0.05$, Table 1). This indicates that *A. antarcticum* is also patchily distributed also at scales smaller (dozens of meters) than the area covered by the transects (Fig. 3). Comparative densities of *A. antarcticum* on three transects revealed a discontinuity in the density values which varied between 0 and 116 ind. 100 m^{-2}. For example, in station 1 of EASIZ I (see Fig. 3 left), the lowest abundance in units that showed presence of *A. antarcticum* was 5 ind. 100 m^{-2}, whereas in the next 200 m 116 ind. 100 m^{-2} were recorded.

Reproductive features

All colonies examined were found to be reproductive. *A. antarcticum* is a gonochoric species, and the sex ratio is approximately 1:1 (χ^2; $p>0.05$). The polyp leaves of *A. antarcticum* are dichotomously ramified (Fig. 2). Internally, gastrovascular cavities are longitudinally arranged and separated by thin mesogloea walls covered by the gastrodermic epithelium, although the cavities of contiguous polyps are not always completely separated (Fig. 2). The gonads fill all the available space in the canals (Fig. 2, 4 a, b), and have the general structure shown by other octocorals (Fig. 4 c, d).

Oogenesis is similar to that described for other anthozoans. Alterations in the nucleus do not take place until the oocyte reaches the final size, when the distinct nucleolus and line between germ vesicle and cytoplasm, observed during the early oogenesis, disappear during the maturation of the large oocytes. Mature oocytes are finally detached from the mesenteries. No embryonic or planula stages have been observed in the gastrovascular cavities of the polyp leaves.

The average number of oocytes per single gastrovascular cavity (polyp) was 2.99 (SD±1.88), and the average number of spermatic cysts was 1.46 (SD±1.42). Results of the 3-way ANOVA for number of gonads are shown in Table 2. Significant interactions precluded us from testing for the main effects but the Bonferroni/Dunn post hoc test revealed that there were no significant differences in the average number of gonads per polyp between cruises (Table 2, Fig. 5 a). Differences in the mean number of gonads were found between the medial-basal and the apical-basal zones in males but not in females. Significant differences were also detected between medial-basal and apical-basal zones in EASIZ I, and between the medial-basal zones in EASIZ II. Numbers of gonads between females and males were significantly different in EASIZ II. Differences in numbers of gonads between females and males have been detected for both cruises in the basal zone.

Results of the 3-way ANOVA for gonad size are shown in Table 3. Again, significant interactions precluded us from testing for the main effects. The Bonferroni/Dunn post hoc test revealed significant differences in gonad size among the three cruises (Table 3, Fig. 5 b). In all cases, the larger gonads of both males and females were located in the apical and medial. Significant differences in gonad size have been detected for both sexes in the three zones (Table 3). Significant differences were also detected among the three zones in EASIZ I and EASIZ II and between medial-basal and apical-basal in EASIZ III. The analysis also showed significant differences in the size of gonads between females and males in all cruises and also among the different levels of the colony (Table 3).

Frequency distributions of the oocytes in females, and of sperm cysts in males, from summer and autumn samples are shown in Fig 6. Two modes in gamete size were clearly distinguishable in females, but were less obvious in males. Summer samples showed a first class of oocytes of about 25-400 µm in diameter in females, and a second size class, mainly oocytes in the last stages and early embryos of about 400-700 µm. The largest size class of oocytes was more abundant in the apical and medial zones of the colonies, whereas those between 25 and 400 µm predominantly occurred in the basal part (Fig. 6). In both cases the first mode was larger than the second one. The autumn samples for females presented almost only one distinct mode, which corresponded to the first summer mode (size). The first size class ranging between 25 and 400 µm in the summer samples showed a displacement to a larger diameter in both sexes in autumn.

In males it was possible to distinguish only one mode both in summer and autumn. In summer, the size of spermatic cysts ranged between <50-1000 µm, while in autumn the size range was no so widespread (Fig. 6). The size of the spermatic cysts also varied between seasons for the different zones of the colony. In the autumn samples the sizes of the spermatic cysts were homogeneous among zones of the colony, while in summer smaller spermatic cysts were more abundant in the basal zone.

Discussion

Distribution and Reproductive patterns

The density and spatial distributional patterns observed for *A. antarcticum* in the Weddell Sea are similar to those observed in other Antarctic gorgonians (Gili et al. 1999). The low mean densities form a strong contrast with the high densities typically observed for shallow water and continental shelf gorgonians in temperate and tropical regions (e.g , Kinzie 1973, Grigg 1977, Gili & Ros 1985).

Density and fecundity at the polyp level seem to be inversely correlated in benthic cnidarians. For example *Umbellula lindahli* exhibits very low densities but high fecundity at the polyp level (Tyler et al. 1995). Conversely, the pennatulacean *Ptilosarcus guerney* presents high densities and fecundity is very low at the polyp level (but high at the colony level) (Chia & Crawford 1973). *A. antarcticum* seems to follow the latter pattern.

The distance between females and males is a critical factor in the reproduction in benthic sessile invertebrates (Coma & Lasker 1997). Pennington (1985) showed that echinoid sperm shed into sea-water is sufficiently diluted, by turbulent mixing, to prevent fertilisation of eggs more than a few metres away from the male. This may not be a major problem in mobile forms such as the echinoids, which can aggregate to ensure successful fertilisation (Young et al. 1992). A similar behaviour has also been observed in the Antarctic limpet *Nacella concinna*, which forms short-term spawning aggregations (Picken 1980). However, in sessile organisms occurring at low densities, distance between females and males must be of paramount importance in determining reproductive success. The aggregated (contagious) distribution observed in many sessile benthic invertebrates is thus critical to their successful reproduction (Rice et al. 1992). Aggregated distributions have been reported for cnidarian species of continental shelves in other latitudes (e.g. *Kophobelemnon stelliferum*, Rice et al. 1992, Hecker 1994), and were also found in *A. antarcticum*. Both aggregation and increased fecundity may favour reproduction success, although other factors, such as synchrony of spawning, may positively affect fertilisation of this free-spawning species (e.g Langton et al. 1987).

Fecundity

Our data are comparable with results from studies of anthozoans from other latitudes. *A. antarcticum* exhibits a reproductive strategy characterised by a relatively low number of oocytes per polyp but a high number of polyps in the colony. The different values of gonad number/polyp observed in both sexes arise because not all the polyps contribute the same reproductive effort to the total fecundity of the polyp leaf. This contribution probably depends on the age of the polyps, which correlates with the length of their respective gastrovascular cavities.

Fecundity in gorgonians is frequently correlated with colony size (e.g. Kinzie 1974, Grigg 1977, Wahle 1983, Benayahu & Loya 1984, Coma et al. 1995b). In contrast we did not find a relationship between colony size of *A. antarcticum* and reproductive effort, but this may be a result of the low number of complete colonies available for examination. A large adult *A. antarcticum* is capable of producing 17,000 oocytes/colony with a maximum value of 12 oocytes/polyp and this compares favourably with colony oocyte output from other cnidarian species, showing different strategies. Thus, Chia & Crawford (1973) showed that the shallow water sea pen *Ptilosarcus guemeyi* has a fecundity of 200,000 oocytes/colony and 20-25 oocytes/polyp (this last figure is a rough approximation based on large colonies). The Mediterranean gorgonian *Eunicella singularis* produces 6,000 planulae/colony with an average of 4 oocytes/polyp, for a medium size female of approximately 35 cm (Weinberg & Weinberg 1979), and the Antarctic gorgonian *Thouarella variabilis* follows a similar strategy (13,500 ooytes/colony, 1 oocyte/polyp) (rough approximation based on a colony of about 20 cm length and the reproductive data by Brito et al. (1997)). On the other hand, the pennatulacean *Umbellula lindahli* has only 2,000 oocytes/colony (Tyler et al. 1995) but about 200 oocytes/polyp (for a specimen of ten polyps and 30 cm length). A relatively small number of oocytes per polyp can thus be compensated by the high number of polyps in the colony.

Intra-colonial variation in fecundity

Variability in fecundity within an individual colony has been studied frequently in octocorals (e.g. Brazeau & Lasker 1990, Coma et al. 1995a). Similar functional characteristics have been postulated for all segments along a colony branch, on the basis of the branch formation pattern (Brazeau & Lasker 1988), but recent reproductive studies have contradicted this assumption by revealing differences in reproductive effort within individual colonies (Coma et al. 1995b). For example, the tropical gorgonian *Briareum asbestinum* shows a more fecund zone in the central portion of its branches (Brazeau & Lasker 1990), whereas in the Mediterranean *Paramuricea clavata* the apical segments are the most fecund ones (Coma et al. 1995a).

Soong & Lang (1992) postulated that a decreasing fecundity related with increasing branch order might be caused by different capture rates along the colonies, themselves related to differences in access to water flow. The authors suggested that the low food availability in tropical waters could be the cause of the low fecundity of the basal portions of the tropical scleractinians *Acropora cervicornis* and *Porites furcata*. A similar pattern was found in *P. clavata* where polyps at the top of the colonies capture the major number of prey (Coma et al. 1994).

In the Antarctic gorgonian *Thouarella variabilis* (Brito et al. 1997) the distal regions of both male and female colonies contain more polyps in the first reproductive or immature stages, with the mature stages distributed relatively evenly between the middle and proximal regions of the secondary branches. Brito et al. (1997) hypothesised that the polyps in a colony could have different functions, which may explain the different distribution of reproductive polyps along the colony, and that the reproductive polyps enter a quiescent stage receiving the food through the solenia from the most distal non-reproductive polyps in the secondary branches. In *A. antarcticum* the most fecund zones are the apical and medial. Two possible explanations could be considered: (1) prey capture is higher in the upper colony parts and is translated into a higher investment in reproduction, and (2) polyp function might be differentiated throughout the colony (Hughes 1989), which would mean that the basal polyps invest more energy into creating colony structure than in reproduction. At present we do not have the data to verify these two hypotheses.

Gametogenesis

Studies on the duration and seasonality of gametogenesis in octocorals have been undertaken in several geographical areas. Different gametogenesis modes have been observed, related in some cases to biological processes. For example, Dahan & Benayahu (1997) suggested that the two annual relatively persistent phytoplankton blooms at Eilat (Red Sea) supply the metabolic demands for gametogenesis in the soft coral *Dendronephthya hemprichi*, allowing the year-round gamete release. In contrast most deep-sea anemones have a seasonal reproductive cycle (e.g. Van Praet 1990, Van Praet et al. 1990), although Rice et al. (1992) could find no evidence of seasonal reproduction in the pennatulacean *Kophobelemnon stelliferum* at 365 – 1600m depth in the Porcupine Seabight (365-1600 m depth). A reproductive cycle of more than one year has been observed in some octocoral species. This is the case in the tropical gorgonian *Plexaura A* (Brazeau & Lasker 1989), the alcyonaceans, *Lobophytum crassum* (Yamazo et al. 1981) and *Sarcophytum glaucum* (Benayahu & Loya 1986), and in the Mediterranean gorgonian *Corallium rubrum* (Vighi 1970). *A. antarcticum* shows two modes in the frequency distribution of the oocytes in summer, which might correspond to two generations of oocytes. This suggests that the reproductive cycle in this species may last at least 18 months and possibly as long as two years, as has been observed in several deep-sea anemones, alcyonaceans and gorgonians (e.g. Benayahu & Loya 1986, Van Praet 1990, Van Praet et al. 1990).

In contrast to the oocyes, the size frequency distributions of spermatic cysts in *A. antarcticum* did not show a clear division into two size classes. This could indicate a development cycle of less than one-year cycle of development, as has been demonstrated for some soft corals (see Benayahu et al. 1990, Dahan & Benayahu 1997), stony corals (see Harrison & Wallace 1990) and gorgonians, in which spermaries develop quickly to maturity within weeks prior to spawning (Brazeau & Lasker 1989, Coma et al. 1995a).

Similarities have been found in the gametogenesis features of *A. antarcticum* and the deep-sea anthozoan species (e.g. Riemann-Zürneck 1976 for the actiniarian *Actinostola spetsbergensis*). These similarities between Antarctic and deep-sea species have also been observed among other benthic invertebrates (Arntz et al. 1994). Brey et al. (1996) suggested that the reproductive strategies of species living on the Antarctic shelf could be similar to those species living in the deep sea because of the migration of continental shelf species into deeper water at times of maximal glacial extension.

Oocyte size as an indicator of reproductive mode

Number and size of oocytes are related to reproductive modes in octocorals (Coma et al. 1995a). Species with non-feeding, non-pelagic, lecithotrophic larvae, produce a few large eggs that are brooded until the larva is mature (Chia & Crawford 1973). In *A. antarcticum* the maximum oocyte size is 900 µm in diameter. This is unusually large, suggesting a brooding strategy (Chia & Crawford 1973). In general, large oocyte sizes (usually > 600 µm) are found in species with internal fertilisation and brooding incubation mode (e.g. *Muricea fruticosa* (Grigg 1977), *Anthelia* *glauca* (Benayahu & Schleyer 1998) and *Thouarella variabilis* (Brito et al. 1997)). However we did not find any direct evidence whether *A. antarcticum* is either a brooding or a broadcasting species.

The decrease in the frequency of large oocytes is clear between summer and autumn samples indicates that spawning of (presumably non-fertilized) oocytes occurs during late summer and autumn. This would be consistent with observations from other octocoral species at lower latitudes (Table 4); (e.g. Benayahu et al. 1989 for *Heteroxenia fuscescens* and Grigg 1977 *for Muricea californica*). However, differences among geographical regions could also be the result of differences in time invested in egg production as a consequence of local trophic constraints. This might be the case in polar regions, which are characterised by a markedly seasonal primary production. Looking at Fig. 7 it can be seen that in all investigated Antarctic and deep-sea species, the oocytes are big (> 600 µm), whereas in other regions the range is much wider. However, it is also important to take into account that the information about Antarctic and deep-sea species is still limited, and conclusions may change as more data become available.

Direct and larval development and their ecological implications

Observations of Antarctic octocorals and other invertebrate species during the EASIZ III cruise (autumn-early winter) showed an increased incidence of embryo or larval release, and of numbers of embryos and larvae ready to be released, compared to the summer. According to Starr et al. (1990), spawning in many marine invertebrates is coupled with phytoplankton blooms. This obviously makes sense in species with planktotrophic larvae, which have a seasonal occurrence in the plankton, such as the octocoral *Dendronephthya hemprichi* (Dahan & Benayahu 1997). The presence of planulae in the water column all year round has been recently demonstrated by Stanwell-Smith et al. (1999) at Signy Island, Antarctica. Planktonic embryos in autumn have also been observed in bivalves (see Bosch & Pearse 1998), as well as ripe gonads in echinoderms (Pearse & Giese 1966).

These observations strengthen the idea that many Antarctic invertebrates release lecithotrophic larval during autumn to have juveniles ready to settle during the best feeding (spring and summer) period.

Species with lecithotrophic larvae are less closely coupled to the seasonal phytoplankton bloom because they do not require an external source of nutrition during early development. Hartnoll (1975) observed such a case in the soft coral *Alcyonium digitatum*, which spawns in mid-winter. The planktonic non-feeding larvae of *A. digitatum* exhibit a long life span, and for this reason a high potential for dispersal before settling prior to the spring plankton bloom. When the bloom commences, larvae are able to take immediate advantage of the abundant food. Another example of long lived planulae has been observed by Shlesinger & Loya (1991) in the scleractinians *Favia favus* and *Platygyra lamellina*, which completely developed their primary polyp 20-24 days and 26-30 days after spawning, respectively. Wilson & Harrison (1998) provided the first data demonstrating that some species of broadcast-spawning reef corals produce larvae with considerable longevity and extended settlement-competition periods, with a maximum value of 78 days having been recorded for *Acanthastrea lordhowensis.* According to Brito et al. (1997) spawning of the Antarctic gorgonian *Thouarella variabilis* occurs presumably throughout the Antarctic summer and the swimming planulae settle soon after release. These results are in line with the evidence that the development of the first feeding polyp after larval settlement in gorgonians, and probably also in other sessile invertebrates such as the rhagon stage in sponges, takes longer than previously reported, especially in polar regions (e.g. Simpson 1984). Thus, only the functional polyp will profit from the plankton blooms during the favourable season, together with the planktotrophic larvae produced by other benthic organisms. An extended period of polyp development could be a life cycle strategy to avoid the unfavourable trophic season in polar regions.

In conclusion, *A. antarcticum* is characterized by an extended oogenesis period (more than one year), which agrees with the reduction in development rates with decreasing temperature as has been demonstrated for a wide range of invertebrate species (reviewed in Pechenik 1987). In *A. antarcticum* spawning seems to be delayed until the autumn-winter season, as we also observed in some *Thoaurella* spp. during the EASIZ III cruise (pers. obs.). The decrease in the relative frequency of large oocytes in autumn has been used as an indicator of the spawning season (following Brondson 1993, Van Praet 1990). The absence of larval stages of *A. antarcticum* during the EASIZ III cruise was surprising, considering that many octocoral species had larvae ready to be released, leaving the reproduction of *A. antarcticum* still as a mystery. The type of fertilization (externally or internally) could not be determined. However, the absence of embryonic or larval stages in the polyp channels and the decrease of large oocyte frequency suggest that the process of fertilisation probably occurs in the water layers close to the sea floor during autumn or winter.

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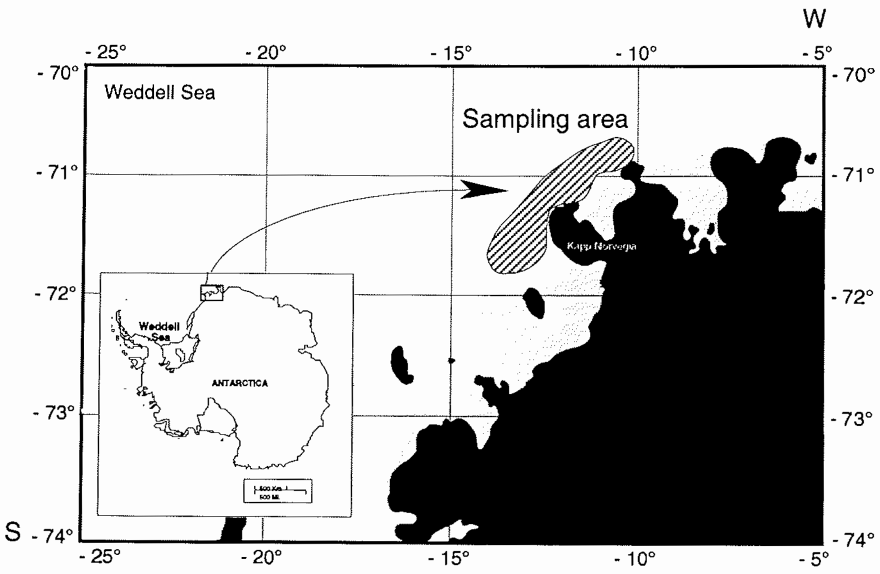

Fig. 1 Map of the sampling area, in the eastern Weddell Sea (Antarctica).

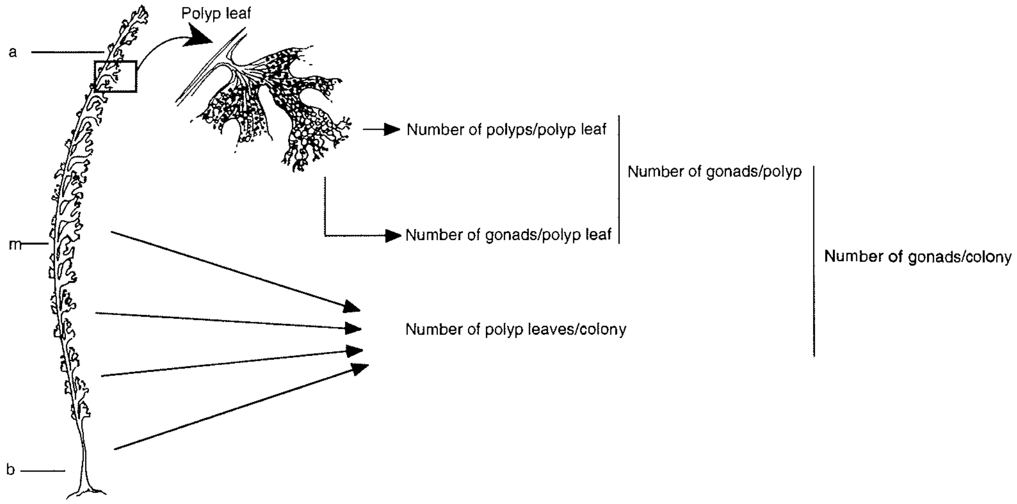

Fig. 2 Morphology of a colony of *Ainigmaptilon antarcticum*. Apical (a), medial (m), and basal (b) zones are indicated, as well as the methodology employed to calculate the fecundity of a colony.

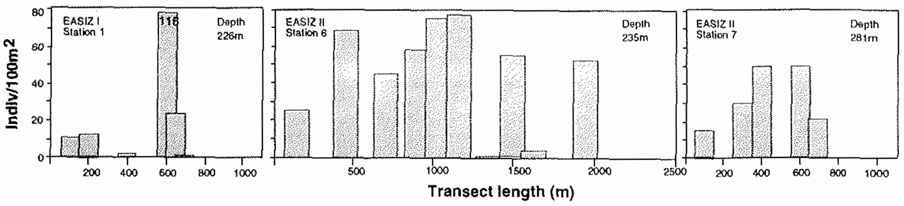

Fig. 3 Density of *Ainigmaptilon antarcticum* in three different transects in the area of Kapp Norvegia (Weddell Sea).

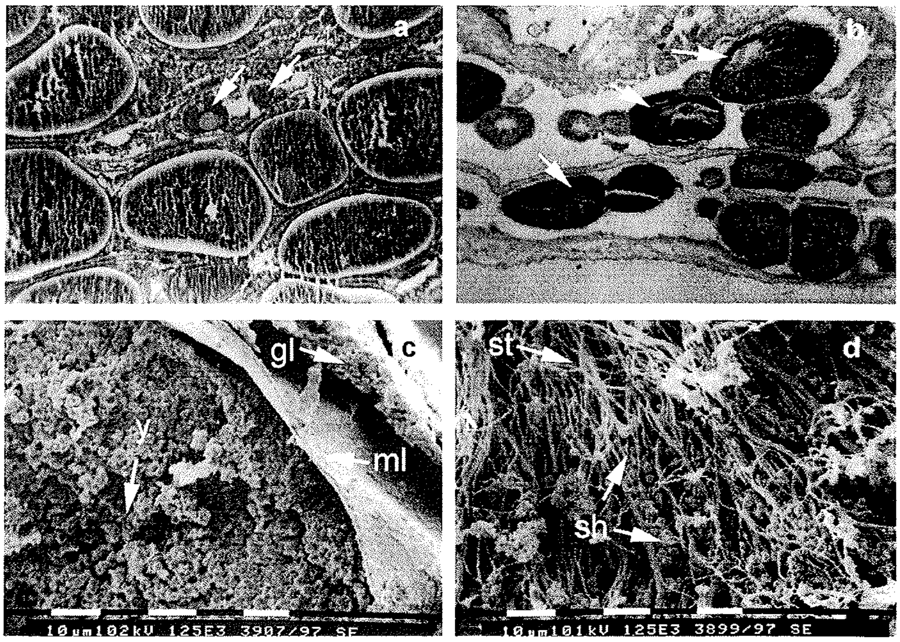

Fig. 4 Gonadal histology and anatomy of *Ainigmaptilon antarcticum*. a) Female colony showing the two different generation of oocytes. b) Male colony showing the spermatic cysts. c) SEM image of an oocyte section. d) SEM image of a spermatic cyst section.

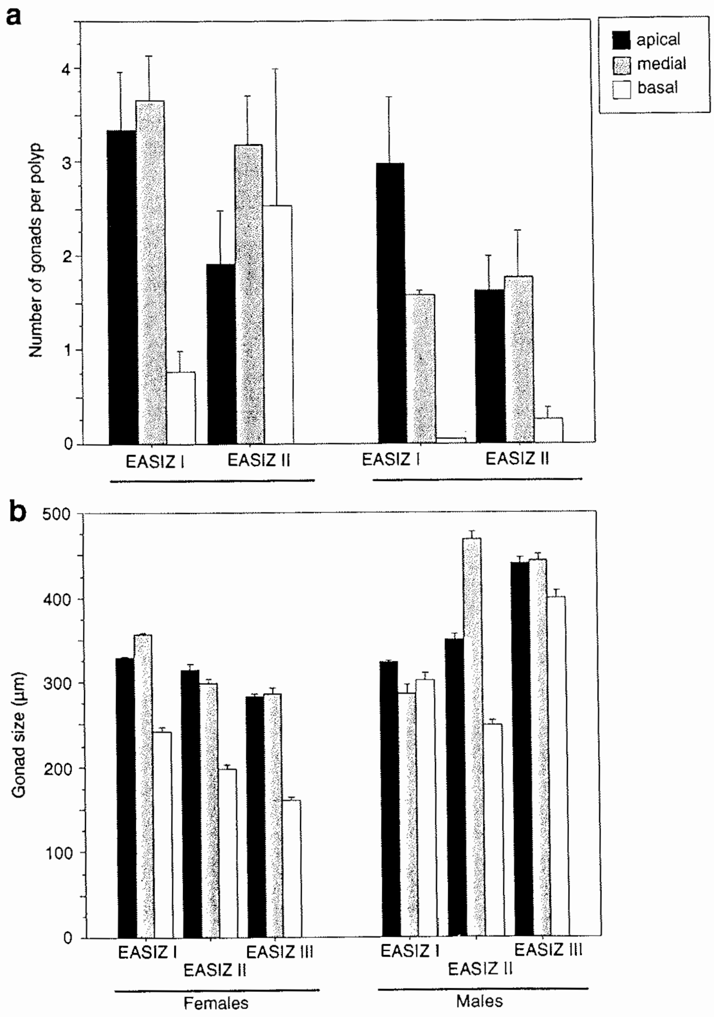

Fig. 5 a) Mean number of gonads along the colony (apical, medial and basal zones) per polyp in both sexes, for the EASIZ I and EASIZ II cruises. b) Mean size of the gonads along the colony (apical, medial and basal zones) per polyp in both sexes, for the EASIZ I, EASIZ II and EASIZ II cruises.

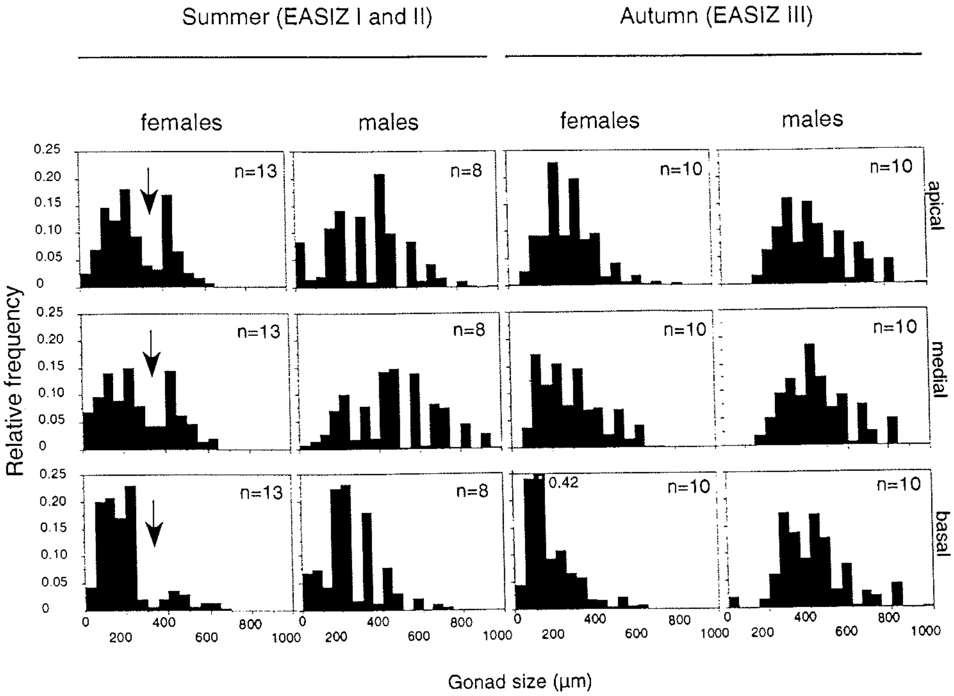

Fig. 6 Size frequency distribution of oocyte and spermatic cysts along the three zones of the colony (apical, medial, basal) in summer and autumn.

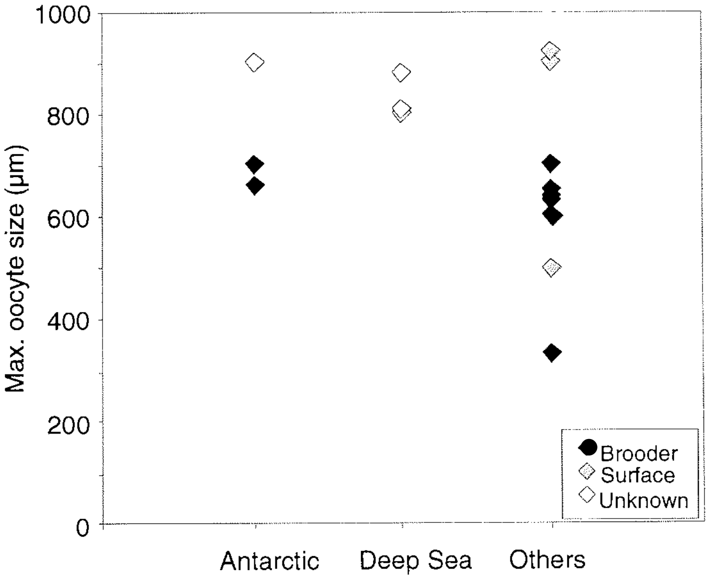

Fig. 7 Maximum oocyte size by mode of incubation in different latitudes (Sources: references Table 4).

Table 1. Density values of *A. antarcticum* in the Weddell Sea with values of $S^2/\bar{x}$ and Morisita's Index (I_d). SW/KN: Southwest of Kapp Norvegia; NW/KN: North west of Kapp Norvegia; W/KN: West of Kapp Norvegia; NE/KN: Northeast of Kapp Norvegia; N/KN: North of Kapp Norvegia; KN: Kapp Norvegia; AB: Atka Bay. An asterisk indicates a significant deviation from random for both $S^2/\bar{x}$ and I_d at the 5% level (χ^2-test). (Data for $\bar{x}$ and SD are based on 4 random $100m^2$ blocks within each transect).

Cruise	Area	Transect	Position		Depth	Total area sampled (m^2)	$\bar{x}$ + SD	$S^2/\bar{x}$	I_d
			Lat (S)	Long (W)	(m)		ind./100 m^2		
EASIZ I	SW/KN	1	71° 40.54'	12° 44.48'	226	705	37 ± 55	79.77*	2.60*
EASIZ I	NW/KN	2	71° 18.13'	12° 15.99'	175	1203	2 ± 2	3.78	2.67*
EASIZ I	W/KN	3	71° 33.09'	12° 20.58'	363	654	4 ± 2	1.62	1.14
EASIZ I	NE/KN	4	71° 07.33'	11° 26.79'	142	1341	0	-	-
EASIZ I	NW/KN	5	71° 20.50'	12° 23.90'	198	1115	0	-	-
EASIZ II	N/KN	1	70° 52.04'	10° 32.40'	229	503	3 ± 5	6.85	2.46*
EASIZ II	N/KN	2	70° 53.82'	10° 33.85'	244	378	1 ± 1	2.00.	2.00
EASIZ II	N/KN	3	70° 52.15'	10° 29.34'	233	1325	1 + 1	0.67	0.00
EASIZ II	N/KN	4	70° 53.28'	10° 27.80'	242	495	0	-	-
EASIZ II	N/KN	5	70° 51.93'	10° 32.32'	231	774	1 ± 2	1.80	1.60
EASIZ II	N/KN	6	70° 50.77'	10° 30.50'	235	567	1 ± 2	3.00	4.00*
EASIZ II	N/KN	7	70° 49.32'	10° 28.92'	281	1696	33 ± 25	18.61*	1.41*
EASIZ II	KN	8	71° 13.56'	12° 25.48'	253	841	19 ± 23	27.13*	2.03*
EASIZ II	KN	9	70° 50.56'	10° 34.97'	261	590	55 ± 41	30.48*	1.40*
EASIZ II	AB	10	70° 47.37'	10° 24.83'	297	568	37 ± 30	24.78*	1.48*
EASIZ II	AB	11	70° 51.71'	10° 45.24'	312	652	2 ± 1	1.10	1.07
EASIZ II	KN	12	71° 13.79'	12° 14.93'	275	517	5 ± 6	7.79	2.02*

Table 2. Three-way ANOVA comparing numbers of gonads of *A. antarcticum* (BoxCox transformed) between a) cruises, b) colony zone, and c) sexes.

	df	SS	MS	F	P
Cruise	1	3.541	3.541	9.512	0.0034*
Colony zone	2	17.919	8.960	24.068	<0.0001**
Sex	1	12.564	12.564	33.749	<0.0001**
Cruise x Colony zone	2	12.389	6.195	16.640	<0.0001**
Cruise x Sex	1	0.076	0.076	0.203	0.6544
Colony zone x Sex	2	11.683	5.842	15.692	<0.0001**
Cruise x Colony zone x Sex	2	0.174	0.087	0.234	0.7924

Bonferroni/Dunn post-hoc test

	Sex		Cruise		Colony zone		
	Female	Male	EASIZ I	EASIZ II	Apical	Medial	Basal
a) **Cruise**							
EASIZ I-EASIZ II	ns	ns					
b) **Colony zone**							
Apical-Medial	ns	ns	ns	ns			
Medial-Basal	ns	**	**	*			
Apical-Basal	ns	**	**	ns			
c) **Sex**							
Female-Male			ns	*	ns	ns	*

df: degrees of freedom; SS: sums of squares; MS: mean square; F: F-ratio; P: probability.
ns = not significant
* = $p<0.05$
** = $p<0.0001$

Table 3. Three-way ANOVA comparing gonad size (µm) of *A. antarcticum* (BoxCox transformed between a) cruises, b) colony zone, and c) sexes.

	df	SS	MS	F	P
Cruise	2	21.386	10.693	36.359	<0.0001**
Colony zone	2	361.206	180.603	614.086	<0.0001**
Sex	1	364.260	364.260	1.238.555	<0.0001**
Cruise x Colony zone	4	30.392	7.598	25.835	<0.0001**
Cruise x Sex	2	246.983	123.492	419.896	<0.0001**
Colony zone x Sex	2	51.089	25.544	86.856	<0.0001**
Cruise x Colony zone x Sex	4	87.437	21.859	74.326	<0.0001**

Bonferroni/Dunn post-hoc test

	Sex		Cruise			Colony zone		
	Female	Male	EASIZ I	EASIZ II	EASIZ III	Apical	Medial	Basal
a) **Cruise**								
EASIZ I-EASIZ II	**	**						
EASIZ II- EASIZ III	**	**						
EASIZ I-EASIZ III	**	**						
b) **Colony zone**								
Apical-Medial	*	**	*	*	ns			
Medial-Basal	**	**	**	**	**			
Apical-Basal	**	**	**	**	**			
c) **Sex**								
Female-Male			*	**	**	**	**	**

df: degrees of freedom; SS: sums of squares; MS: mean square; F: F ratio; P: probability.
ns = not significant
• = p<0.05
** = p<0.0001

Table 4. Maximum oocyte size, fertilization type and incubation mode, and geographic area for different gorgonian species (data are arranged by oocyte sizes).

Species	Max oocyte size (µm)	Fertilization	Incubation mode	Geographic area	Reference
Corallium rubrum	330	internal	brooder	Mediterranean	Vighi 1970
Paramuricea clavata	500	-	surface	Mediterranean	Coma et al. 1995
Muricea fructicosa	600	internal	brooder	NE Pacific	Grigg 1977
Ptilosarcus guerney	600	external	-	NE Pacific	Chia & Crawford 1973
Plexaura A	600	external	-	E Pacific	Brazeau & Lasker 1989
Anthelia glauca	633	internal	brooder	SW Indic	Benayahu & Schleyer 1988
Plexaura homomalla	640	external	-	Caribbean	Martin 1982
Sarcophytum glaucum	650	external	-	Red Sea	Benayahu & Loya 1986
Thouarella variabilis	660	internal	brooder	Antarctic Peninsula	Brito et al. 1997
Muricea californica	700	internal	brooder	NE Pacific	Grigg 1977
Fannyella rossii	700	internal	brooder	E Weddell Sea	(in preparation Orejas et al.)
Pennatula aculeata	880	external	-	NW Atlanctic	Eckelbarger et al. 1998
Ainigmaptilon antarcticum	900	internal	-	E Weddell Sea	This study
Heteroxenia fuscescens	900	internal/external	brooder	Red Sea	Benayahu et al. 1989
Briaremum asbestinum	900	internal	surface	Caribbean	Brazeau & Lasker 1989
Heliophora coerulea	920	internal	surface	SW Pacific	Babcock 1990
Eunicella singularis	-	internal	brooder	Mediterranean	Weinberg & Weinberg 1979

Publication IV

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Reproductive patterns of four Antarctic octocorals in the Weddell Sea: comparisons across different species, morphologies and latitudes

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Abstract

The reproductive patterns of four Antarctic gorgonian species have been investigated. Two of them, *Dasystenella acanthina* and *Thouarella* sp. present bottle-brush shapes; the other two, *Fannyella rossii* and *Fannyella spinosa* are fan-shaped. Two different reproductive patterns have been observed in these species: *D. acanthina* and *Thouarella* sp. present two modes in the frequency distribution of oocytes and spermatic cyst size classes, *F. rossi* and *F. spinosa* show only one size class. The presence of larvae in the gastrovascular cavities of both Fannyella species is a clear sign of larvae release during the austral summer.

The observed patterns, as well as the oocyte and spermatic cyst sizes, are comparable to reproductive trends and features of gorgonians from other latitudes. These coincident strategies seem to be related with morphological similarities and food limitation rather than with latitude or water temperature.

The results of this study indicate that octocoral morphology together with trophic constraints may play a crucial role in determining their reproductive output.

Introduction

Over the past three decades, there has been a substantial increase in research into Antarctic benthic marine communities, mostly on the continental shelf. Although aspects of reproduction have been studied in a variety of taxa, a significant fraction of this work has focused almost entirely on solitary (non-colonial) animals (see Pearse et al. 1991, Barnes & Clarke 1998). Information on reproductive patterns and trends for benthic organisms in Antarctic waters comprises decapods (e.g. Arntz et al. 1992, Gorny et al. 1992), amphipods (e.g. Klages 1993), molluscs (e.g. Hain & Arnaud 1992, gastropods: e.g. Stanwell-Smith & Clarke 1998, bivalves: e.g. Berkman et al. 1991), brachiopods (e.g. Peck & Robinson 1994), holothurians (e.g. Gutt 1991, Gutt et al. 1992), sponges (e.g. Barthel & Gutt 1992), polychaetes (e.g. Stiller 1996) and echinoderms (e.g. Poulin & Féral 1996, McClintock & Baker 1997, Stanwell-Smith & Peck 1998). A few papers focused on modular organisms (e.g. Barnes 1996, Barnes & Clarke 1998), but to our knowledge only four have dealt with soft octocorals (Bayer 1996, Brito et al. 1997, Slattery & McClintock 1997, Orejas et al. submitted). The high abundance of suspension feeders, including octocorals, in Antarctic waters (e.g. White 1984, Mühlenhardt-Siegel 1988, Starmans et al. 1999) calls for the study of the biology and ecology of these organisms, in order to determine their role in the Antarctic ecosystem.

According to Clarke (1987), reproduction and growth should be more efficient in polar waters than at lower latitudes, because the lower basal metabolism of the Antarctic species should allow them to invest more energy in these processes. However, reproductive patterns in the Antarctic are mostly defined by such characteristics as prolonged gametogenesis, delayed maturation, seasonal reproduction, low fecundity, large yolky eggs, predominance of non-pelagic or at least lecitotrophic development, brooding, brood protection, viviparity, slow embryonic development, advanced newly-hatched juvenile stages and slow growth (Thorson 1950, Arnaud 1974, White 1977, reviewed in Pearse et al. 1991). The long developmental times observed in Antarctic organisms (e.g. Hain & Arnaud 1992, Gorny et al. 1992, Gorny et al. 1993, Klages 1993, Gorny & George 1997) seem to be connected with large oocyte sizes and, consequently, with low fecundity (see Arntz et al. 1994). However, the degree of retardation of embryonic development and maturation varies largely among groups and species in the Antarctic (Pearse et al. 1991, Arntz et al. 1994).

Octocoral reproduction has been studied quantitatively in temperate and tropical latitudes (mostly in terms of oocyte number and size), and their reproductive biology is now fairly well known (for a review see Coma et al. 1995a), as are the environmental and biological factors which control the reproductive processes.

This study focused on the quantification of the reproductive patterns of four high Antarctic octocoral species of different colony morphology, comparing these patterns with those of other Antarctic invertebrates. The second objective was a comparison of the reproductive strategies of these polar species and the strategies of octocorals from other latitudes, in order to identify the controlling environmental (e.g. temperature) and biological (e.g. food availability) factors.

Material and methods

Study area

Sampling was carried out in the eastern Weddell Sea (Antarctica) (Fig. 1) from the German RV "Polarstern" (for details on the expeditions see Arntz & Gutt 1997, 1999), during the EASIZ (Ecology of the Antarctic Sea Ice Zone) cruises I (ANT XIII/3, January-March 1996) and II (ANT XV/3, January-March 1998). The eastern Weddell Sea differs from many other Antarctic areas in that it has no shallow areas. The ice edge usually prevents work in areas shallower than 200m, and even in the inlets the seafloor is several hundred metres deep (Arntz et al. 1992). The area was characterised by Voß (1988) who noted the presence of sandy bottoms but also sponge spicules, bryozoan debris and a few stones and described for the first time the benthic assemblages. The communities of Kapp Norvegia, where our studies were carried out, are characterised by high species richness, diversity and evenness (Galéron et al. 1992).

Studied species

The four gorgonian species investigated belong to the Primnoidae, the most important family, in number of species, of gorgonian octocorals in Antarctic communities. *Dasystenella acanthina* (Wright & Studer 1889) and *Thouarella* sp. presented a branched shape with bottle-brush form (Fig 2A). *Fannyella rossii* (Gray 1873) and *Fannyella spinosa* (Thomson & Bennet 1931) showed a dichotomous branched pattern (Fig 2B). All the colonies studied were collected living on soft substratum, attached to stones, in a depth range between 200 and 500 m approximately.

Reproduction study

Sampling was performed with Agassiz, bottom and bentho-pelagic trawls and with a small dredge at depths between 250 and 600 m. All specimens were preserved in 4% formalin prior to further work in the laboratory.

Twenty colonies (10 females and 10 males) for *Dasystenella acanthina, Thouarella* sp. *and Fannyella spinosa*, and 17 (10 females and 7 males) for *Fannyella rossii* were examined. The developmental stage, and the number and size of the gonads were studied in each colony at apical, medial and basal colony zones (Fig. 2A,B), following the methodology described by Brazeau & Lasker (1990), Coma et al. (1995b), and Brito et al. (1997). Additionally, the maturity stage and number of gonads in the proximal, central and distal portion with respect to the axis (Fig. 2A) were also investigated for those species having a principal axis, i.e., *D. acanthina* and *Thouarella* sp.

In the colonies of *D. acanthina* and *Thouarella* sp., 15 polyps from each described colony zone (5 from each portion respect to the axis: proximal, central, distal) were dissected, and for *F.rossii* and *F. spinosa* 10 polyps of each colony zone (apical, medial and basal). In all cases, the polyps were selected randomly and the total of gonads in each polyp gastrovascular cavity were counted and measured.

The dissection of specimens was done under a binocular; gonads were measured with a light microscope using an eyepiece calibrated against a stage micrometer.

Our data set for number and size of gonads was not distributed normally, despite different transformations (data were subjected to a square root transformation (number of gonads) and a logarithmic transformation (size of gonads) (Sokal & Rohlf 1995)). However, in order to evaluate individual effects and interactions of the factors sex, colony zone and position with respect to the axis, and the influence of them on the variability of number and size of gonads, we applied a 3-way ANOVA instead of a non-parametric test for *D. acanthina* and *Thouarella* sp. To evaluate the effects and interactions of the factors sex and colony zone, a 2-way ANOVA test for *F. rossii* and *F. spinosa* was applied. In case of significant differences, a Bonferroni/Dunn post-hoc analysis of means was performed. For data transformation and further statistical analyses the statistical package Statview (SAS Institute 1998) was used.

Results

According to the classification system for the sexual modes of modular organisms of Wasson & Newberry (1997), the four species are gonochoric at module, genet and colony level.

The 3-way ANOVA analyses for *D. acanthina* and *Thouarella* sp. lead to the following results:

Number of gonads

The average (±SD) number of oocytes was 1.1±1.1 and 1.3±0.9 for *D. acanthina* and *Thouarella* sp., and that of spermatic cysts was 2.8±1.2 and 3.2±2.4, respectively (Fig. 3a). Statistically significant differences between females and males in both species were observed (Table 1A, 2A). Significant differences in the number of gonads between different colony zones and positions with respect to the axis (Table 1A, 2A, Figs. 3a, 4a, 5a) were also observed. The highest number of oocytes and spermatic cysts was found in the medial and basal zones in both species (Fig. 3a). In females and males of *D. acanthina,* gonads were more abundant in the proximal and central positions (Fig. 4a), whereas in *Thouarella* sp. this was the case in the central and distal ones (Fig. 5a).

Gonad size

The mean (±SD) size of oocytes was 373.7±259.4 µm and 270.7±134.5 µm, and of spermatic cysts 304.8±172.3µm and 252.1±106.4 µm, respectively for *D. acanthina* and *Thouarella* sp. (Fig. 3b). Statistically significant differences between females and males were found (Table 1B, 2B) in all colony zones for *D. acanthina*, while in *Thouarella* sp. only in the apical zone. Significant differences in the gonad size between different colony zones and positions with respect to the axis were also detected for both species (Table 1B, 2A, Figs. 3b, 4b, 5b). The largest gonads were in the apical and medial zones in the females and in the medial and basal in the males of *D. acanthina.* The oocytes from the proximal and central position and the spermatic cysts from the central and distal were the largest (Fig. 4b). *Thouarella* sp. had the largest oocytes in the basal zone and in the central and distal position with respect to the axis. The basal zone and the central and distal parts presented the largest spermatic cysts (Fig. 5b).

The results of the 2-way ANOVA analysis for *Fannyella rossii* and *Fanyella spinosa* can be summarised as follows:

Gonad number

The average number of oocytes per polyp (±SD) was 1.6±0.6 and 1.5±0.7, and of spermatic cysts 5.2±3.0 and 3.1±1.5 for *F. rossii* and *F. spinosa*, respectively (Fig. 3a). Statistically significant differences between females and males (Table 3A, 4A) were found. No statistically significant differences in the number of oocytes between different colony zones in *F. rossii* (Table 3A, Fig. 3a) were observed, but in the number of spermatic cysts (Table 3A, Fig 3a). For *F. spinosa* the number of oocytes and spermatic cysts were significantly different for the different colony zones (Table 4A, Fig. 3a). In both species, the medial zone had the highest number of gonads, except in the case of *F. rossii*, having the highest number of spermatic cysts in the basal one.

Gonad size

The average size of the oocytes was 239.8±129.4 µm and 182.0±95.5 and of the spermatic cysts 113.7±62.7 µm and 161.4±83.8 µm for *F. rossii* and *F. spinosa*, respectively (Fig. 3b). Statistically significant differences between females and males in all colony zones were found for *F. rossii* (Table 3B) and in the apical and medial zones for *F. spinosa* (Table 4B).

Gonad size frequency distribution:

Dasystenella acanthina and *Thouarella* sp

The frequency distribution of gonad size in these species showed, in both females and males, two modes which probably correspond to two oocyte and spermatic cyst generations (Fig. 6a,b, 7a,b). In *D. acanthina* there seems to be a third size class although it is not clear if this corresponds to a third mode or if it is just a remnant from the last spawn event. The two modes of *Thouarella* sp. (Fig. 7a,b) are not as well defined as in *D. acanthina* because they were not distinguishable in all the colony zones. There were no significant differences in the frequency distribution of gonad size in *D. acanthina* between the different colony zones, but there was in the positions with respect to the axis. The largest oocytes were located in the central and distal part (Fig. 6a). The colony zones of the males were very similar, in contrast to the position respect to the axis, with the largest spermatic cysts in the central and distal positions (Fig. 6b). In *Thouarella* sp. there were neither significant differences in the frequency distribution of gonad size in the females between different colony zones nor in the position with respect to the axis. However, the largest ooycte classes were located in the apical and basal zones, and in the proximal and central part with respect to the axis (Fig. 7a). The colony zones were significantly different in the males. The largest spermatic cyst class was present in the central and basal zone. No statistically significant differences were detected with respect to the axis position.

Fannyella rossii and *Fannyella spinosa*

There were no significant differences in the frequency distribution of oocyte sizes between the different colony zones. The largest oocytes for *F. rossii* were located in the medial and basal zones while in the apical and medial zones for *F. spinosa.* Although both species presented one mode, the rest of a larger oocyte size class was also detected. This rest should be a signal of release of sexual products (Fig. 8a, 9a). In the males, there were significant differences in the size frequency distribution between all colony zones in *F. rossii,* and between the apical and basal zones in *F. spinosa.* In *F. rossii* the largest spermatic cysts appeared in the medial zone, following in importance the apical and basal ones (Fig. 8b), whereas in *F. spinosa* they were mainly in the basal and apical zone (Fig. 9b).

No larvae were present in the studied colonies of *D. acanthina*, in contrast with *Thouarella* sp., which had larvae in two of the studied colonies. One of these colonies had three in the basal zone, the other had one in the apical zone. In *F. rossii* two colonies had three and two larvae, respectively, in the medial zone, and a third one had one in the basal zone. In one of the studied colonies of *F. spinosa* there were two larvae in the apical zone.

Discussion

General patterns in octocoral reproduction

Reproductive features of Antarctic invertebrates have been studied by many authors (e.g., Arntz et al. 1992, Barthel & Gutt 1992, Poulin & Féral

1996, Brito et al. 1997, Barnes & Clarke 1998). Despite the efforts to identify a general polar trend in reproduction (e.g. Thorson 1950, for a review see Pearse et al. 1991) up to now only a variety of strategies, ranging from production of planktotrophic larvae to brooding, and from seasonal to continuous reproduction, has been described.

To our knowledge, the only data on the reproductive biology of Antarctic octocorals available are on *Thouarella variabilis* (Brito et al. 1997) and *Ainigmaptilon antarcticum* (Orejas et al. submitted), and on the stoloniferan *Clavularia* cf *frankliniana* (Slattery & Mc Clintock 1997), although descriptive information on reproductive modes of some Antarctic octocorals was obtained a long time ago (in Brito et al. 1997: e.g. Wright & Studer 1889, Versluys 1906). These studies showed gonochorism and brooding to be common features of Antarctic and deep-sea octocorals.

The species studied in this publication fit with the pattern related to gonochorism, and at least three of them (*Thouarella* sp., *Fannyella rossii* and *Fannyella spinosa)* are clearly brooders, as shown by the presence of larvae in their gastrovascular cavities. In the case of *Dasystenella acanthina* the lack of larvae in the studied polyps and colonies prevents any clear definition of the incubation mode of the species.

Many authors have attempted to identify the factors that determine patterns of reproduction in reef anthozoans. Colony morphology and polyp size (Fadlallah & Pearse 1982a,b, Fadlallah 1983), patterns of gamete development (Rinkevich & Loya 1979), habitat (Stimson 1978), and levels of disturbance (Szmant 1986) have all been proposed as important correlates of reproductive strategies. However, these models have not adequately explained the diversity of reproductive patterns observed (Brazeau & Lasker 1990). There are three modes of sexual reproduction in reef soft corals: broadcasting of gametes, external surface brooding, and internal brooding of planulae (for a review see Benayahu et al. 1990). Most of the species studied to date are gonochoric, whereas hermaphrodites are rare (Dahan & Benayahu 1997).

It is surprising that so many traits are shared by species despite the differences in geographical location and colony morphology (Brazeau & Lasker 1990). Since the patterns of reproduction of anthozoans are well studied in temperate and tropical regions (e.g. Weinberg & Weinberg 1979, Hughes & Jackson 1980, Martin 1982, Brazeau & Lasker 1990, Coma et al. 1995a), gonochorism and a sex ratio of 1:1 have been considered as the general patterns for this group in the Caribbean Sea (Kinzie 1970, 1974, Goldberg & Hamilton 1974, Behety-González & Guardiola 1979, Martin 1982), the Pacific Ocean (Grigg 1977) and the Mediterranean Sea (Coma et al. 1995a).

Oocyte number and size as indicators of gamete development duration and incubation mode: a latitudinal comparison

Oocyte production ranges from 1.1 polyp^{-1} for *Dasystenella acanthina* to 1.6 polyp^{-1} for *Fannyella rossii*. Among gorgonians from other latitudes, it ranges from 1.6 polyp^{-1} for *Muricea californica* (Grigg 1977) to 13 oocytes per mature polyp for *Paramuricea clavata* (Coma et al. 1995b), with the majority of species producing 2 to 7 oocytes per polyp. The Antarctic octocorals *Ainigmaptilon antarcticum* and *Primnoella* sp., both with a flagelliform shape, have an average of 3 oocytes polyp^{-1} (Orejas et al. submitted) and 9 oocytes polyp^{-1} (own unpublished data), respectively. This means that the oocyte number of the Antarctic species does not differ from the pattern observed in other latitudes.

The size of the oocytes might define the duration of the maturation period: large oocytes may indicate a long period of development (Harrison & Wallace 1990) and the presence of lecitotrophic larvae. However, this is a controversial subject and some authors do not consider the oocyte size to be an indicator of the incubation mode in octocoral species (e.g. Rinkevich & Loya 1979, Fadlallah 1983, Kruger et al. 1998).

The oocyte size between the four studied gorgonians ranged from 40 to approximately 900 µm, in agreement with the values found in other octocoral species (see Coma et al. 1995a). The suggestion of Harrison & Wallace (1990) that large oocytes are often associated with longer oogenic development, does not fit with the large oocytes (450-750 µm) commonly found in soft corals (Benayahu & Loya 1986), irrespective of the duration of oogenesis (Benayahu & Loya 1983, 1984, 1986) and regardless of their mode of reproduction (Rinkevich & Loya 1979, Fadlallah 1983). Benayahu &

Loya (1986) suggested that large oocyte size is not the consequence of a prolonged oocyte development, but that prolonged gametogenesis is found in species with high fecundity, synchronised maturation and brief spawning periods. Furthermore, Levitan (1993, 1996a,b) has argued that large oocytes are a larger target for sperm and thus increase the probability of fertilization. There are hard corals with extended oogenic cycles that only produce small oocytes, as the case of *Paracyanthus stearnsii* (Fadlallah & Pearse 1982b). The hypothesis of Rinkevich & Loya (1979) that broadcast-spawning hard corals produce large oocytes while brooders produce small oocytes is clearly not applicable to soft corals (Benayahu & Loya 1986) and the species studied here corroborate that. In agreement with previous studies on brooders: Benayahu & Loya (1983, 1984), Benayahu (1989), Benayahu et al. (1989), and broadcasters: Benayahu & Loya (1986), Aliño & Coll (1989) our results indicate that both produce large oocytes, ranging between 400 and 900 µm, as has also been shown by Kruger et al. (1998).

Duration of gametogenesis

The differences in number and size of gonads found in the different parts of the colony of *D. acanthina* (Fig. 4a,b) might indicate a lack of synchronisation of reproduction within a colony. Nevertheless, synchronisation could exist as in *Xenia macrospiculata*. This gorgonian is markedly synchronised within the same colony, but because of the prolonged period of gonadal initiation, the population contains colonies of various sexual stages, and a wide range of sizes in oocytes and sperm sacs is evident almost year-round (Benayahu & Loya 1984). The presence of two-three oocyte and spermatic cyst size classes in *D. acanthina* points to a reproduction cycle of 2-3 years with long maturation periods, and probably non-seasonal spawning events. The low mean number of oocytes per polyp (1.1) is due to the large size of them (up to 900 µm approximately). This pattern fits also with the - probably delayed - maturation (Harrison & Wallace 1990) and spawning period. *D. acanthina*, with its two-three oocyte size classes, presents a similar pattern as the Caribbean gorgonian *Plexaura* A (Brazeau & Lasker 1989). Additionally the pattern of oocyte development in *Plexaura* A seems to be quite similar to the pattern expected for *D. acanthina* as the oocytes are present in *Plexaura A* colonies throughout the year. This is the only such case known for a coral and the trend suggests that more than a single season of oocyte maturation time is required (Brazeau & Lasker 1989), as probably occurs with *D. acanthina*. This may represent a mechanism through which mature oocyte production can be adjusted later in the developmental season rather than at the time of primary oocyte appearance (Brazeau & Lasker 1989). In *Thouarella* sp (Fig. 7a,b), there is a significantly higher frequency of immature oocytes than of mature and spermatic cysts. This situation, together with the remainder of a larger oocyte size class and the larvae observed in the polyps is a sign of recent larval release.

Thouarella sp. shows reproduction patterns similar to other octocoral species with a two year maturation time: the alcyonaceans *Lobophytum crassum* (Yamazo et al. 1981) and *Sarcophytum glaucum* (Benayahu & Loya 1986), and the gorgonian *Corallium rubrum* (Vighi 1972, in Yamazo et al. 1981). In the polyps of these species, as in *Thouarella* sp. (Fig. 7a,b), two discrete size classes of oocytes can be identified. In *Sarcophyton glaucum*, where oogenesis occurs every year, the oocyte maturation requires 22-23 months, resulting in the presence of two cohorts of oocytes in each female. Two size classes are also present in the polyps of *Heteroxenia coheni* with primordial oocytes developing between the large oocytes and three spermatogenic stages usually found in a single polyp (Benayahu et al. 1990).

Other polar organisms also require two successive summer periods to complete the gametogenesis, due to the shortage of food available for gonad synthesis during the intervening winter, e.g. the isopod *Serolis polita* (Luxmoore 1982) and some caridean decapods (Gorny et al. 1993).

F. rossii and *F. spinosa* present a pattern quite different to the above described for *D. acanthina* and *Thouarella* sp. In both cases it is possible to distinguish a unique oocyte class and the remainder of a larger class, which was probably released during the period of sampling. In the case of the coral *Parerythropodium fulvum fulvum*, the annual development of female and male gonads exhibited the same pattern, which was markedly synchronized within the population. This species shows only one gonad generation (Benayahu & Loya 1983) as seems to occur in *F. rossii* and *F. spinosa*.

Among other cnidarians, the shallow water sea pen *Ptilosarcus gurney* reproduces annually (Chia & Crawford 1973), whereas the upper bathyal species *Kophobolemnon stelliferum* shows no signs of seasonal reproduction (Rice et al. 1992).

The size of the oocytes is smaller in *F. rossii* and *F. spinosa* than in *D. acanthina* and *Thouarella* sp. This is likely a consequence of the different gametogenesis cycle duration since *F. rossii* and *F. spinosa*, due to their annual cycle, probably have a shorter maturation period.

Role of the shape in the reproductive features

Although the fecundity of clonal organisms is size dependent (see reviews by Harper 1977, Hughes 1989, Harrison & Wallace 1990), colony size does not always have an effect on oocyte or spermatic cyst number per polyp (Hall & Hughes 1996). The number of gravid modules in a colony varies greatly between species, caused in part by differences in module size and spacing, and partly by colony morphology. The branch type and growth form of the corals influence the reproductive patterns and provide further evidence that the reproductive output of colonies is not a simple multiple of polyp fecundity (Hall & Hughes 1996). Hughes & Jackson (1980) argued that sterile areas in corals may also act as buffer zones against partial mortality, and that reproductively valuable tissue is located in "safer", central regions of the colony (e.g. away from peripheral encounters with competitors and predators). Similarly, Grosberg (1988) argued for a colonial ascidian, that the periphery of a colony or clone may be structurally specialised for defence against predation or agressive encounters with competitors. In *D. acanthina*, one of the bottle-brush morphotypes studied (Fig 2A), a higher number of gonads was observed in the proximal and central part of the branches relative to the axis (Fig. 4a) and in the medial and basal part of the colonies (Fig. 3a). This pattern agrees with that detected for the same morphotype at other latitudes: Kojis & Quinn (1982) and Szmant-Froehlich (1985) reported that among large colonies of bottle-brush octocorals, the modules at the periphery of the colony are often non - reproductive (Kapela & Lasker 1999). Peripheral modules in octocoral species are typically younger, faster growing, and non-reproductive. For example, in the soft coral *Sarcophyton glaucum*, young and sexually immature polyps are located along the margins of the colony (Benayahu & Loya 1986). The specimens of *Thouarella* sp. studied here did not show this tendency very clearly. The colony zone pattern is the same as for *D. acanthina* (Fig. 3), but in contrast, the central and distal zone had a higher number of gonads per polyp (Fig 5a). However Brito et al. (1997) reported that another species of the genus Thouarella (*T. variabilis*) seems to have the same pattern as *D. acanthina*. These different reproductive stages in a colony have been hypothesised by Brito et al. (1997) as differential polyp functionality: the reproductive polyps, near to the axis, enter in a quiescent stage receiving the food through the solenia from the most distal non-reproductive polyps in the secondary branches. The reduced reproductive effort in polyps near the growing tip of branching colonies has also been noticed in some hard corals (e.g. Rinkevich & Loya 1979, Wallace 1985, Chornesky & Peters 1987), being explained by Connell (1973) in terms of diversion of colony resources to growth rather than gamete production, and/or polyp age.

The gonad distribution shown by *Thouarella* sp., *F. rossii* and *F. spinosa* did not fit with the above described patterns for scleractinian and octocorals. They therefore can not be explained with the information presently available. This is also true for the tropical gorgonian *Plexaura* A, implying that this is not a specific Antarctic feature. The inclusion of taxonomic/morphologic constraints and/or additional ecological parameters seems to be required to explain the reproductive patterns seen in octocorals (Brazeau & Lasker 1989).

Trophic control of the reproduction processes

Over the last decade, studies of benthic suspension feeders, both in cold (Antarctic: e.g. Barnes & Clarke 1995), and temperate (Mediterranean: Coma et al. 1998) environments have demonstrated that trophic control is a better explanation than temperature in understanding the seasonality of marine faunal life cycles. According to Hughes (1989) and Coma et al. (1998), the energy investment in reproduction coincides with the seasonal increase of food supply to the benthos, which suggests a trophic control of life cycles in many benthic organisms. Trophic control of gametogenesis has been observed among a wide variety of invertebrates (e.g. Andrew 1986, Giese & Kanatani 1987), but this topic has seldom been examined for corals. In the cold water soft coral *Alcyonium digitatum* a direct relationship was found between its gonad development and the seasonal abundance of plankton (Hartnoll 1975). Dahan & Benayahu (1997) suggest that the two relatively persistent phytoplankton blooms each year at Eilat (Genin et al. 1995) supply the metabolic demands for gametogenesis in *D. hemprichi*, thus allowing year-round gamete release.

The seasonality of primary production in the Antarctic should influence herbivores and suspension feeders directly (Clarke 1983, Clarke & Peck 1991). However, it has been shown that various suspension feeders are able to use the fraction of seston, which remains less seasonal through the year (Clarke & Leakey 1996) as a food source (Barnes & Clarke 1995, Orejas et al. in press, Orejas et al. submitted).

Clarke (1991) argues that the comparatively slow rates of reproduction and development of Antarctic organisms cannot be taken as an evidence of lack of temperature compensation, but rather as adaptations to low food supplies during most of the year. The possible disadvantages of a winter spawning strategy include a slower developmental rate and a diminished food supply. Slow developmental rates may be associated with the extra energetic requirement of increased overall maintenance metabolic costs, while reduced food availability is a disadvantage for winter larvae. However, Rivkin et al (1986) showed that asteroid larvae could feed on bacteria, and Peck (1993) found that larvae of the Antarctic nemertean *Parbolarsia corrugatus* were capable of feeding on particles less than 1 µm diameter.

Although the seasonal pulse of primary productivity is very sharp, the pattern becomes less distinct further along the food chain. Some benthic organisms breed all year around, suggesting only minor fluctuations in their food supply (White 1977, Picken 1979, Barnes & Clarke 1995). In three of the octocoral species studied, larvae have been observed in the gastrovascular cavities of the polyps. According to Rivkin et al. (1986) larvae are known to feed on bacterioplankton that are relatively abundant the whole year, therefore they may not be as dependent on the mid-summer phytoplankton blooms as had originally been suspected (White 1977, Picken 1980).

Stanwell-Smith et al. (1999) found planulae from octocorals at Signy Island throughout the year. At this same location the cushion star *Odontaster validus* reproduces via feeding pelagic larvae which are released into the water column in early winter, although the phytoplankton levels are decreasing during this season (Stanwell-Smith et al. 1999). Most planulae would not be expected to be tightly associated with the summer phytoplankton blooms because they are predominantly lecitotrophic.

From our data we are not able to know if the release of larvae occurs during the Antarctic summer, during other years or seasons, or continuously. The presence of more than one gonad size class in the same polyp and colony indicates continuous gametogenesis, which would also imply continuous release of larvae all year round.

In summary, Antarctic octocorals present reproduction features and patterns which seem not to be different from octocorals at other latitudes. Oocyte numbers and sizes fit into the observed pattern at other latitudes, as does the duration of gametogenic cycles. Presence of one or more oocyte size class points to cycles of one or several years duration, respectively, as also occurs in octocorals from tropical seas. Different shape patterns have been detected in agreement with observations of corals from different latitudes. The consideration of "architectural" parameters is required to identify possible features related with the shape of these organisms. Additionally, trophic control has been identified as one of the main factors probably responsible for reproductive processes as observed in other latitudes.

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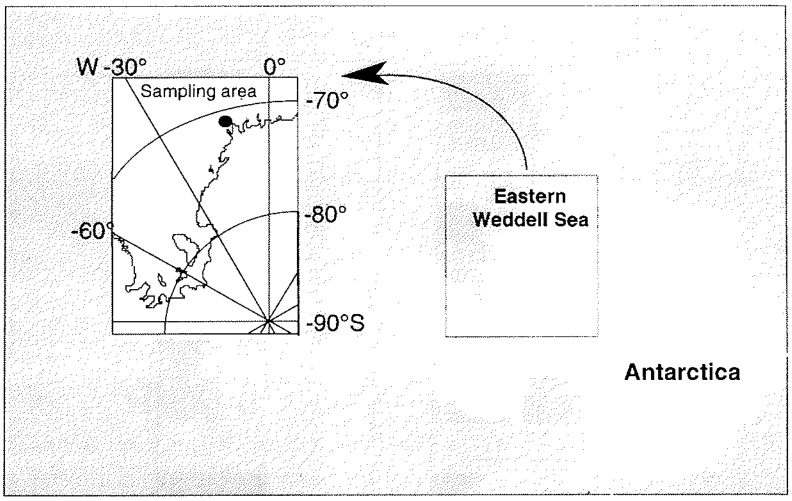

Fig.1 Sampling area. Eastern Weddell Sea. The black circle shows the area where the sampling has been done

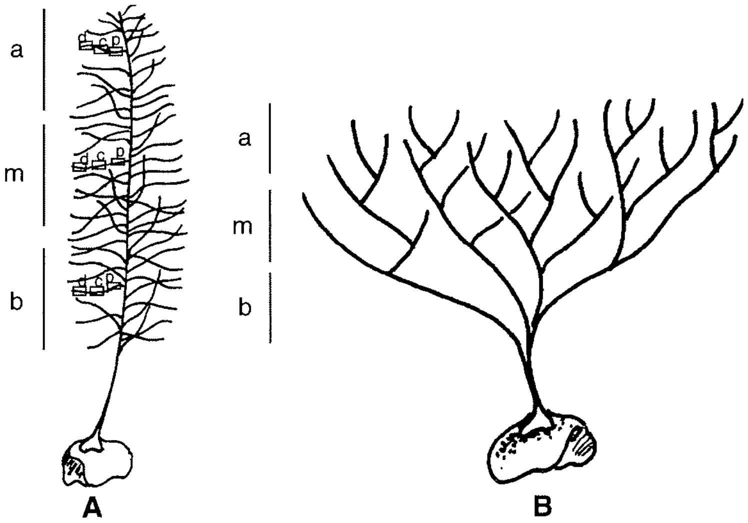

Fig. 2 Schematic aspect of the two studied morphotypes. *Dasystenella acanthina* and *Thouarella* sp. belong to the bottle-brush (A), and *Fannyella rossii* and *Fannyella spinosa* to the dichotomous type (B). The letters a, m and b indicate the colony zones apical, medial and basal respectively; p, c and d indicate the position with respect to the axis: proximal, central and distal, respectively.

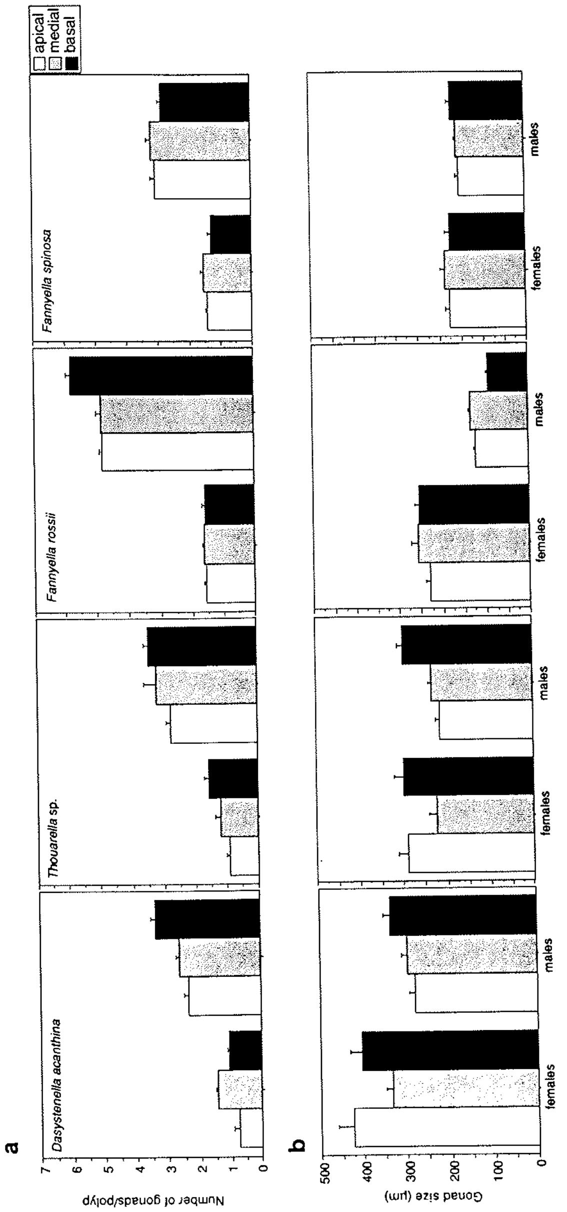

Fig. 3 Number (a) and gonad size (b) in the different colony zones (a, m, b) of the four species of this study.

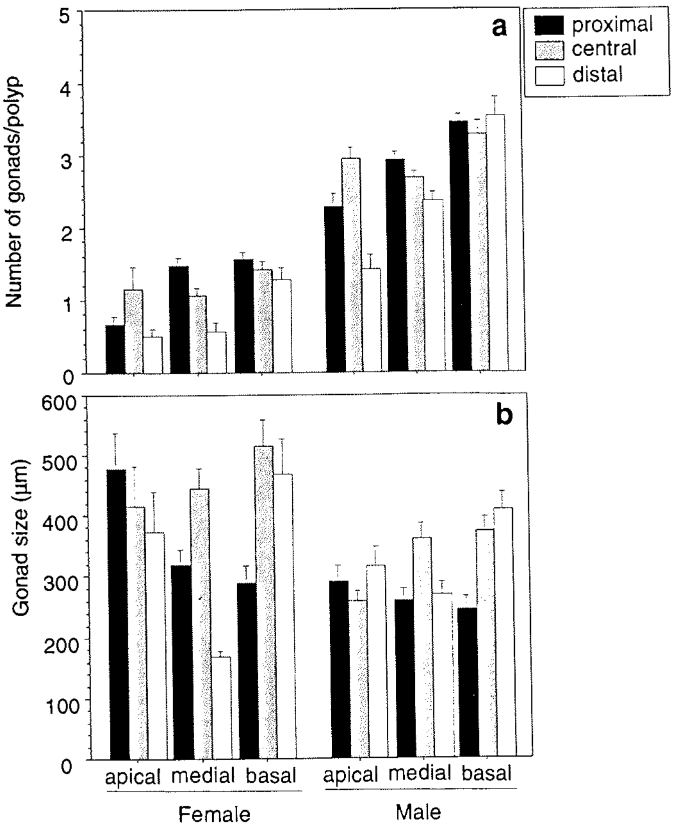

Fig. 4 a) Number of gonads related to axis position (p, c, d) *for Dasystenella acanthina*. b) Size of gonads related to axis position (p, c, d) *for Dasystenella acanthina*.

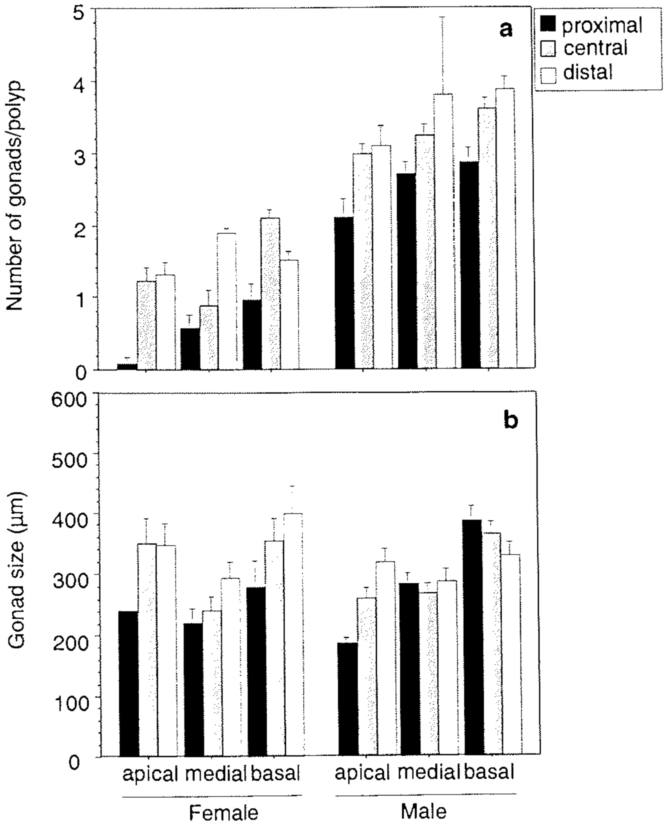

Fig. 5 a) Number of gonads related to axis position (p, c, d) for *Thouarella* sp. b) Size of gonads related to axis position (p, c, d) for *Thouarella* sp.

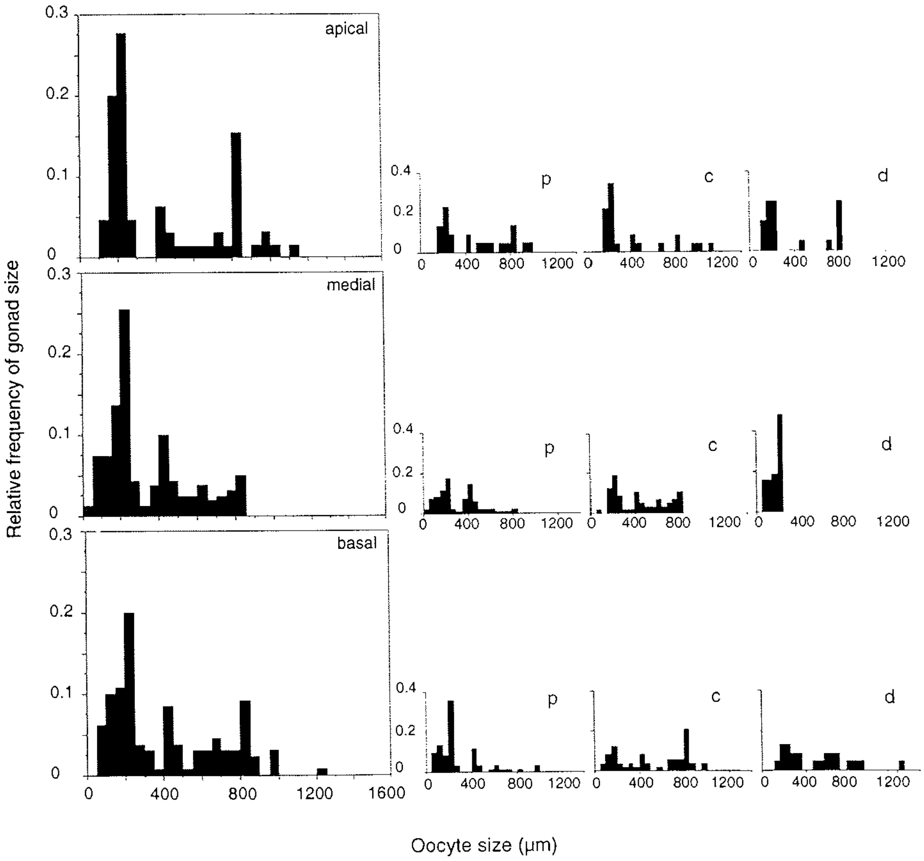

Fig. 6a Frequency distribution of oocyte size for *Dasystenella acanthina*.

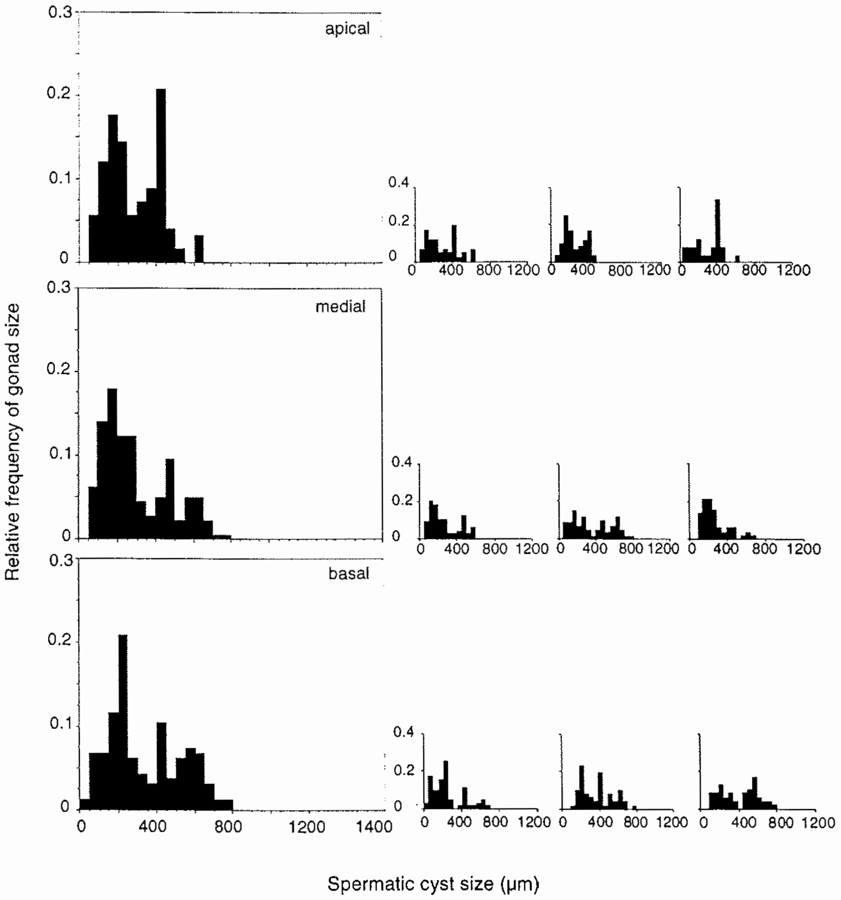

Fig. 6b Frequency distribution of spermatic cyst size for *Dasystenella acanthina*.

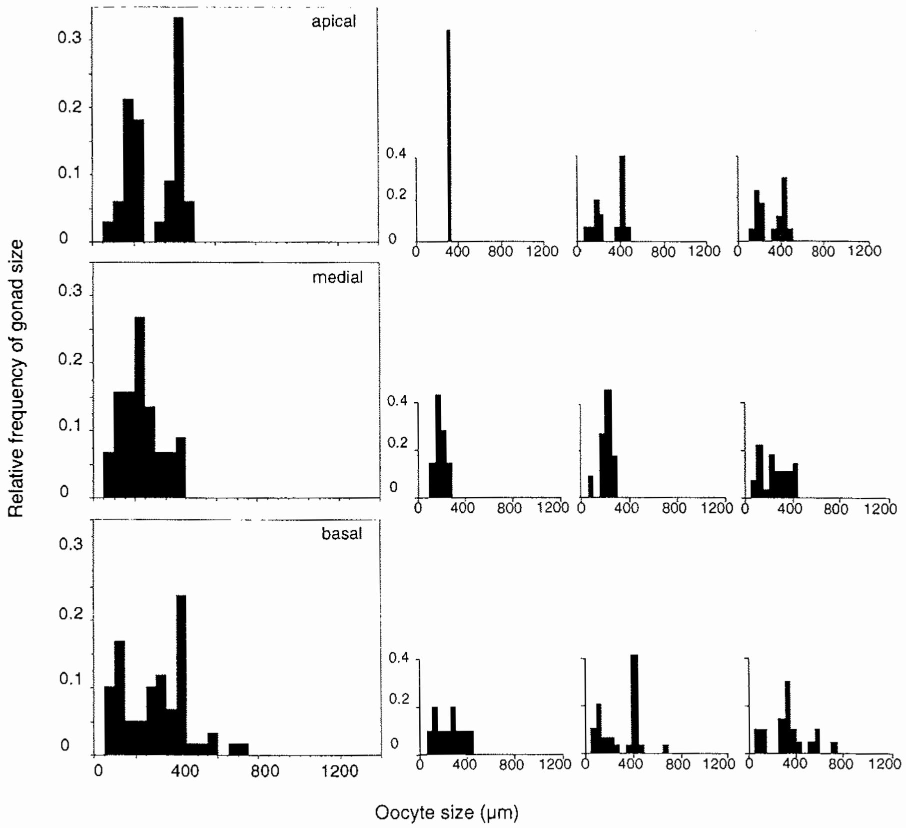

Fig. 7a Frequency distribution of oocyte sizefor *Thouarella* sp.

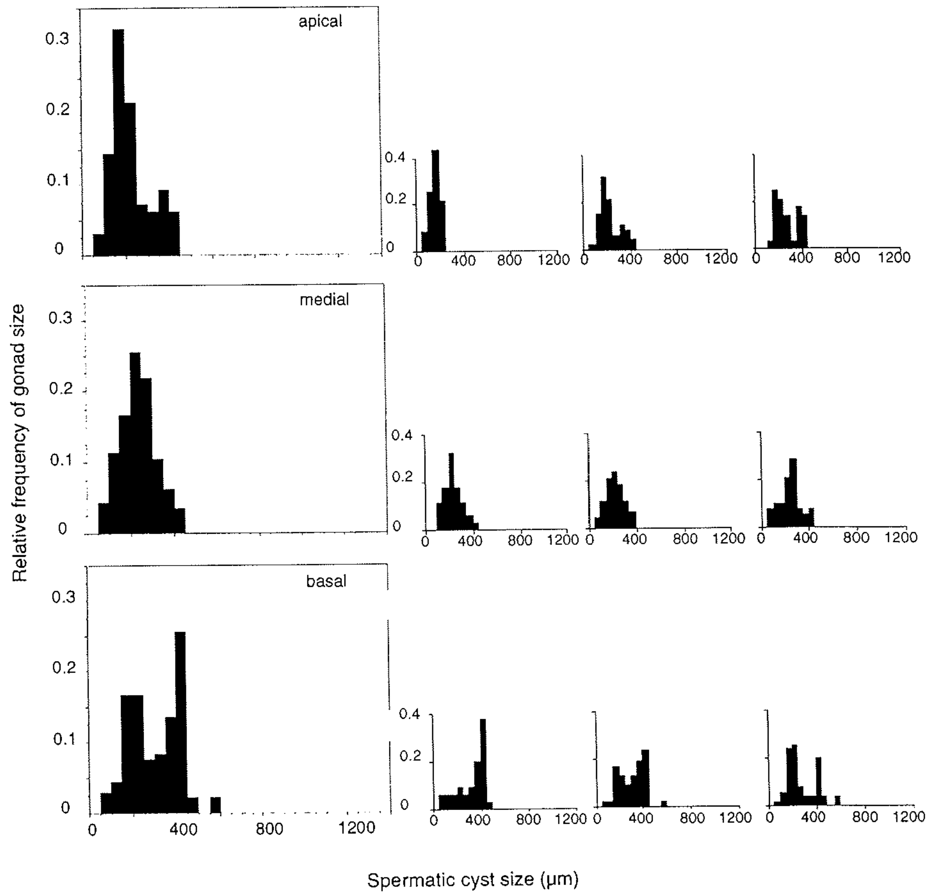

Fig. 7b Frequency distribution of spermatic cyst size for *Thouarella* sp.

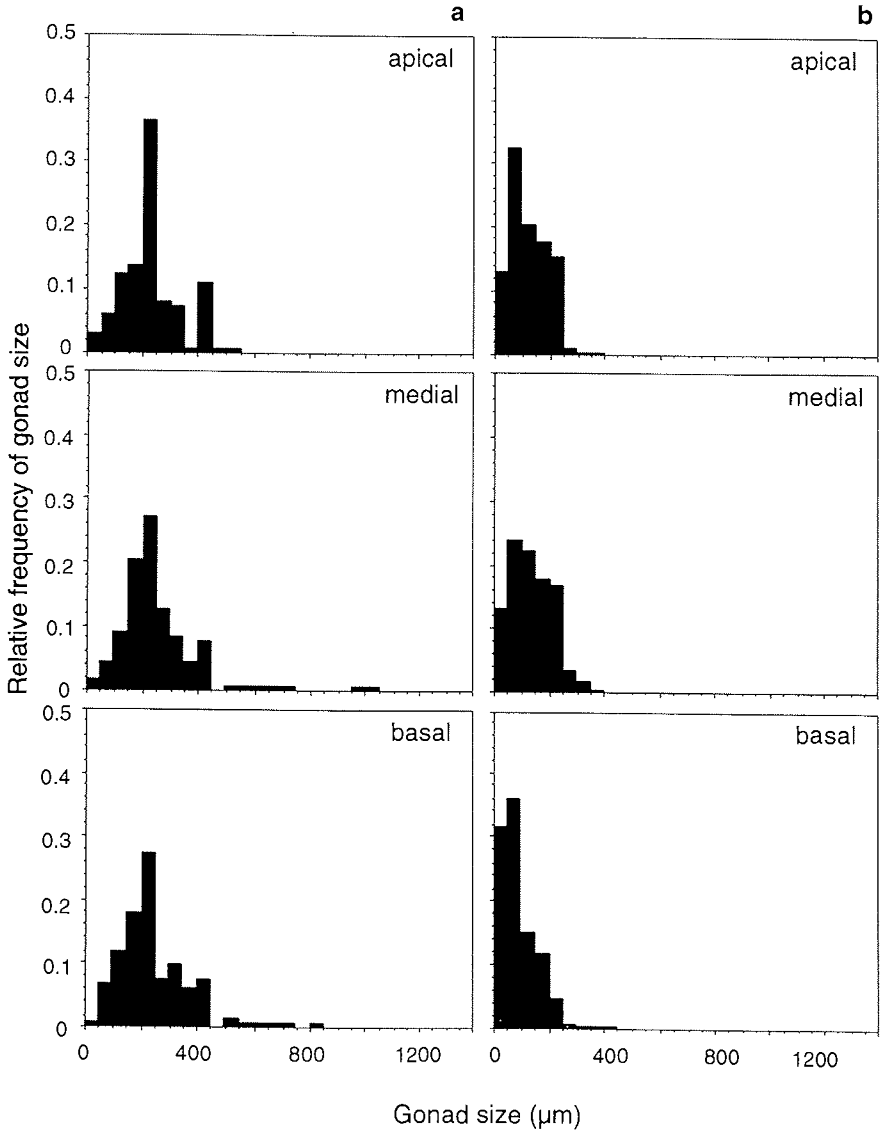

Fig. 8 Frequency distribution of gonad size for *Fannyella rossii*. a) oocytes, b) spermatic cysts.

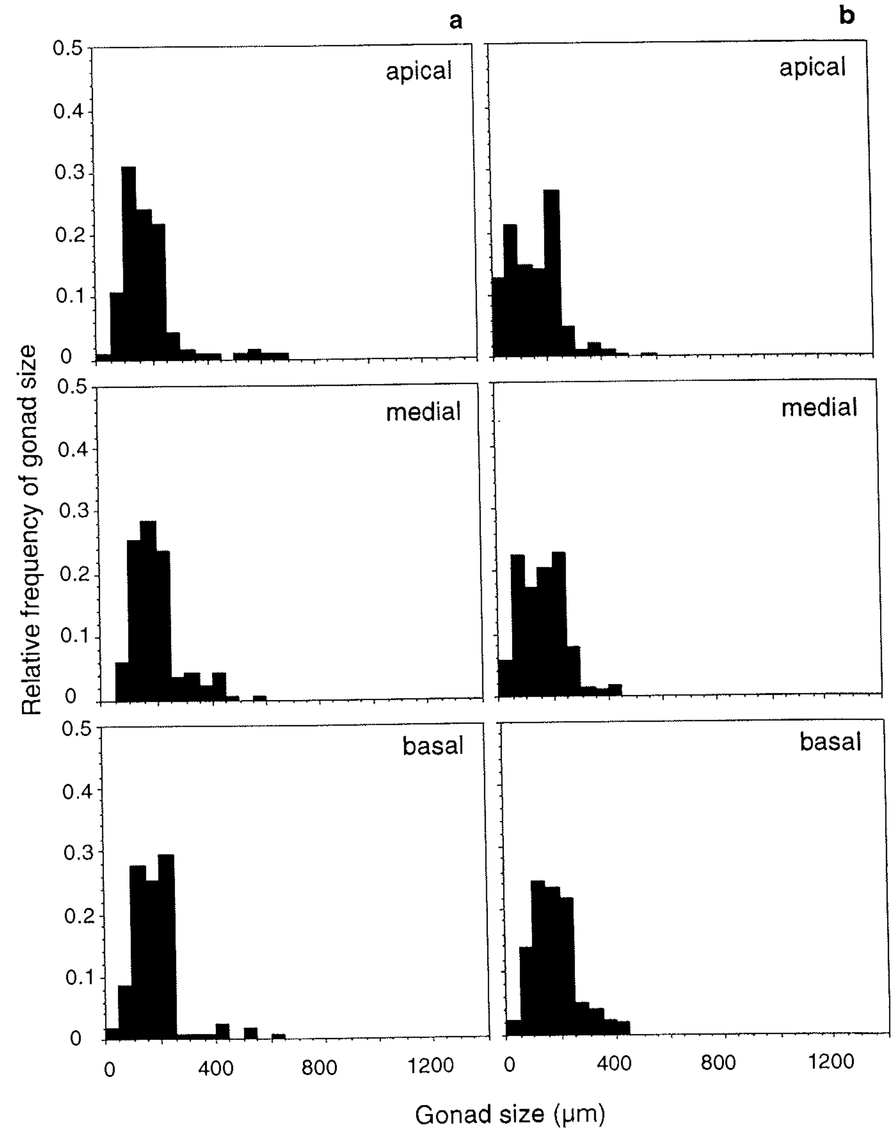

Fig. 9 Frequency distribution of gonad size for *Fannyella spinosa*. a) oocytes, b) spermatic cysts.

Table 1. **A**) Three-way ANOVA comparing numbers of gonads for *Dasystenella acanthina* (square root transformed): a) sex and colony zone, b) sex and axis position, c) colony zone and axis position. **B**) Three-way ANOVA comparing gonad size for *Dasystenella acanthina* (Log transformed): a) sex and colony zone, b) sex and axis position, c) colony zone and axis position.

A

	df	SS	MS	F	P
Sex	1	85.200	85.200	644.280	<0.0001
Colony zone	2	12.933	6.467	48.901	<0.0001
Axis position	2	7.174	3.587	27.126	<0.0001
Sex x Colony zone	2	5.386	2.693	20.3663	<0.0001
Sex x Axis position	2	0.171	0.086	0.648	0.5233
Colony zone x Axis position	4	3.114	0.779	5.887	0.0001
Sex x Colony zone x Axis position	4	2.998	0.749	5.667	0.0002
Residual	1035	136.87	0.132		

Bonferroni/Dunn post-hoc test

	Axis position			Colony zone			Sex	
	Proximal	Central	Distal	Apical	Medial	Basal	Female	Male
a) Sex								
Female-Male	**	**	**	**	**	**		
b) Colony zone								
Apical-Medial	**	ns	**				**	*
Medial-Basal	ns	ns	ns				*	**
Apical-Basal	**	ns	**				*	**
c) Axis position								
Proximal-Central				*	ns	ns	ns	ns
Central-Distal				**	ns	ns	*	*
Proximal-Distal				*	*	*	**	*

B

	df	SS	MS	F	P
Sex	1	0.643	0.643	8.887	0.0030
Colony zone	2	1.345	0.673	9.289	0.0001
Axis position	2	1.836	0.918	12.679	<0.0001
Sex x Colony zone	2	0.409	0.204	2.824	0.0599
Sex x Axis position	2	0.871	0.436	6.018	0.0025
Colony zone x Axis position	4	4.074	1.019	14.068	<0.0001
Sex x Colony zone x Axis position	4	0.409	0.102	1.412	0.2282
Residual	807	58.429	0.072		

Bonferroni/Dunn post-hoc test

	Axis position			Colony zone			Sex	
	Proximal	Central	Distal	Apical	Medial	Basal	Female	Male
a) Sex								
Female-Male	*	**	*	*	ns	ns		
b) Colony zone								
Apical-Medial	*	*	*				*	ns
Medial-Basal	ns	ns	**				ns	ns
Apical-Basal	*	**	*				ns	ns
c) Axis position								
Proximal-Central				ns	**	**	**	**
Central-Distal				ns	**	ns	**	ns
Proximal-Distal				ns	ns	**	ns	**

df: degrees of freedom, SS: sums of squares, MS: mean square, F: F-ratio, P: probability
ns = not significant
* = $p<0.05$
** = $p<0.0001$

Table 2. **A**) Three-way ANOVA comparing numbers of gonads for *Thouarella* sp. (square root transformed): a) sex and colony zone, b) sex and axis position, c) colony zone and axis position. **B**) Three-way ANOVA comparing gonad size for *Thouarella* sp. (Log transformed): a) sex and colony zone, b) sex and axis position, c) colony zone and axis position.

A

	df	SS	MS	F	P
Sex	1	44.393	44.393	308.866	<0.0001
Colony zone	2	4.572	2.286	15.906	<0.0001
Axis position	2	10.443	5.221	36.328	<0.0001
Sex x Colony zone	2	0.105	0.052	0.365	0.6942
Sex x Axis position	2	1.035	0.518	3.601	0.0280
Colony zone x Axis position	4	1.575	0.394	2.739	0.0281
Sex x Colony zone x Axis position	4	1.718	0.430	2.988	0.0186
Residual	527	75.75	0.144		

Bonferroni/Dunn post-hoc test

	Axis position			Colony zone			Sex	
	Proximal	Central	Distal	Apical	Medial	Basal	Female	Male
a) Sex								
Female-Male	**	**	**	**	**	**		
b) Colony zone								
Apical-Medial	*	ns	ns				*	ns
Medial-Basal	ns	*	ns				*	*
Apical-Basal	*	*	*				**	*
c) Axis position								
Proximal-Central				**	ns	*	**	*
Central-Distal				ns	ns	ns	ns	ns
Proximal-Distal				*	*	**	**	**

B

	df	SS	MS	F	P
Sex	1	0,0001	0,0001	0.003	0.9571
Colony zone	2	0.624	0.312	7.886	0.0004
Axis position	2	0.192	0.096	2.427	0.0894
Sex x Colony zone	2	0.125	0.063	1.579	0.2072
Sex x Axis position	2	0.033	0.016	0.415	0.6604
Colony zone x Axis position	4	0.083	0.021	0.527	0.7162
Sex x Colony zone x Axis position	4	0.175	0.044	1.104	0.3542
Residual	463	18.327	0.040		

Bonferroni/Dunn post-hoc test

	Axis position			Colony zone			Sex	
	Proximal	Central	Distal	Apical	Medial	Basal	Female	Male
a) Sex								
Female-Male	ns	ns	ns	*	ns	ns		
b) Colony zone								
Apical-Medial	*	ns	ns				ns	ns
Medial-Basal	*	*	*				ns	**
Apical-Basal	**	*	ns				ns	**
c) Axis position								
Proximal-Central				*	ns	ns	ns	ns
Central-Distal				*	ns	ns	ns	ns
Proximal-Distal				**	ns	ns	ns	ns

df: degrees of freedom, SS: sums of squares, MS: mean square, F: F-ratio, P: probability
ns = not significant
* = p<0.05
** = p<0.0001

Table 3. A) Two-way ANOVA comparing numbers of gonads for *Fannyella rossii* (square root transformed): a) sex and colony zone, b) sex and axis position, c) colony zone and axis position. B) Two-way ANOVA comparing gonad size for *Fannyella rossii* (Log transformed): a) sex and colony zone, b) sex and axis position, c) colony zone and axis position.

A

	df	SS	MS	F	P
Sex	1	306.940	306.940	754.765	<0.0001
Colony zone	2	2.718	1.359	3.342	0.0355
Sex x Colony zone	2	2.663	1.332	3.274	0.0380
Residual	2524	1026.44	0.407		

Bonferroni/Dunn post-hoc test

	Colony zone			Sex	
	Apical	Medial	Basal	Female	Male
a) Sex					
Female-Male	**	**	**		
b) Colony zone					
Apical-Medial				ns	ns
Medial-Basal				ns	**
Apical-Basal				ns	**

B

	df	SS	MS	F	P
Sex	1	36.688	38.688	711.620	<0.0001
Colony zone	2	1.859	0.929	17.094	<0.0001
Sex x Colony zone	2	1.700	0.850	15.633	<0.0001
Residual	2521	137.057	0.054		

Bonferroni/Dunn post-hoc test

	Colony zone			Sex	
	Apical	Medial	Basal	Female	Male
a) Sex					
Female-Male	**	**	**		
b) Colony zone					
Apical-Medial				ns	**
Medial-Basal				ns	ns
Apical-Basal				ns	**

df: degrees of freedom, SS: sums of squares, MS: mean square, F: F-ratio, P: probability.

ns = not significant

* = $p<0.05$

** = $p<0.0001$

Table 4. **A**) Two-way ANOVA comparing numbers of gonad for *Fannyella spinosa* (square root transformed): between a) sex and colony zone, b) sex and axis position, c) colony zone and axis position. **B**) Two-way ANOVA comparing gonad size for *Fannyella spinosa* (Log transformed): between a) sex and colony zone, b) sex and axis position, c) colony zone and axis position.

A

	df	SS	MS	F	P
Sex	1	57.193	57.193	421.383	<0.0001
Colony zone	2	0.021	0.011	0.078	0.9252
Sex x Colony zone	2	1.233	0.617	4.542	0.0109
Residual	1087	147.535	0.136		

Bonferroni/Dunn post-hoc test

	Colony zone			Sex	
	Apical	Medial	Basal	Female	Male
a) Sex					
Female-Male	**	**	**		
b) Colony zone					
Apical-Medial				ns	ns
Medial-Basal				*	*
Apical-Basal				ns	ns

B

	df	SS	MS	F	P
Sex	1	1.022	1.022	20.268	<0.0001
Colony zone	2	0.311	0.156	3.084	0.0462
Sex x Colony zone	2	0.285	0.142	2.820	0.0600
Residual	1024	51.649	0.050		

Bonferroni/Dunn post-hoc test

	Colony zone			Sex	
	Apical	Medial	Basal	Female	Male
a) Sex					
Female-Male	*	**	ns		
b) Colony zone					
Apical-Medial				ns	ns
Medial-Basal				ns	ns
Apical-Basal				ns	*

df: degrees of freedom, SS: sums of squares, MS: mean square, F: F-ratio, P: probability.
ns = not significant
* = $p<0.05$
** = $p<0.0001$

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