Polar Biol (1994) 14: 243-251

© Springer-Verlag 1994

ORIGINAL PAPER

To Phil Pugh, wishing a long and prosperous collaboration, Francesc Pagès 20-6-94

F. Pagès · F. Kurbjeweit

# Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica

Received: 28 June 1993/Accepted: 21 September 1993

**Abstract** The composition, abundance and vertical distribution of mesoplanktonic cnidarians collected along a transect across the Weddell Sea have been analysed. The transect was characterized by a thermocline, approximately between 200 and 100 m, which deepened significantly towards the shelf edges. In total, 10 species of medusae and 18 species of siphonophores were identified. The most abundant medusae were *Pantachogon scotti* (up to 11,671 specimens/1,000 m$^3$) and *Arctapodema ampla* (up to 960 specimens/1000 m$^3$). The most abundant siphonophores were *Muggiaea bargmannae* (up to 1,172 nectophores/1,000 m$^3$) and *Dimophyes arctica* (up to 230 nectophores/1,000 m$^3$). Five assemblages of planktonic cnidarians were distinguished: (a) epipelagic species located in and above the thermocline; (b) epi- and upper mesopelagic species located in, above and just below the thermocline; (c) epi- and mesopelagic species located in and below the thermocline; (d) mesopelagic species; (e) lower mesopelagic species. Differences in the depth distribution of the various species gave rise to a clear partitioning of the mesoplanktonic cnidarian population throughout the water column. This vertical partitioning was related to the existence of a thermocline, the structure of the water column and the vertical distribution of prey.

## Introduction

In recent years, numerous studies on the systematic composition, abundance and distribution of zooplankton communities in the Southern Ocean have been published, e.g. Chojnacki and Weglenska (1984), Hopkins (1985), Witek et al. (1985), Atkinson and Peck (1988), Hubold et al. (1988), Foster (1989), Hopkins and Torres (1988), Piatkowski (1989), Lancraft et al. (1989), Tucker and Burton (1990), Boysen-Ennen et al. (1991), Siegel et al. (1992), Hopkins et al. (1993). Most of these deal with copepods and euphausiids, the main components of the Antarctic zooplankton. A review of the systematic groups examined in these publications shows a remarkable lack of data about the so-called gelatinous zooplankton, aptly called "the forgotten fauna" by Pugh (1989), which includes medusae, siphonophores, ctenophores and tunicates as the most important groups.

The early publications dealing with these gelatinous groups in the Southern Ocean were mainly concerned with descriptions of new species collected during the first expeditions to Antarctica (Apstein 1908; Moser 1909, 1925; Browne 1910; Lohmann and Buchmann 1926). Some years later, the Discovery Reports provided data on abundances and distribution (Totton 1954; Kramp 1957; Foxton 1966) and established their presence and importance in Antarctic waters. Later, the few publications on gelatinous zooplankton in Antarctic waters have mainly dealt with the salps which are very abundant in the spring, coincident with the phytoplankton bloom (e.g. Nast 1986).

Recently, it has become necessary to reappraise the ecological role of the gelatinous zooplankton in the Southern Ocean. Some considerations from an energetic point of view (Clarke and Peck 1991) and data on its proximate and elemental composition (Clarke et al. 1992) have been published, but data about species composition, abundance and distribution still are scarce. There is no doubt that the role of gelatinous zooplankton in the Antarctic food web has been underestimated, as the work of Larson (1986) on scyphozoan medusae shows.

This study was undertaken to examine the vertical distribution and abundance of mesoplanktonic cnidarians

F. Pagès[1] · F. Kurbjeweit (✉)
Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstrasse,
D-27568 Bremerhaven, Germany

*Present address:*
[1] Institut de Ciències del Mar (CSIC), Passeig Nacional s/n, 08039 Barcelona, Spain

on a transect across the Weddell Sea, as a first step towards gaining a better understanding of their role in the zooplankton community of Antarctic waters. Planktonic cnidarians are carnivorous predators that feed on a wide variety of prey, principally copepods (Purcell 1984; Matsakis and Conover 1991). Their abundance is low in comparison with copepods, but one has to take into account the fact that a single medusa measuring 45 mm in diameter can capture and digest up to 607 copepods per day (Båmstedt 1990) and a single calycophoran siphonophore (5 mm high) can take up to 15 copepods in the same time (Purcell and Kremer 1983).

## Materials and methods

The mesoplanktonic cnidarian population of the Weddell Sea was studied by analysing samples collected between 22 November and 15 December 1990, along a transect between the northern tip of the Antarctic Peninsula and Cape Norvegia (Fig. 1) by the *RV Polarstern* during the Antarktis IX/2 cruise (Bathmann et al. 1992). A multiple opening/closing net system (0.25 m$^2$, 100 μm; Weikert and John 1981) was hauled vertically at 11 stations. The depth intervals sampled were chosen according to the hydrographic conditions revealed by conductivity-temperature-depth casts before each haul. In order, the depth intervals sampled in the oceanic stations were 1,000–500, 500–200, 200–100, 100–50 and 50–0 m. On the stations located over the shelves, the deepest net was towed from near the bottom to 250 m and the remaining intervals were 250–150, 150–100, 100–50 and 50–0 m. The volume of filtered water was calculated using a flowmeter (Hydrobios, Kiel).

All siphonophores [both polygastric (asexual) and eudoxid (sexual) stages] and medusae were identified according to our present knowledge of the systematics of both groups. All specimens (whole colonies in physonects; nectophores, bracts or eudoxids in calycophores) were counted and the counts standardized to number of specimens per 1,000 m$^3$.

Cluster analyses were carried out in order to obtain an objective description of the distribution pattern of the most abundant species, and to characterize assemblages of species according to their affinities, based on their presence or absence in the samples. Czekanowski's index of similarity (Legendre and Legendre 1979), also called percentage similarity (Pielou 1984), and the UPGMA algorithm (Sneath and Sokal 1973) were used.

## Results

### Hydrography

The Weddell Sea transect, in the upper 1,000 m of water column, was generally characterized by a thermocline approximately between 200 and 100 m. However, the thermocline deepened significantly towards the shelf edges, down to 700 m on the eastern and almost 1,000 m on the western shelf (Fig. 2). This thermocline was formed by Modified Warm Deep Water (MWDW) with temperatures between 0 and −1.5°C. It separated the upper cold Winter Water (WW) with temperatures of −1.8°C, from the Warm Deep Water (WDW) with a temperature maximum greater than 0°C. The maximum was more pronounced at shelf edges than in the oceanic region with temperatures up to 0.8°C in the east and 0.4°C in the west indicating an inflow and an outflow, respectively (Bathmann et al. 1992). The Western (WSW) and Eastern (ESW) Shelf Waters were characterized by very cold water (temperature range −1.80 to −1.85°C) with high and low salinities, respectively. Ice coverage ranged from about seven-tenths in the western half of the transect to about nine-tenths in the eastern half.

### Species distribution

In total, 28 species of planktonic cnidarians (10 medusae and 18 siphonophores) were collected across the transect.

The medusae consisted of 3 anthomedusae, 1 narcomedusa, 4 trachymedusae and 2 scyphomedusae.

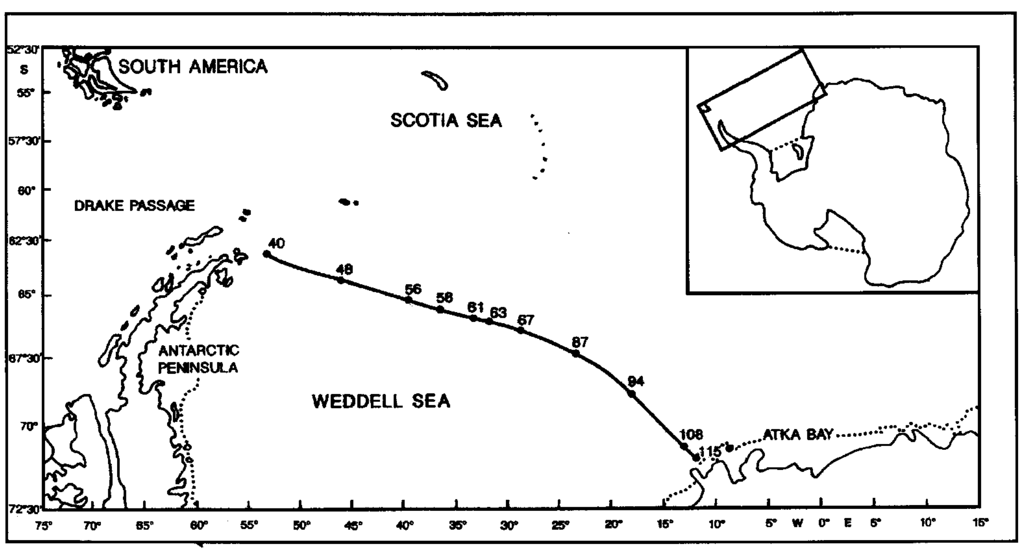



**Fig. 1** Map of the Weddell Sea showing the transect made by the *RV Polarstern* during cruise Antarktis IX/2

**Table 1** Total number of specimens (N) and mean densities per 1000 m$^3$ ($\pm$SD) by depth interval in the transect across the Weddell Sea, for each medusan species. Systematics according to Bouillon et al. (1992)

| Species | N | DEPTH INTERVAL (m) 50–0 $n = 11$ | 100–50 $n = 11$ | 200–100 $n = 11$ | 500–200 $n = 13$ | 1000–500 $n = 9$ |
|---|---|---|---|---|---|---|
| **Class Hydrozoa** | | | | | | |
| **Subclass Hydroidomedusae** | | | | | | |
| Order Anthomedusae | | | | | | |
| Tubulariidae sp. A | 67 | 0 | 0 | 0 | 0 | 7.4 $\pm$ 22.4 |
| Corymorphidae sp. A | 29 | 0 | 0 | 0 | 2.1 $\pm$ 5.3 | 0 |
| *Calycopsis borchgrevinki* (Browne, 1910) | 16 | 0 | 0 | 0 | 1.2 $\pm$ 4.4 | 0 |
| Order Narcomedusae | | | | | | |
| *Solmundella bitentaculata* (Quoy and Gaimard, 1833) | 905 | 7.6 $\pm$ 25.4 | 0 | 29.5 $\pm$ 74.2 | 19.3 $\pm$ 25.7 | 6.58 $\pm$ 11.1 |
| Order Trachymedusae | | | | | | |
| *Botrynema brucei* Browne, 1908 | 35 | 0 | 0 | 0 | 0 | 3.8 $\pm$ 6.4 |
| *Arctapodema ampla* (Vanhöffen, 1902) | 6400 | 0 | 0 | 0 | 244.5$\pm$271.4 | 357.6$\pm$167.4 |
| *Haliscera conica* Vanhöffen, 1902 | 453 | 0 | 0 | 0 | 25.5 $\pm$ 39.9 | 13.2 $\pm$ 11.7 |
| *Pantachogon scotti* Browne, 1910 | 66906 | 368.0$\pm$687.0 | 3133.9$\pm$3677.9 | 2147.8$\pm$1568.7 | 364.5 $\pm$ 373.3 | 1.7 $\pm$ 3.4 |
| **Class Scyphozoa** | | | | | | |
| Order Coronatae | | | | | | |
| *Periphylla periphylla* (Péron and Lesueur, 1810) | 34 | 0 | 0 | 3.1 $\pm$ 10.3 | 0 | 0 |
| *Tetraplatia sp.* | 9 | 0 | 0 | 0 | 0 | 0.9 $\pm$ 2.8 |

Eight of these are well known in the Southern Ocean but two undescribed anthomedusan species (Tubulariidae sp. A and Corymorphidae sp. A) were also found.

The siphonophores consisted of 5 physonects and 13 calycophores. Only 2 physonects were easily identified. The others were an undescribed species of the family Apolemidae (Apolemidae sp. D), a specimen belonging to the family Agalmidae but of doubtful identity, and several post-larval stages probably belonging to the genus *Bargmannia* and previously recorded in Antarctic waters (Pagès and Gili 1989).

Among the calycophores, there were several interesting species, including an unidentified species of *Sphaeronectes*. *Lensia asymmetrica*, originally described from material collected in the Kamchatka Trench (Stepanjants 1970), was recorded again just after its first record in Antarctic waters (Margulis 1992) and its sexual stage identified. Two unascribable eudoxids belonging to the genus *Lensia* as well as another unknown eudoxid of doubtful affinity (Eudoxia X) were also collected. The remaining species are common in Antarctic waters or have been collected at meso- and bathypelagic depths in the three great oceans.

*Pantachogon scotti* and *Arctapodema ampla* were the most abundant medusae along the transect. *P. scotti* (1–4 mm in diameter) was caught at all stations except those located over the continental shelves (Fig. 2). It was mainly concentrated between 500 and 50 m depth (up to 11,671 specimens/1,000 m$^3$) although several specimens were collected above and below this depth range. *A. ampla* (1–5 mm in diameter) was collected below 200 m at all stations (up to 960 specimens/1,000 m$^3$) except those over the western continental shelf (Fig. 3).

*Haliscera conica* (1–10 mm in diameter) was also caught at all stations except those located over both continental shelves. It was always present below 200 m, with highest abundances in the 500–200 m depth stratum (up to 109 specimens/1,000 m$^3$).

Individuals of the remaining species were present only in small densities and their mean abundances and depth distributions are shown in Table 1.

*Muggiaea bargmannae* was the most abundant siphonophore across the transect (up to 1,172 nectophores/1,000 m$^3$). Nectophores (1–6 mm high) were present at all stations and throughout the whole sampled water column but they were clearly concentrated in the 500–100 m depth horizon (Fig. 4). Eudoxids (1–2 mm high) were collected almost exclusively below 200 m and mostly in the 500–200 m stratum. They were less abundant (up to 447 eudoxids/1,000 m$^3$) than the nectophores. Only a few nectophores were collected in the upper cold water mass (WW = $-1.8$°C).

*Dimophyes arctica* (4–9 mm water anterior nectophore height) showed a distribution almost identical to that of *M. bargmannae* (Fig. 5). The depth distribution

**Table 2** Total number (N) of specimens (whole colony in physonects, nectophores, eudoxids or bracts in calycophores) and mean densities per 1,000 m$^3$ ($\pm$SD) by depth interval on the transect across the Weddell Sea, for each siphonophoran species (*an* anterior nectophore, *b* bract, *e* eudoxid)

| Species | N | DEPTH INTERVAL (m) 50–0 $n = 11$ | 100–50 $n = 11$ | 200–100 $n = 11$ | 500–200 $n = 13$ | 1000–500 $n = 9$ |
|---|---|---|---|---|---|---|
| **Class Hydrozoa** | | | | | | |
| **Order Siphonophorae** | | | | | | |
| **Suborder Physonectae** | | | | | | |
| Apolemidae sp. D | 8 | 0 | 0 | 0 | 0 | 0.8 ± 2.6 |
| Agalmidae sp. A | 41 | 0 | 0 | 3.6 ± 12.2 | 0 | 0 |
| *Moseria convoluta* (Moser, 1925) | 20 | 0 | 0 | 0 | 0.8 ± 3.1 | 1.0 ± 3.1 |
| *Pyrostephos vanhöffeni* Moser, 1925 | 112 | 6.2 ± 20.7 | 0 | 0 | 0 | 0 |
| ?Bargmannia post-larvae | 570 | 34.9 ± 115.8 | 0 | 13.0 ± 43.4 | 3.8 ± 12.7 | 0 |
| **Suborder Calycophorae** | | | | | | |
| *Vogtia serrata* (Moser, 1925) | 79 | 0 | 0 | 0 | 5.5 ± 12.5 | 0.7 ± 2.2 |
| *Diphyes antarctica* Moser, 1925 an | 135 | 0 | 6.9 ± 23.0 | 0 | 0.8 ± 3.1 | 0 |
| e | 298 | 0 | 4.7 ± 15.7 | 8.1 ± 18.7 | 3.0 ± 5.7 | 0 |
| *Lensia asymmetrica* Stepanjants, 1970 an | 314 | 0 | 0 | 0 | 0 | 34.8 ± 24.0 |
| b | 423 | 0 | 0 | 0 | 0 | 46.8 ± 34.3 |
| *L. havock* Totton, 1941 an | 10 | 0 | 0 | 0 | 0 | 1.0 ± 3.2 |
| *L. reticulata* Totton 1954 b | 171 | 0 | 0 | 0 | 0 | 16.4 ± 1.0 |
| *Lensia* sp. 1 e | 24 | 0 | 0 | 0 | 0 | 2.5 ± 3.9 |
| *Lensia* sp 2 e | 9 | 0 | 0 | 0 | 0 | 1.0 ± 3.1 |
| *Dimophyes arctica* (Chun, 1897) an | 2124 | 0 | 16.4 ± 36.8 | 11.4 ± 154.5 | 48.3 ± 31.3 | 2.1 ± 6.4 |
| e | 1945 | 0 | 0 | 45.5 ± 58.7 | 154.1 ± 223.2 | 52.5 ± 23.5 |
| *Muggiaea bargmannae* Totton, 1954 n | 10639 | 39.5 ± 48.8 | 20.7 ± 35.7 | 515.2 ± 421.5 | 329.9 ± 206.2 | 58.5 ± 37.2 |
| e | 4781 | 0 | 0 | 9.8 ± 22.8 | 231.5 ± 172.4 | 184.6 ± 90.8 |
| *Heteropyramis crystallina* (Moser, 1925) n | 622 | 0 | 0 | 0 | 2.5 ± 6.4 | 65.6 ± 13.4 |
| | 843 | 0 | 0 | 0 | 0 | 93.6 ± 20.5 |
| *Crystallophyes amygdalina* Moser, 1925 an | 439 | 0 | 0 | 0 | 6.5 ± 11.1 | 20.5 ± 13.3 |
| *Sphaeronectes* sp. n | 2784 | 54.8 ± 57.0 | 136.9 ± 222.2 | 34.5 ± 35.6 | 29.2 ± 83.3 | 0 |
| e | 4012 | 12.4 ± 28.6 | 140.3 ± 219.9 | 96.3 ± 177.8 | 97.8 ± 241.4 | 0 |
| Eudoxia X | 19 | 0 | 0 | 0 | 0 | 2.1 ± 6.4 |

was between 1000 and 50 m but mainly concentrated in the 500–100 m range (up to 230 anterior nectophores/1,000 m$^3$). Eudoxids (5–8 mm high) were collected between 1,000 and 100 m but their abundance was lower (up to 130 eudoxids/1,000 m$^3$).

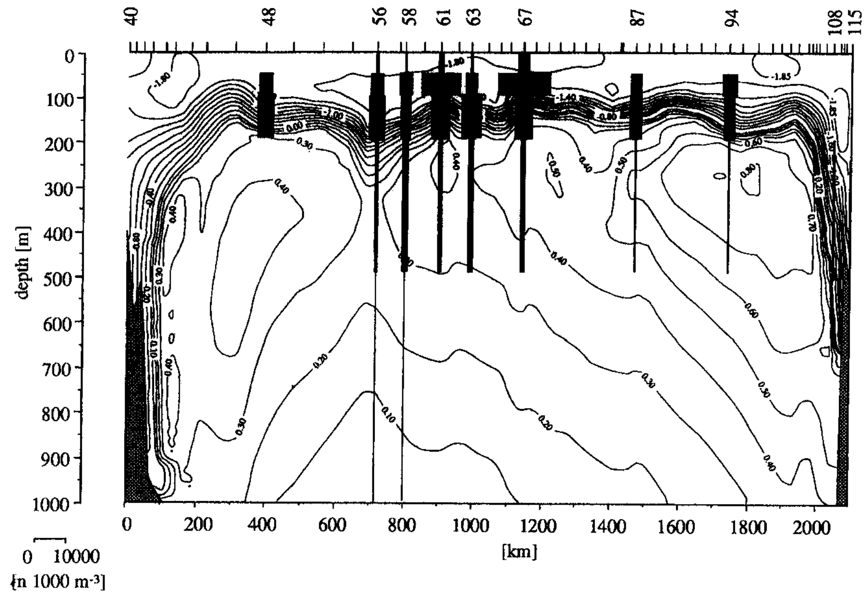
*Crystallophyes amygdalina* (5 mm anterior nectophore height) was collected only beneath the thermocline (Fig. 6). At all oceanic stations it was present in the 1,000–500 m stratum (up to 48 anterior nectophores/1,000 m$^3$), but it was also caught in the 500–200 m depth range at the central stations of the transect (up to 31 anterior nectophores/1,000 m$^3$).

Specimens of *Heteropyramis crystallina* (3–6 mm high) were collected at all stations, almost exclusively in the 1,000–500 m stratum (Fig. 7). Both stages had low and similar densities (up to 87 nectophores/1,000 m$^3$ and up to 119 eudoxids/1,000 m$^3$).

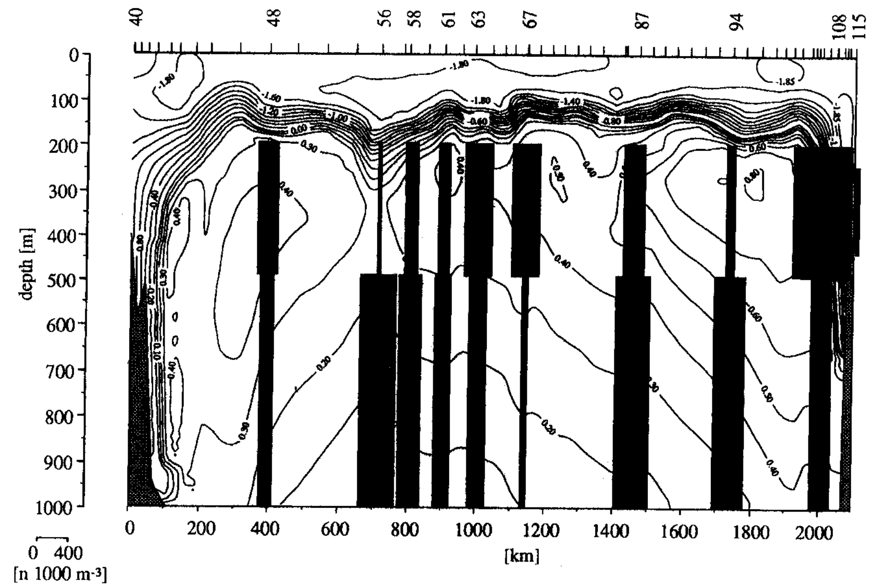
*Lensia asymmetrica* (1–3 mm anterior nectophore height, 1–2 mm bract height) was present exclusively in the 1,000–500 m stratum of all oceanic stations. As in the case of *H. crystallina*, both stages showed low abundances (up to 79 nectophores/1,000 m$^3$ and up to 102 bracts/1,000 m$^3$).

Eudoxids of *Lensia reticulata* (1–2 mm bract height) were also restricted to the 1,000–500 m stratum (Fig. 8). They were collected at all the oceanic stations (up to 32 eudoxids/1,000 m$^3$).

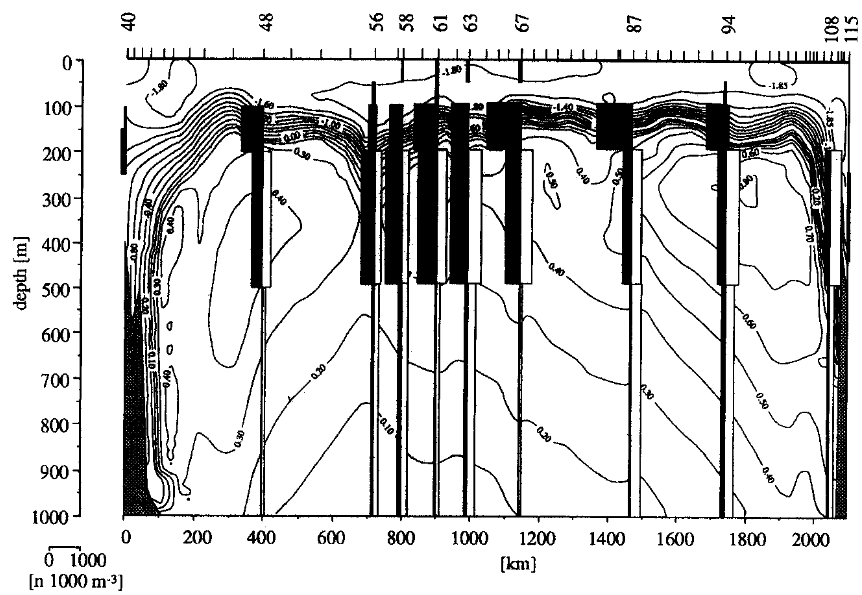
*Sphaeronectes* sp. (1–4 mm nectophore height, 1–3 mm eudoxid height) was the only siphonophore collected in and above the thermocline (Fig. 9). At the



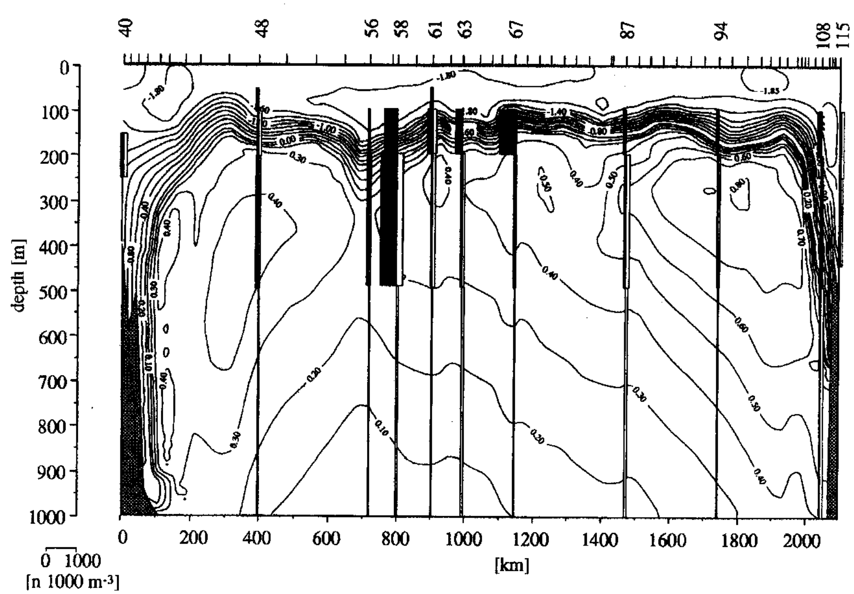

2




3




4



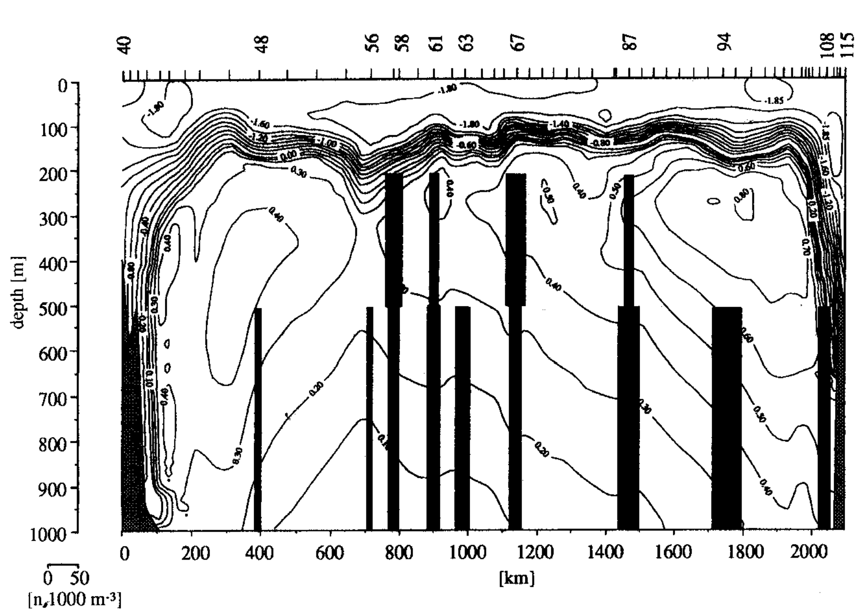

5

**Fig. 2** Depth distribution and abundance of *Pantachogon scotti* along the transect

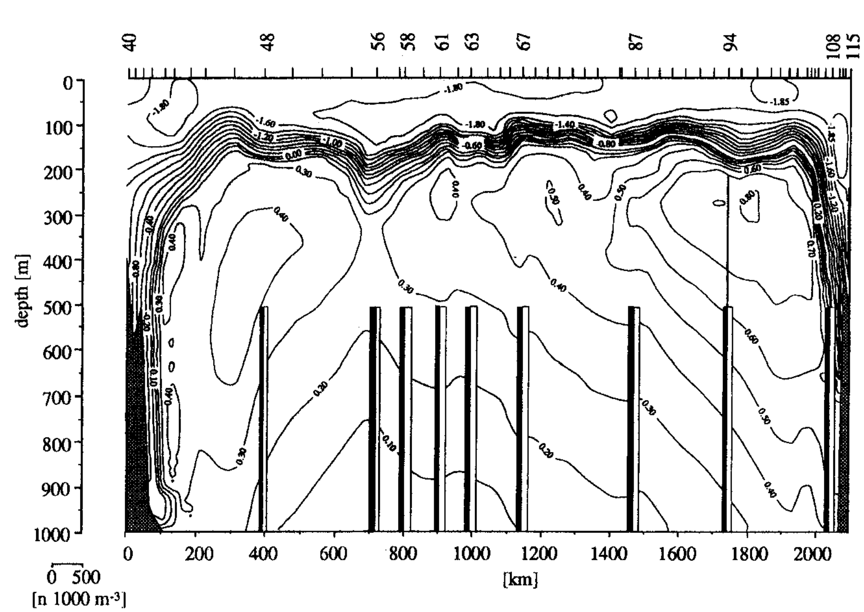
**Fig. 3** Depth distribution and abundance of *Arctapodema ampla* along the transect

**Fig. 4** Depth distribution and abundance of *Muggiaea bargmannae* along the transect. Nectophores are *shaded*, eudoxids are *outlined*

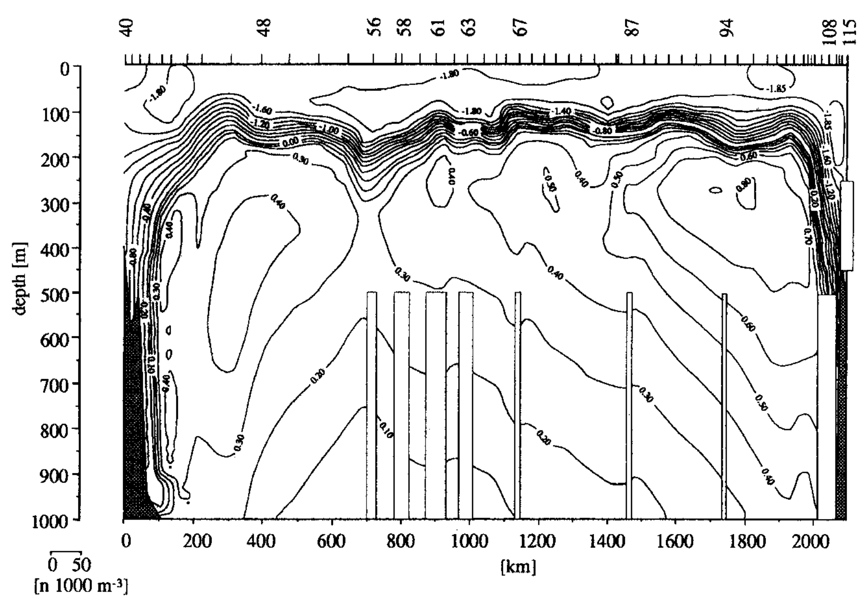
**Fig. 5** Depth distribution and abundance of *Dimophyes arctica* along the transect. Nectophores are *shaded*, eudoxids are *outlined*



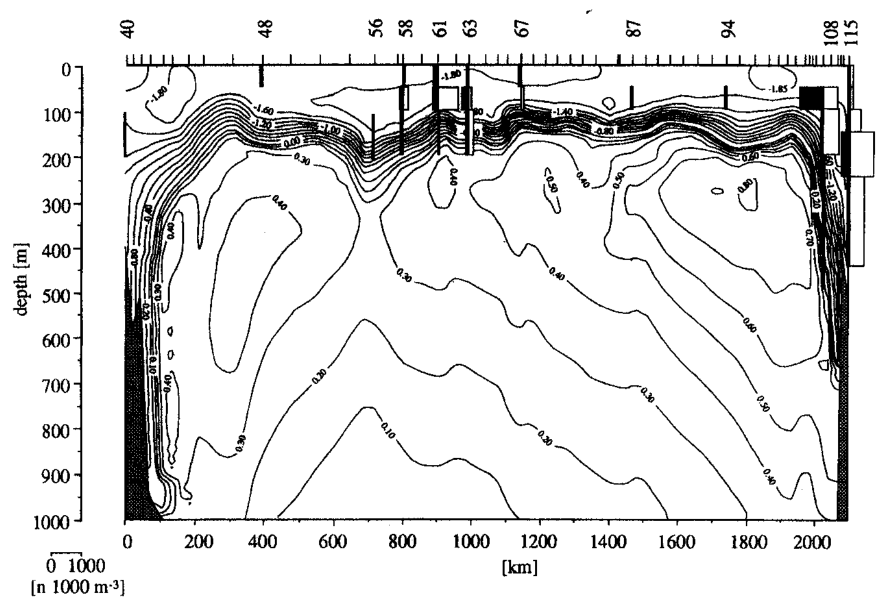

6




7




8




9

**Fig. 6** Depth distribution and abundance of nectophores of *Crystallophyes amygdalina*

**Fig. 8** Depth distribution of the eudoxids of *Lensia reticulata* along the transect

**Fig. 7** Depth distribution and abundance of *Heteropyramis crystallina* along the transect. Nectophores are *shaded*, eudoxids are *outlined*

**Fig. 9** Depth distribution and abundance of *Sphaeronectes* sp. along the transect. Nectophores are *shaded*, eudoxids are *outlined* central stations of the transect, it was restricted to the upper 200 m, but its bathymetric distribution was extended to 500 m near the eastern shelf edge, following the deepening of the thermocline. Both stages showed similar abundances (up to 768 nectophores/1,000 $m^3$ and up to 802 eudoxids/1,000 $m^3$) but the eudoxids were absent in the top 50 m and were more abundant in the deeper strata in comparison with the nectophores.

Colonies of the remaining species were present only at low densities. Their mean abundances and depth distributions are shown in Table 2.

## Discussion

Vertical distribution patterns of the planktonic cnidarian population collected along the transect were closely associated with the location of the thermocline and structure of the water column. Cluster analyses support this idea and distinguish four main species groups (Fig. 10):

1. Epipelagic species located in and above the thermocline (T = −1.8–0.2°C)

The siphonophore *Sphaeronectes* sp. nov. belongs to this group. Its distribution shows that it lives in very cold waters. Nothing is known about the biology of this species.

2. Species located throughout the water column

Careful examination of the vertical distribution of the species of this group, taking into account the depth range of the bulk of their populations, enables the distinction of two additional species groups:

*a) Epi- and upper mesopelagic species located in, above and just below the thermocline (T = −1.8–0.2°C)*

The trachymedusan *Pantachogon scotti* and the siphonophore *Diphyes antarctica* belong to this association. The distribution of *D. antarctica* was erratic across the transect and did not show any clear distribution pattern. *P. scotti* is discussed in a later section.

*b) Epi- and mesopelagic species located in and below the thermocline (T = −1.7–0.7°C)*

Nectophores of *Muggiaea bargmannae* and both stages of *Dimophyes arctica* are included in this group. The bulk of the population of *M. bargmannae* was concentrated in the thermocline and decreased with depth. *D. arctica* showed the same vertical pattern, which matched that described by Pugh (1974) in Canary Islands and by Mapstone and Arai (1992) for British Columbia waters, where nectophores were most abundant higher in the water column and eudoxids were deeper and much less abundant. As both these species are similar in size and shape, and often co-occur in Antarctic waters (Pagès, unpublished data), it is possible that they feed on different prey or have evolved different feeding strategies.

Across the transect, a distribution pattern similar to that of the above two siphonophores is known for *Microcalanus pygmaeus*, the most abundant calanoid copepod along the transect (Kurbjeweit 1993). Since copepods are the main prey items of siphonophores (Purcell 1981, 1982, 1983, 1984), we believe that the vertical distributions of *M. bargmannae* and *D. arctica* are related not only to hydrography but probably also to their prey. This has been recently suggested by Mapstone and Arai (1992) for *D. arctica* in British Columbia waters. More rigorous and broader studies about the distribution, abundance, feeding and reproduction of both species are required because of their relatively high abundances in Antarctic waters.

3. Mesopelagic species (T = 0–0.7°C)

*Crystallophyes amygdalina*, the eudoxids of *M. bargmannae* and the trachymedusae *Arctapodema ampla* and *Haliscera conica* were distributed exclusively between 1,000 and 200 m. *C. amygdalina* was originally described from three anterior nectophores collected in Antarctic waters in the 400–0 m stratum (Moser 1925). Its presence in the 500–200 m stratum of the central stations suggests that it inhabits the upper mesopelagic layers in oceanic waters, while it is found beneath 500 m

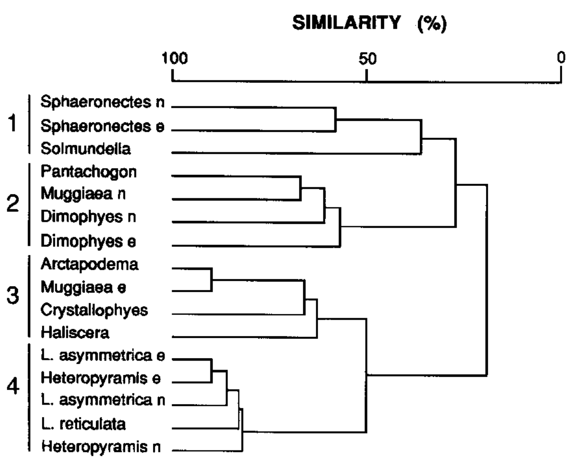



**Fig. 10** Dendrogram of similarities (using the Czekanowski index) between the most abundant species collected along the transect on the basis of their presence or absence. *1* refers to the species distributed in and above the thermocline. *2* comprises the species collected at all depths sampled. *3* refers to the species distributed exclusively below the thermocline. *4* consists in lower mesopelagic species (*n* nectophore, *e* eudoxid)

close to the continental shelf. Records of its vertical distribution (Leloup and Hentschel 1935; Totton 1954) show that it lives mainly between 250 and 750 m although it has been found down to a 2,320 m depth (Alvariño 1967).

The fact that the eudoxids of *M. bargmannae* were located deeper than the bulk of nectophores, below the thermocline, suggests that temperature may be a more important factor than prey availability for its reproduction. Carré and Carré (1991) showed that the reproduction of *M. kochi*, a similar species that inhabits warm waters, is strictly a function of temperature. During three weeks in the laboratory, development was accelerated and more eudoxids were produced after increasing the temperature from 18 to 24°C, while the polygastric stage was stationary and no eudoxids were produced at 13°C. Although *M. bargmannae* is a cold-water species, it is suggested that reproduction occurs in the upper range of its optimum temperature interval, at temperatures higher than 0°C.

4. Lower mesopelagic species (T = 0–0.6°C)

The siphonophores *Heteropyramis crytallina*, *Lensia asymmetrica* and *L. reticulata* belong to this group since they were only collected in the 1,000–500 m stratum. These small siphonophores have been collected previously, mainly at meso- and bathypelagic depths. In fact, it is probable that they also live even deeper in Antarctic waters, as the polygastric stage of *L. reticulata* was not collected in the present study. Nothing is known about their biology.

The five species groups mentioned show a clear partitioning of the siphonophore population throughout the water column. In the case of the medusae, we have considered only the most abundant species, *Pantachogon scotti* and *Arctapodema ampla*. The former predominated in and above the thermocline while the latter predominated below it. Both species belong to the same family and are similar in size and shape. The smaller umbrella:stomach size-ratio of *A. ampla* in comparison to *P. scotti* is the most obvious difference between both species. It is suggested that this is related to the feeding strategy of each species and their preferred type of prey. Microscopical examination of several specimens of *A. ampla* showed a considerable percentage of copepods in their stomachs. Feeding probably occurred in the net but we cannot quantify it. The large specimens (4–5 mm) contained copepodite stages III and IV (cephalothorax length 0.8–0.99 mm and 1.0–1.3 mm, respectively) of *Metridia gerlachei*. This species was distributed throughout the water column at all stations, but it was more abundant below the thermocline at the oceanic stations (Kurbjeweit 1993). The two species of medusae appear to have different vertical distributions that are probably related to hydrography and food preferences. On the one hand, *A. ampla* lives at temperatures above 0°C and has a large stomach for keeping and digesting all kinds of available prey below the thermocline, taking into account the decrease of prey density with depth and the low flux in organic matter from epipelagic layers. In contrast, although no prey items were found in the stomachs of *P. scotti*, the smaller size of its stomach suggests that it feeds on smaller prey, such as *Microcalanus pygmaeus* (0.3–0.7 mm cephalothorax length), which is concentrated in and above the thermocline.

In conclusion, vertical variations in distribution and abundance gave rise to a distinct partitioning of the mesoplanktonic cnidarian population throughout the water column. This vertical partitioning is considered to be caused by the existence of a thermocline, the structure of the water column and the vertical distribution of prey.

**Acknowledgements** We are grateful for the constructive comments made by J-M Gili, PR Pugh and SB Schiel on the first draft of the manuscript. We thank C Carré, A Clarke and CE Mills for their helpful and constructive comments on the original manuscript. Thanks are also given to M Klages and S Kühne for their help with the COMM program. Hydrographical data were provided by E Fahrbach and coworkers. Technical assistance was given by M Puls. The captain and crew of *RV Polarstern* provided their professional assistance. This work was supported by the Spanish Ministry of Education and Science (EX92 46331867). Contribution no. 639 of the Alfred-Wegener-Institut für Polar- und Meeresforschung.

## References

Alvariño A (1967) Bathymetric distribution of Chaetognatha, Siphonophorae, Medusae, and Ctenophorae off San Diego, California. Pac Sci 21:474–485

Apstein C (1908) Die Salpen der deutschen Südpolar-Expedition. Ergeb Dtsch Südpolar-Expedition 1901–03 (Zool 1):155–203

Atkinson A, Peck JM (1988) A summer-winter comparison of zooplankton in the oceanic area around South Georgia. Polar Biol 8:463–473

Båmstedt U (1990) Trophodynamics of the scyphomedusae *Aurelia aurita*. Predation rate in relation to abundance, size and type of prey organism. J. Plankton Res 12:215–229

Bathmann U, Schulz-Baldes M, Fahrbach E, Smetacek V, Hubberten H-W (1992) Die Expeditionen ANTARKTIS IX/1–4 des Forchungsschiffes "POLARSTERN" 1990/91. Ber Polarforsch 100:1–403.

Bouillon J, Boero F, Cicogna F, Gili JM, Hughes RG (1992) Non-Siphonophoran Hydrozoa: what are we talking about? Sci Mar 56:279–284

Boysen-Ennen E, Hagen W, Hubold G, Piatkowski U (1991) Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. Mar Biol 111:227–235

Browne ET (1910) Coelenterates. V. Medusae, National Antarctic Expedition. Nat Hist 5:1–62

Carré C, Carré D (1991) A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. Philos Trans R Soc London Ser B 334:27–32

Chojnacki J, Weglenska T (1984) Periodicity of composition, abundance, and vertical distribution of summer zooplankton (1977/78) in Ezcurra Inlet, Admiralty Bay (King George Island, South Shetland). J Plankton Res 6:997–1017

Clarke A, Peck LS (1991) The physiology of polar marine zooplankton. Polar Res 10:355–369

Clarke A, Holmes LJ, Gore DJ (1992) Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. J Exp Mar Biol Ecol 155:55–68

Foster BA (1989) Time and depth comparisons of sub-ice zooplankton in McMurdo Sound, Antarctica. Polar Biol 9:431–435

Foxton P (1966) The distribution and life history of *Salpa thompsoni* Foxton with observations in a related species, *Salpa gerlachei* Foxton. Discovery Rep 34:1–116

Hopkins TL (1985) Food web of an Antarctic midwater ecosystem. Mar Biol 89:197–212

Hopkins TL, Torres JJ (1988) The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. Polar Biol 9:79–97

Hopkins TL, Lancraft TM, Torres JJ, Donnelly J (1993) Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). Deep-Sea Res 40:81–105

Hubold G, Hempel I, Meyer M (1988) Zooplankton communities in the southern Weddell Sea (Antarctica). Polar Biol 8:225–233

Kramp PL (1957) Hydromedusae from the Discovery collections. Discovery Rep 29:1–128

Kurbjeweit F (1993) Reproduktion und lebenszyklen dominanter Copepodemanten aus dem Weddellmeer, Antarktis. Ber Polarforsch 129:1–238

Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). Polar Biol 9:225–233

Larson RJ (1986) Pelagic Scyphomedusae (Scyphozoa: Coronatae and Semaeostomae) of the Southern Ocean. Biology of the Antarctic Seas XVI. Antarct Res Ser 41:59–165

Legendre L, Legendre P (1979) Écologie Numérique. 2. La structure des Données Ecologiques. Masson, Paris

Leloup E, Hentschel E (1935) Die Verbreitung der calycophoren Siphonophoren im Südatlantischen Ozean. Dtsch Atl Expedition "Meteor" 12:1–31

Lohmann H, Buchmann A (1926) Die Appendicularien der Deutschen Südpolar-Expedition 1901–03. Ergeb Dtsch Südpolar-Expedition 18 (Zool 10):63–231

Mapstone GM, Arai MN (1992) Abundance and vertical distribution of siphonophores (Cnidaria) from the Central Strait of Georgia, British Columbia, during spring and summer. Contr Nat Sci 15:1–8

Margulis RY (1992) Siphonophora from the Indian Sector of the Antarctic (in Russian) In: The Antarctic. Committee Reports No. 30. Nauka, Moskow

Matsakis S, Conover RJ (1991) Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can J Fish Aquat Sci 48:1419–1430

Moser F (1909) Die Ctenophoren der Deutschen Südpolar-Expedition 1901–03. Ergeb Dtsch Südpolar-Expedition 11:1–192

Moser F (1925) Die Siphonophoren der Deutschen Südpolar-Expedition, 1901–03. Ergeb Dtsch Südpolar-Expedition 17 (Zool 9):1–541

Nast F (1986) Changes in krill abundance and in other zooplankton relative to the Weddell–Scotia Confluence around Elephant Island in November 1983. Arch Fisherei wiss 37:73–94

Pagès F, Gili JM (1989) Siphonophores (Cnidaria: Hydrozoa) collected during the "Magga Dan" Expedition (1966–67) from Africa to Antarctica. Sci Mar 53:53–57

Piatkowski U (1989) Macroplankton communities in Antarctic surface waters: spatial changes related to hydrography. Mar Ecol Prog Ser 55:251–259

Pielou EC (1984) The interpretation of ecological data. A primer on classification and ordination. John Wiley and Sons, New York

Pugh PR (1974) The vertical distribution of siphonophores collected during the SOND cruise, 1965. J Mar Biol Ass U.K. 54:25–90

Pugh PR (1989) Gelatinous zooplankton – the forgotten fauna. Prog Underwater Sci 14:67–78

Purcell JE (1981) Dietary composition and diel feeding patterns of epipelagic siphonophores. Mar Biol 65:83–90

Purcell JE (1982) Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). J Exp Mar Biol Ecol 62:39–54

Purcell JE (1983) Digestion rates and assimilation efficiencies of siphonophores fed zooplankton prey. Mar Biol 73:257–261

Purcell JE (1984) The function of nematocysts in prey capture by epipelagic siphonophores (Coelenterata, Hydrozoa). Biol Bull 166:310–327

Purcell JE, Kremer P (1983) Feeding and metabolism of the siphonophore *Sphaeronectes gracilis*. J Plankton Res 5:95–106

Siegel V, Skibowski A, Harm U (1992) Community structure of the epipelagic zooplankton community under the sea-ice of the northern Weddell Sea. Polar Biol 12:15–24

Sneath PH, Sokal RR (1973) Numerical taxonomy. The principles and practice of numerical classification. Freeman, San Francisco

Stepanjants SD (1970) Siphonophora of the southern part of the Kurile–Kamschatka Trench and adjacent marine areas. Trudy Inst Okeanol Akad Nauk SSSR 86:222–236 (translation of Russian text: 234–249)

Totton AK (1954) Siphonophora of the Indian Ocean together with systematic and biological notes on related species from other oceans. Discovery Rep 27:1–161

Tucker MJ, Burton HR (1990) Seasonal and spatial variations in the zooplankton community of an eastern Antarctic coastal location. Polar Biol 10:571–579

Weickert H, John H-C (1981) Experiences with a modified Be multiple opening-closing plankton net. J Plankton Res 3:167–177

Witek Z, Kittel W, Czykieta H, Zmijewska MI, Presler E (1985) Macrozooplankton in the southern Drake Passage and in the Bransfield Strait during BIOMASS-SIBEX (December 1983–January 1984). Pol Polar Res 6:95–115