# The composition, abundance, biomass and diversity of the epipelagic zooplankton communities of the southern Bellingshausen Sea (Antarctic) with special reference to krill and salps

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## Abstract

Zooplankton was sampled in the southern Bellingshausen Sea with RMT 1+8 gear during austral summer 1994. A total of 121 zooplankton species were found. Although zooplankton diversity was high in oceanic and neritic waters, abundances and biomass were among the lowest recorded for Antarctic epipelagic zooplankton. Copepods and chaetognaths dominated numerically, while chaetognaths and krill *Euphausia superba* dominated in biomass wet weight. *Salpa thompsoni* occurred in low densities (median 0.1 to 0.4/1000 $m^3$), although during the same period a mass development was recorded from the South Shetland Island region. Density values for *Euphausia crystallorophias* were in the same range as reported from the southern Weddell Sea. Krill, *Euphausia superba*, biomass was lower than generally found in the Antarctic Peninsula and Elephant Island region. A distinct spatial separation for size groups was observed for salps, *Euphausia crystallorophias* and krill. Small salp size groups dominated in the East Wind Drift zone and larger ones further north under the influence of West Wind Drift waters. Larger size classes of *E. crystallorophias* concentrated in nearshore areas. Krill was smaller in neritc and larger in oceanic waters. The overall krill length frequency distribution was similar to that reported from the South Shetland Island region for the same period. The recruitment index for *E. crystallorophias* and *Thysanoessa macrura* age group 1+ indicated a very successful year-class 1992/93 in the region ($R_1 = 0.412$ and $R_1 = 0.609$, respectively), while krill showed the opposite, a poor recruitment of the 1992/93 year class ($R_1 = 0.076$). Spawning was late during the 1994 season for *E. crystallorophias* and *E. superba*; no larvae were found in the area. These findings are discussed in the light of recently described correlations between winter sea-ice conditions and krill spawning and recruitment success, and lead to the conclusion that recruitment of the 1993/94 krill year-class will be poor.

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## Kurzfassung

**Die Zusammensetzung, Abundanz, Biomasse und Diversität der epipelagischen Zooplanktongemeinschaften der südlichen Bellingshausensee (Antarktis) unter besonderer Berücksichtigung von Krill und Salpen.**

In RMT 1+8 Netzfängen wurden im Sommer 1994 in der südlichen Bellingshausensee 121 Zooplankton Arten gefunden. Obwohl die Diversität im Plankton der ozeanischen und neritischen Zone hoch war, lagen Gesamtabundanz und Biomasse im untersten Bereich der bisher in der Antarktis gemessenen Werte. Copepoda und Chaetognatha waren numerisch dominant, während Chaetognatha und der Krill *Euphausia superba* nach Biomasse dominierten. *Salpa thompsoni* trat nur in geringen Dichten auf (Medianwert 0,1 bis 0,4 Individuen pro 1000 $m^3$), obwohl die Art im selben Zeitraum im Gebiet der Süd Shetland Inseln eine Massenentwicklung zeigte. *Euphausia crystallorophias* wies Dichteanzahlen auf, wie sie aus der südlichen Weddell See bekannt sind. Die Biomasse von *Euphausia superba* war geringer, als sie allgemein im Gebiet der Antarktischen Halbinsel und um Elephant Island gefunden wird. Eine deutliche geographische Trennung von Längengruppen wurde für Salpen, *E. crystallorophias* und den Krill beobachtet. Salpen geringer Größe dominierten in der Ostwinddrift Zone, während die größeren Längengruppen im Einflußbereich der Westwinddrift auftraten. Die großen Längengruppen von *E. crystallorophias* wurden überwiegend in Küstennähe angetroffen. Krill war über dem Schelf von deutlich geringerer Größe als in ozeanischen Bereichen. Die Gesamtlängenverteilung für Krill und der Bestandsaufbau zeigten eine Übereinstimmung zwischen der Bellingshausen See und dem Seegebiet um die Süd Shetland Inseln. Der Rekrutierungs-Index der Altersgruppe 1 von *E. crystallorophias* und *Thysanoessa macrura* deutet auf einen sehr erfolgreichen Jahrgang 1992/93 in der Region hin ($R_1$ = 0,412 bzw. $R_1$ = 0,609). Demgegenüber wies Krill für den Jahrgang 1992/93 eine schwache Rekrutierung auf ($R_1$ = 0,076). Das Laichen von *E. crystallorophias* und Krill fand in der untersuchten Saison 1994 sehr spät statt. Die vorliegenden Ergebnisse wurden in Verbindung mit kürzlich beschriebenen Abhängigkeiten zwischen Winter-Eisverhältnissen und dem Krilllaichen sowie Rekrutierungserfolg diskutiert.



## Résumé

**Composition, abondance et biomasse des communautés de zooplancton épipelagique de la Mer Bellingshausen du Sud (Antarctique) compte tenu des conditions particulières du krill et du salpe**

Au cours de l'été 1994, 121 espèces de zooplanctons ont été recueilli à l'aide d'un chalut en RMT 1+8 au Sud de la Mer Bellingshausen. Bien que la variété entre les communautés de plancton soit nombreuse dans les eaux océaniques et néritiques, l'abondance générale et la biomasse dans la région la plus basse se trouvaient en dessous du niveau des valeurs relevées jusqu'à présent dans l'Antarctique. Les Copepoda et Chaetognatha étaient en nombre dominant tandis que les Chaetognatha et le krill *Euphausia superba* dominaient en biomasse. La *Salpa thompsoni* apparurent en densité faible (valeur moyenne allant de 0,1 à 0,4 individus par 1 000 $m^3$), bien que l'espèce connaisse pour la même période un développement en masse au Sud des Iles Shetland. Les *Euphausia crystallorophias* montrèrent une densité proche de celle connue dans le Sud de la Mer Weddel. La biomasse de la *Euphausia superba* était plus faibles que celles rencontrées en général dans la région des Iles Antarctiques et de l'Ile de l'Eléphant. On distingua une coupure géographique nette par groupes de taille chez les salpes, *E. crystallorophia* et chez le krill. Les salpes de petites tailles dominent dans les eaux de courants à vents Est tandis que les groupes plus gros apparaissent plutôt dans les eaux influencées par les courants de vents Ouest. Les groupes plus importants des *E. crystallorophias* ont été rencontrés essentiellement proche des côtes. Le krill était de taille nettement plus petite que dans les eaux océaniques. La répartition de taille du krill et la structure des quantités montraient une similitude entre la Mer de Bellingshausen et des eaux aux alentours du Sud des Iles Shetland. L'index de recrutement par groupe d'âge 1 des *E. crystallorophias* et *Thysanoessa macrura* indique l'année 1992-1993 comme une année très bonne pour la région. (de $R_1$= 0,412 à $R_1$= 0,609). L'année 1992/93 était au contraire pour le crill une année très modeste ($R_1$= 0,076). Le frai des *E. crystallorophias* et du krill a eu lieu très tard pendant la saison 1994. Les résultats présentés ont été analysés en mettant en relation les dépendances entre l'état de la glace en hiver et le frai du krill ainsi que le succès de la recrue.

## Introduction

The Bellingshausen Sea remains one of the poorly known regions of the Southern Ocean. Long seasonal ice cover – even during summer the pack ice does not disappear from the shelf areas – make access to this remote region difficult. Relatively few data exist on the composition of the zooplankton in the Bellingshausen Sea and even less is known about quantitative aspects of the plankton community. However, this kind of information is essential for the discussion of the implications within the pelagic system and for higher trophic levels.

First basic geographical descriptions of the Bellingshausen Sea were given by Cook (1903) on the drift of the 'Belgica' in 1898/99 south of 69° S. From this cruise we also gain the first information on the occurrence of ice algae and large quantities of krill feeding on diatoms under the ice flows as well as the occurrence of krill in crabeater seal stomachs in the southern Bellingshausen Sea (Hansen 1908). Decades later, studies centered around the Antarctic Peninsula sampled limited areas of the eastern Bellingshausen Sea. During 1929-31 British expeditions with 'William Scoresby' and 'Discovery II' conducted plankton net sampling on stations running north of the ice edge westwards from Adelaide Island to a point beyond Peter I Island. Mackintosh (1934) reported sparse zooplankton in the waters of the eastern Bellingshausen Sea, while it was numerically richer to the west. He also mentioned the scarcity of euphausiids in the area. In his later publication Mackintosh (1973) found evidence for a Bellingshausen krill stock, because of a higher krill density in the area between 72° and 97° W.

Former Soviet Union cruises working in the Peninsula area also collected data from the open waters of the eastern Bellingshausen Sea, describing krill size composition (Makarov 1979), oceanographic conditions and geostrophic currents (Makarov *et al.* 1982) as well as krill biomass and distribution (Latogursky *et al.* 1990).

During austral summer 1978/79 a Polish research cruise covered the area along the Antarctic Peninsula and partly investigated the eastern Bellingshausen Sea. Results were published on phytoplankton and krill (Witek *et al.* 1982), occurrence of krill larvae (Witek *et al.* 1980) and acoustic observations on krill aggregations (Kalinowski and Witek 1980). The investigation of macroplankton samples collected during an Anglo-German expedition along the Antarctic Peninsula in February 1982 resulted in the description of different communities which also extended into the northern Bellingshausen Sea (Piatkowski 1989). An acoustic krill biomass survey was carried out in Nov/Dec 1992 during the British JGOFS cruise between 65° S to 69° S around 85° W just north of the marginal ice edge zone (Murray *et al.* 1995).

Almost each of these cruises concentrated on the northern part of the Bellingshausen Sea north of 69° S, i.e. outside the pack-ice zone and beyond the continental shelf of the Bellingshausen Sea. However, data of Murray *et al.* (in press), Makarov (1979), and Latogursky et al. (1990) show that the northern distribution limit of krill is gradually moving south to 67° S when moving west from the Peninsula to Peter I Island. For this reason, it was the intention of the 1994 'Polarstern' cruise to extend the studies from the open water areas into the poorly known permanently ice covered shelf areas, to describe the zooplankton composition, to support quantitative data on zooplankton density and biomass, and compare the stock composition of krill and salps with survey data collected simultaneously in regions further to the north.

## Material and Methods

Zooplankton was sampled onboard RV 'Polarstern' from January 25 to March 11, 1994 on 22 stations south of 66° S (Fig.1). Details on general scientific objectives of the cruise, station lists and cruise tracks are summarized by Miller (in press). Zooplankton was collected using the RMT 1+8 (single Rectangular Midwater Trawl). A detailed descrip-

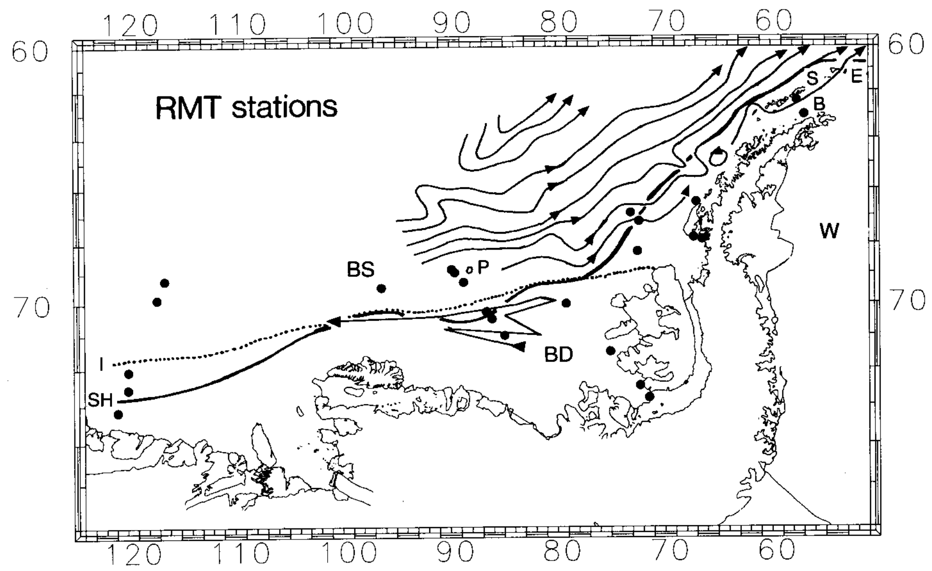



*Figure 1:* Geographical location of RMT sampling stations, geostrophic currents after Makarov *et al.* (1982), and BD = drift of the 'Belgica' in 1898/1899, the fast straight drift to the west occurred during the summer months. BS: Bellingshausen Sea, W: Weddell Sea, P: Peter I Island, E: Elephant Island, S: South Shetland Islands, B: Bransfield Strait, SH: shelf break, I: ice edge in January-March 1994

tion of the net system is given by Baker et al. (1973). Standard oblique tows were made for the depth stratum 0 to 200 m. Filtered water volumes were calculated considering net speed, net angle and flow data according to Pommeranz *et al.* (1982). The net was deployed in open water and in leads within in pack-ice zone. When sampling in ice a sufficient sized area of free water was formed behind the ship by propeller action to allow deployment and retrieval of the net from the stern. When the net reached a depth of 20 m during hauling, the propeller was stopped to minimize the effects on the net operations and to avoid damage of the samples.

Immediately after each haul samples were stored in 4% buffered formalin seawater solution. Sorting, counting and measuring was carried out a few days later onboard ship. Taxa were identified to the species level, adult fish were excluded from the analysis, because their abundance is strongly affected by net avoidance. Species biomass and abundances were standardized to grams or numbers per 1000 $m^3$. Wet weight was generally measured from formalin preserved material in the lab after the cruise, while salps were weighed onboard immediately after the haul. The RMT 1 and RMT 8 nets (mesh sizes 320 $\mu$m and 4.5 mm, respectively) collect a broad size range of zooplankton and samples from both nets were analyzed for this study. Standardized abundance values of each species were compared for both nets, and in each case the higher standardized abundance value was considered to minimise effects of net selection.

Length frequency distributions were produced for euphausiids, measured as total length from the anterior margin of the eye to the tip of the telson for krill and from the tip of the rostrum to tip of the telson for the other species. Length measurements for salps refer to body length according to Foxton (1966). Maturity stages were determined following the classification of Makarov and Denys (1981).

Several diversity indices were calculated to characterize the zooplankton community in different subareas. The most simple and unambiguous index is species richness S, which gives the total number of species in a sample. The Shannon-Wiener index H′ is maximum when all species are represented by the same number of individuals. H′ is zero if there is only one species in the sample. The N2 index measures the number of very abundant species and is based on Simpson's index. For the evenness index we used the modified Hill's ratio E5, because this index is relatively unaffected by the number of species in the sample and tends to be independent of sample size. E5 approaches 1 as number of individuals become more and more evenly distributed among species or zero as a single species becomes dominant. Further details on indices and formulas as well as the software to calculate the indices are given by Ludwig and Reynolds (1988).

The MIX programme of Macdonald and Pitcher (1979) was applied to length frequency data for the distribution mixture analysis of size groups. Variables of the age class 1 component were calculated by stepwise optimization, *i.e.* proportion, mean length and sigma and their standard errors. The recruitment index $R_1$ was determined according to de la Mare (1994). All other statitistical procedures were carried out using the software package CSS Statistica.

## Results

A total of 121 zooplankton species were counted from 22 samples in the epipelagic water layer. The largest taxonomic group was represented by copepods which consisted of 31 species. Ranking second was the group of pelagic fish larvae, with 23 species. Hyperiids and polychaetes each contributed 11 species. A complete species list is presented in Table 1.

### *Diversity of zooplankton*

Species richness, diversity and evenness were calculated separately for shelf and oceanic stations. A Mann-Whitney U test was carried out between the two groups for each of the variables. None of the variables showed a significant difference between shelf and oceanic areas (Richness: $Z = -0.791$ , p-level = 0.429; H': $Z = -1.912$, p-level = 0.060; N2: $Z = -1.583$, p-level = 0.114; E5: $Z = -0.396$, p-level = 0.692). For this reason data from all stations were pooled and recalculated. Results are listed in Table 2 together with results from a study in oceanic waters of the southern Scotia Sea/northern Weddell Sea in 1988 (Siegel *et al.* 1992) for which precisely the same methods were applied. For a direct comparison indices were recalculated from the original data set for the 200 m water layer of the northern Weddell Sea.

Mean species richness was higher in the Bellingshausen Sea (S = 35) than in the open water and the pack-ice zone (S = 31) of the Weddell Sea. The mean partly reflects the difference in total number of species between the regions, which was evidently higher in the Bellingshausen Sea (120 versus 88 species in the Weddell Sea). This difference can mostly be explained by the higher number of copepod (7 species) and the larvae of neritic fish species (14 species) in the Bellingshausen Sea.

The diversity H′ for the Bellingshausen samples is very similar to the results found in the northern Weddell Sea. If only the upper 60 m beneath the closed ice cover is considered, then the diversity is much lower in the northern Weddell Sea. The N2 index is heavily weighted toward the most abundant species in the samples while being less sensitive to species richness. A low N2 value means a high dominance of few species. The relatively low N2 diversity index indicates a dominance of few species in the catches from the Bellingshausen and Weddell Seas. Interestingly the index was highest in the transition belt, the marginal ice zone of the Weddell Sea, demonstrating a more uniform species composition. In general the majority of species were rare.

The rank abundance plot is one graphical method of presenting species abundance data in which percentage abundance is plotted against species rank (see Magurran 1988). The plot for the Bellingshausen community illustrates the typical shape of the log series curve, while the species abundances from the closed pack-ice zone of the northern Weddell Sea follows the geometric series model (Fig. 2). In general the figure shows that the majority of species in the Bellingshausen Sea are rare. Under the closed pack-ice of the Weddell Sea the situation shifts to an extreme with very few abundant and some rare species.

*Table 1:* Species list. Asterisks indicate species which occurred only once in the samples.

**Hydrozoa**
*Calycopsis borchgrevinki*
**Haliscera conica*
**Haliscera racovitzae*
**Russellia mirabilis*
**Solmundella bitentaculata*
**Scyphozoa**
*Periphylla periphylla*
**Siphonophora**
*Dimophyes arctica*
*Diphyes antarctica*
**Marrus antarcticus*
*Pyrostephos vanhoeffeni*
**Vogtia serrata*
**Ctenophora**
**Beroe cucumis*
*Beroe forskalii*
**Cephalopoda**
*Alluroteuthis antarcticus*
**Gastropoda**
*Clio pyramidata*
*Clione limacina*
*Limacina helicina*
*Spongiobranchaea australis*
**Polychaeta**
**Bylgides pelagica*
**Lopadorrhynchus appendiculatus*
*Maupasia gracilis*
*Pelagobia longicrrata*
*Rhynchonereella bongraini*
*Sagitella kowalevskii*
*Tomopteris carpenteri*
**Tomopteris septentrionalis*
**Travisiopsis coniceps*
**Travisiopsis levinseni*
*Vanadis antarctica*
**Copepoda**
*Aetideopsis minor*
**Bathycalanus bradyi*
*Bathycalanus princeps*
*Calanoides acutus*
*Calanus propinquus*
*Candacia maxima*
*Ctenocalanus citer*
*Euaugaptilus antarcticus*
**Euaugaptilus parantarcticus*
*Euchirella rostromagna*
*Gaidius intermedius*
*Gaidius tenuispinus*
*Heterorhabdus farrani*
*Heterorhabdus papilliger*
**Heterorhabdus pustulifer*
*Lucicutia flavicornis*
*Lucicutia wolfendeni*
*Metridia gerlachei*
*Metridia lucens*
**Microcalanus pygmaeus*
*Paraeuchaeta antarctica*
*Paraeuchaeta biloba*
**Paraeuchaeta farrani*
*Paraeuchaeta rasa*
**Pleuromamma robusta*
*Pseudochirella mawsoni*
*Rhincalanus gigas*
*Scaphocalanus antarcticus*
**Scaphocalanus parantarcticus*
*Scolecithricella dentipes*
*Scolecithricella minor*
**Ostracoda**
*Alacia belgicae*
*Alacia hettacra*
**Boroecia antipoda*
**Metaconchoecia isocheira*
*Metaconchoecia skogsbergi*
**Euphausiacea**
*Euphausia crystallorophias*
*Euphausia superba*
*Euphausia triacantha*
*Thysanoessa macrura*
**Decapoda larvae**
*Acanthephyra pelagica*
*Chorismus antarcticus*
**Notocrangon antarcticus*
**Mysidacea**
**Antarctomysis maxima*
**Antarctimysis ohlini*
**Euchaetomera zurstrasseni*
**Hyperiidea**
*Cyllopus lucasii*
*Cyllopus magellanicus*
**Hyperia antarctica*
*Hyperia macrocephala*
*Hyperiella dilatata*
*Hyperiella macronyx*
**Hyperoche medusarum*
*Primno macropa*
**Scina antarctica*
*Themisto gaudichaudii*
*Vibilia antarctica*
**Gammaridea**
*Epimeriella macronyx*
*Eusirus antarcticus*
*Eusirus microps*
*Eusirus propeperdentatus*
*Orchomene plebs*
**Orchomene rossi*
**Chaetognatha**
*Eukrohnia hamata*
*Sagitta gazellae*
*Sagitta marri*
*Sagitta maxima*
**Tunicata**
*Salpa thompsoni*
*Ihlea racovitzai*
**Pisces larvae**
**Artedidraco loennbergi*
**Artedidraco orianae*
**Artedidraco skottsbergi*
**Bathydraco antarcticus*
**Chaenodraco wilsoni*
*Chionodraco rastrospinosus*
**Cryodraco antarcticus*
**Dacodraco hunteri*
*Electrona antarctica*
*Lepidonotothen kempi*
**Lepidonotothen larseni*
**Muraenolepis microps*
*Notolepis annulata*
*Notolepis coatsi*
**Pagetopsis macropterus*
*Pleuragramma antarcticum*
**Pogonophryne marmorata*
**Prionodraco evansii*
**Psilodraco breviceps*
**Racovitzia glacialis*
**Trematomus lepidorhinus*
**Trematomus newnesi*
**Trematomus scotti*

Table 2: Mean species richness, diversity and evenness for zooplankton in the Bellingshausen Sea. Results from a study in the oceanic region of the northern Weddell Sea (from Siegel *et al.* 1992 and * recalculated from original data for 0 to 200 m depth) are listed for comparison. OW = open water, TRANS = outer and inner marginal pack-ice zone, CP = closed pack-ice zone.

| Index | Bellingshausen Sea | Weddell Sea | | | | |
|---|---|---|---|---|---|---|
| | Sea | OW | OW* | TRANS | CP | CP* |
| | 0-200 m | 0-60 m | 0-200 m | 0-200 m | 0-60 m | 0-200 m |
| Richness S | 35.2 | 26.0 | 31 | 27.8 | 17.4 | 31 |
| Diversity H' | 1.997 | 1.743 | 1.923 | 2.128 | 1.435 | 1.985 |
| Diversity N2 | 5.41 | 4.71 | 4.95 | 6.12 | 3.56 | 5.25 |
| Eveness E5 | 0.58 | 0.64 | 0.56 | 0.63 | 0.57 | 0.58 |

### *Distribution, dominance and abundance*

In the Bellingshausen Sea 46 of the recorded species were only found at one or two stations and therefore have a constancy of less than 10 % . These are marked with an asterisk in Table 1. Only 8 species had a very wide distribution and were observed at more than 90 % of all stations. These were the copepods *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus*, *Metridia gerlachei*, the chaetognaths *Eukrohnia hamata*, *Sagitta gazellae*, the euphausiid *Thysanoessa macrura* and the siphonophore *Diphyes antarctica*. Except for the siphonophore these species were also the ones with the highest abundances.

*Several investigations identified the existence of a neritic and an oceanic plankton community in Antarctic waters (e.g.* Boysen-Ennen and Piatkowski 1988; Piatkowski 1989; Siegel and Piatkowski 1990; Hosie 1994). We calculated the abundances separately for the shelf and oceanic stations. Due to the non-normal frequency distribution of the species abundance data we preferred the median instead of the mean abundance. Zero

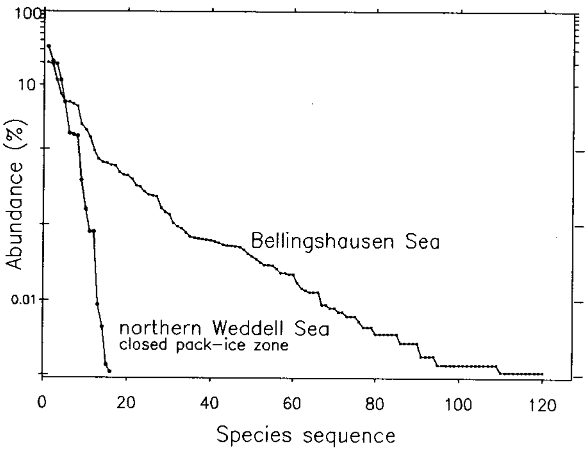



*Figure 2:* Species rank abundance plot for data from the Bellingshausen Sea (present study) and the closed pack-ice zone of the northern Weddell Sea (data from Siegel *et al.* 1992).

catches were included in the calculation of the median. Results for the more abundant species are listed in Table 3. Among the six dominant species we found four copepod and two chaetognath species contributing 80 % of the total number of zooplankton specimens, with *Calanoides acutus* (37.6 %) dominating numerically in the neritic zone. *Thysanoessa macrura* (2.6 %) was ranked seventh, krill twelvth and *Euphausia crystallorophias* fourteenth. *Euphausia crystallorophias* was clearly restricted to neritic waters, as were larvae of almost all fish species. However, even these and other neritic indicator species (*Antarctomysis* spp, Gammaridea, *Pleuragramma antarcticum*) occurred in very low densities, or the distribution was extremely patchy resulting in a low median abundance as for *Euphausia crystallorophias*.

*Table 3:* Median abundances (in n/1000 m$^3$) for the dominant species in oceanic and neritic waters of the Bellingshausen Sea. Results from a study in the oceanic region of the northern Weddell Sea (from Siegel *et al.* 1992) are listed for comparison, abbreviations see Table 2.

| Species | Bellingshausen Sea | | Weddell Sea | | |
|---|---|---|---|---|---|
| | Neritic | Oceanic | OW 0 - 60 m | TRANS 0 - 200 m | CP 0 - 60 m |
| *Calanoides acutus* | 66.4 | 38.5 | 947.6 | 45.5 | 11.0 |
| *Calanus propinquus* | 23.1 | 28.0 | 459.8 | 40.9 | 36.1 |
| *Metridia gerlachei* | 15.4 | 45.6 | 271.0 | 7.5 | 4.0 |
| *Eukrohnia hamata* | 14.5 | 2.9 | 31.8 | 37.9 | 4.1 |
| *Sagitta gazellae* | 11.7 | 9.1 | 3.7 | 10.9 | 0.4 |
| *Rhincalanus gigas* | 9.9 | 16.0 | 2988.9 | 24.7 | 22.0 |
| *Thysanoessa macrura* | 4.6 | 2.5 | 144.1 | 36.7 | 38.8 |
| *Lucicutia flavicornis* | 4.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Alacia belgicae* | 4.2 | 2.1 | 0.0 | 1.4 | 0.0 |
| *Dimophyes arctica* | 3.4 | 0.6 | 0.0 | 0.0 | 0.0 |
| *Paraeuchaeta antarctica* | 2.9 | 1.5 | 0.0 | 0.0 | 0.0 |
| *Euphausia superba* | 2.7 | 0.2 | 0.9 | 2.6 | 62.4 |
| *Scolecithricella dentipes* | 2.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Euphausia crystallorophias* | 2.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pyrostephos vanhoeffeni* | 2.0 | 1.1 | 0.0 | 0.0 | 0.0 |
| *Limacina helicina* | 1.6 | 0.2 | 113.8 | 0.5 | 0.2 |
| *Heterorhabdus farrani* | 1.4 | 2.3 | 0.0 | 0.0 | 0.0 |
| *Alacia hettacra* | 1.4 | 0.2 | 40.8 | 18.8 | 0.2 |
| *Salpa thompsoni* | 0.4 | 0.1 | 101.0 | 2.0 | 0.0 |
| *Hyperiella dilatata* | 0.0 | 0.1 | 16.3 | 0.0 | 0.0 |
| *Euphausia frigida* | | | 43.2 | 0.0 | 0.0 |
| *Vibilia antarctica* | 0.0 | 0.0 | 30.5 | 0.0 | 0.0 |
| *Tomopteris septentrionalis* | 0.0 | 0.0 | 34.1 | 0.0 | 0.0 |
| *Pleuromamma robusta* | 0.0 | 0.0 | 16.4 | 0.0 | 0.0 |
| Median total | 176.8 | 155.1 | 5277.7 | 245.3 | 180.6 |
| Mean total | 576.8 | 981.3 | | | |

The abundance of the dominant species did not differ noticably between shelf and oceanic stations. *Metridia gerlachei* (29.4 %) replaced *Calanoides acutus* (24.8 %) as the dominant species in the oceanic region. Chaetognaths were less abundant in oceanic waters, while *Rhincalanus gigas* occurred in higher densities further to the north. *Thysanoessa macrura,* a common species around the Antarctic continent, occurred everywhere in the study area, but only in relatively small quantities. *Euphausia triacantha* was found at only three of the northernmost oceanic stations.

Comparison with the results from a cruise to the oceanic southern Scotia Sea/northern Weddell Sea in spring 1988/89 clearly demonstrates the overall low total abundance of zooplankton in the Bellingshausen Sea (Table 3). Even the maxima for single stations in the Bellingshausen Sea (577 plankton specimens/1000 $m^3$ at one shelf station and 981/1000 $m^3$ for an oceanic station) were one order of magnitude lower than the overall median abundance found in the open water of the Scotia/Weddell Sea area (5277 specimens/1000 $m^3$). The Bellingshausen Sea plankton reached only the abundance level of the very poor plankton community under the pack ice of the northern Weddell Sea.

*Table 4:* Median wet weight (in g/1000 $m^3$) for the dominant species in oceanic and neritic waters of the Bellingshausen Sea. Results from a study in the oceanic region of the northern Weddell Sea (from Siegel *et al.* 1992) are listed for comparison. OW = open water, TRANS = outer and inner marginal pack-ice zone, CP = closed pack-ice zone.

| Species | Bellingshausen Sea Neritic | Bellingshausen Sea Oceanic | Weddell Sea OW 0 - 60 m | Weddell Sea TRANS 0 - 200 m | Weddell Sea CP 0 - 60 m |
|---|---|---|---|---|---|
| *Sagitta gazellae* | 1.64 | 1.27 | 0.37 | 1.09 | 0.04 |
| *Euphausia superba* | 1.52 | 0.15 | 0.49 | 1.43 | 34.32 |
| *Salpa thompsoni* | 0.73 | 0.14 | 101.00 | 2.00 | 0.00 |
| *Dyhyes antarctica* | 0.39 | 0.46 | 0.09 | 1.26 | 0.41 |
| *Dimophyes arctica* | 0.31 | 0.06 | 0.00 | 0.00 | 0.00 |
| *Eukrohnia hamata* | 0.27 | 0.06 | 0.38 | 0.46 | 0.05 |
| *Pyrostrephos vanhoeffeni* | 0.26 | 0.20 | 0.00 | 0.00 | 0.00 |
| *Calanoides acutus* | 0.26 | 0.15 | 3.32 | 0.16 | 0.04 |
| *Thysanoessa macrura* | 0.18 | 0.08 | 7.21 | 1.83 | 1.94 |
| *Calanus propinquus* | 0.12 | 0.14 | 2.53 | 0.23 | 0.20 |
| *Euphausia crystallorophias* | 0.12 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Rhincalanus gigas* | 0.11 | 0.18 | 28.39 | 0.23 | 0.21 |
| *Paraeuchaeta antarctica* | 0.03 | 0.02 | 0.00 | 0.00 | 0.00 |
| *Metridia gerlachei* | 0.03 | 0.00 | 0.30 | 0.01 | 0.00 |
| *Sagitta maxima* | 0.02 | 0.01 | 0.00 | 0.00 | 0.00 |
| *Sagitta marri* | 0.01 | 0.01 | 0.04 | 0.00 | 0.00 |
| *Heterorhabdus farrani* | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 |
| *Epimeriella macronyx* | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Alacia belgicae* | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Themisto gaudichaudii* | 0.00 | 0.13 | 0.11 | 0.00 | 0.00 |
| Median total | 6.03 | 3.07 | 149.73 | 9.12 | 37.35 |

### *Biomass*

Median total biomass of zooplankton was extremely low with a slightly higher biomass in neritic areas (6.03 g/1000 $m^3$) than in the oceanic region (3.07 g/1000 $m^3$). These values were of a similar magnitude to the marginal ice zone of the northern Weddell Sea in 1988, but were much lower than in the open water and closed pack-ice zone (Table 4). In the open water zone of the Weddell Sea salps contributed 67.5 % to the total zooplankton biomass of 149.73 g/1000 $m^3$. In the closed pack-ice zone krill dominated the zooplankton biomass by 92 % (37.35 g/1000 $m^3$); the remaining zooplankters contributed only 3 g/1000 $m^3$.

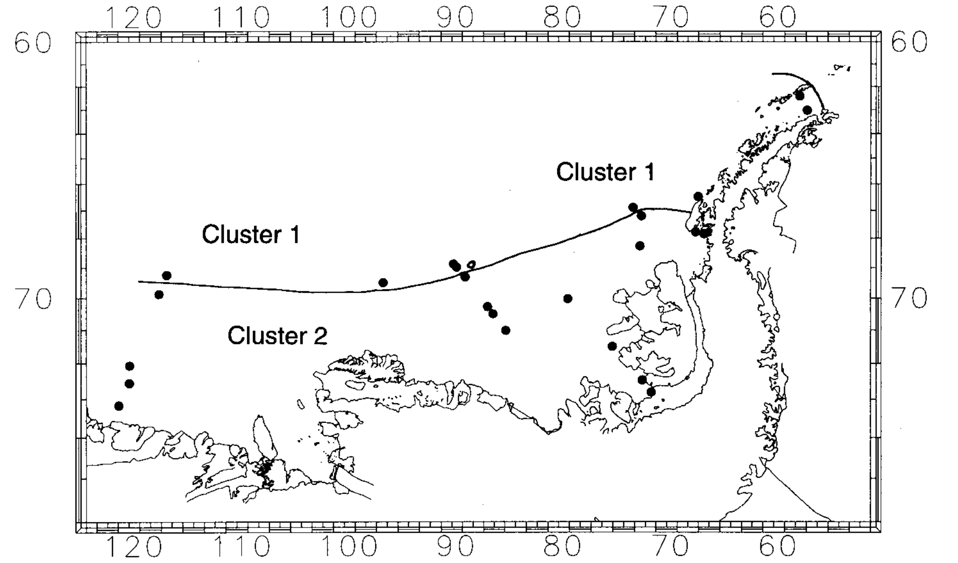
*Krill and salps regularly occurred in the samples of the Bellingshausen Sea, and interestingly they followed the chaetognath Sagitta gazellae* in the dominance of biomass. However, dominance values for krill and salps were not substantially high in neritic waters (25.2 % and 12.1 % respectively) and even lower at oceanic stations. In the oceanic region several siphonophore and copepod species added more, or at least the same, wet weight to the zooplankton standing stock (Table 4). Median biomass of *Euphausia crystallorophias* was as low as 0.12 g/1000 $m^3$, not exceeding 2 % dominance in biomass, although this species regularly occurred in the shelf samples. For neritic waters again siphonophores (15.9 %) and copepods (9.3 %) contributed more to the zooplankton standing stock than this typical neritic euphausiid species, and even *Thysanoessa macrura* showed a slightly higher biomass (3 % dominance).

### *Salps*

Salps occurred in 68 % of the samples from the Bellingshausen Sea, but median abundance was low in offshore and shelf waters (0.1 and 0.4 salps/1000 $m^3$, respectively). Maximum salp abundance in the Bellingshausen Sea was less than 51 salps/1000 $m^3$. This was a striking contrast to the findings at two stations further north in the Bransfield Strait (see Fig. 1), where salps showed a mass occurrence. These catches yielded 161 salps/1000 $m^3$ (358 g/1000 $m^3$) and 263 salps/1000 $m^3$ (1134 g/1000 $m^3$). This resulted in a numerical dominance of 72.9 – 73.2 % or a biomass dominance of 96.5 – 98.9 % of salps in the Bransfield Strait catches.

Salp body length data were collected from both areas and length data were submitted to a hierarchical cluster analysis using relative frequencies of length classes as station parameters to distinguish possible differences in distribution patterns. The Euclidean coefficient was used as the dissimilarity coefficient and clustering was done by the minimum variance linkage rule (Ward's method). At a distance level of 0.60, the size frequency distributions of salps clustered into two distinct groups of stations. There was a strong spatial coherence of the two groups (Fig. 3a), with group 1 located along the Antarctic Peninsula and including the northernmost oceanic stations to the west, while group 2 was restricted to an area south of a line from Adelaide Island to Peter I Island. The modal size of the groups differed by approximately 24 mm body length (Fig 3b). Group 1 in the northern region was the larger sized ($L \approx 40$ mm). Group 2 was distinctly smaller ($L \approx 16$ mm).

a)




b)

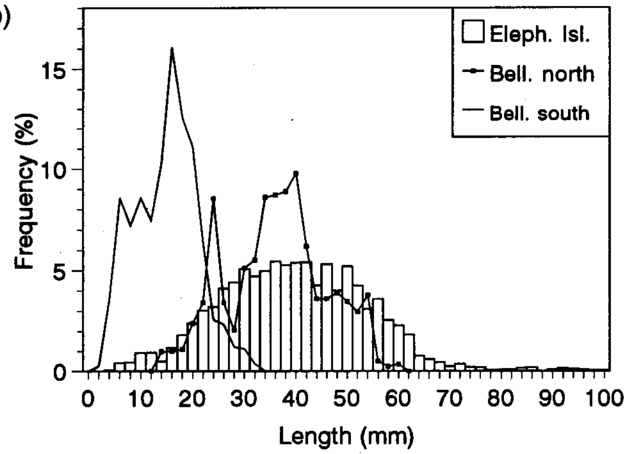



*Figure 3: a)* Spatial distribution of size groups of *Salpa thompsoni* from the southern (cluster 2) and northern Bellingshausen Sea/Bransfield Strait area (cluster 1) during January to March 1994. *b)* Length frequency distribution (body length).

## *Krill and other euphausiids*

Thysanoessa macrura was present in 91 % of all samples. Maximum abundance in the Bellingshausen Sea reached 47 specimens/1000 m$^3$, but the species showed no preference for shelf or oceanic areas. Due to the early spawning season of this species, larvae had already progressed to the furcilia stage. However, larvae were only found at three northern oceanic stations with high densities between 867 and 991 specimens/1000 m$^3$, respectively). Length of the larvae ranged from 3 to 7 mm and this group was clearly separated from the one year old juveniles of 10 to 16 mm length (Fig. 4).

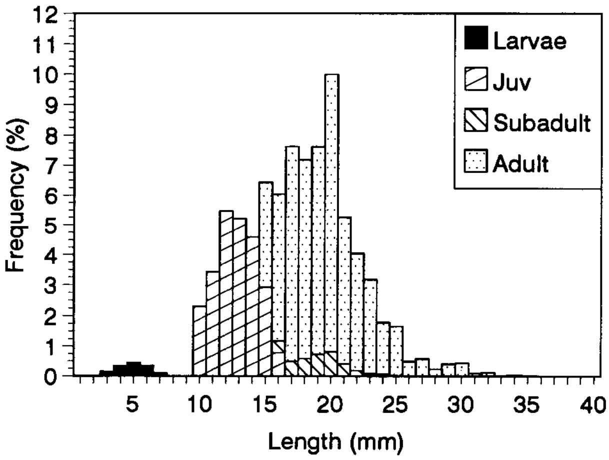



*Figure 4:* Length frequency distribution of *Thysanoessa macrura* from the Bellingshausen Sea during January/March 1994.

The recruitment index was calculated for age group 1 using the formula given by de la Mare (1994). The index can range between 0 (no recruitment) to 1 (stock consists only of recruits). For further details on the estimation of the index see de la Mare (1994) and Siegel and Loeb (1995). This value was relatively high for *Thysanoessa macrura* with $R_1 = 0.609$ ($S_E = 0.046$) indicating a very successful year-class 1992/93. Adult stages dominated the stock with a modal size of 20 mm. 0.5 % of the adult females represented the recently spent maturity stage, while 93 % had already recovered from spawning and belonged to the resting stage.

*Euphausia crystallorophias* was absent at all oceanic stations but did occur in all but one sample from the neritic zone (92 % constancy). However, abundance was extremely patchy. Maximum densities were recorded in nearshore shelf areas, *e.g.* exceeding 310 specimens/1000 m$^3$ in Marguerite Bay (Adelaide Island), whereas outer shelf areas were less densly populated, generally less than 3 specimens/1000 m$^3$. There are indications that larger specimens dominated in nearshore waters (group 2, Fig 5), while smaller size classes were more abundant in the outer shelf zone (group 1, Fig.5).

The overall length frequency distribution is characterized by the strong juvenile mode around 15 mm, representing age group 1+ (Fig. 5). The recruitment index for the 1992/93 year-class was relatively high, $R_1 = 0.412$ ($S_E = 0.006$). A second mode at 26 mm consisted of subadults and adults. 32 % of the adult females were carrying spermatophores and were still in the process of spawning, while 31 % were spent. No advanced larval stages were caught during this study.

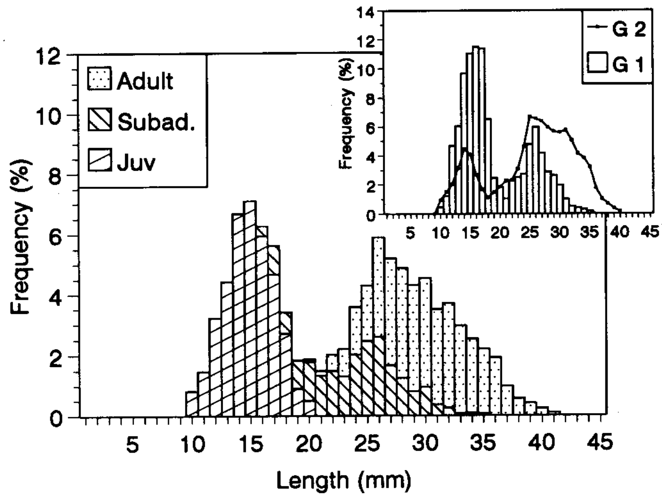



*Figure 5:* Length frequency distribution of *Euphausia crystallorophias* from the shelf areas of the Bellingshausen Sea. Inserted figure shows the difference in length frequencies between Group 1 and Group 2 occurring in outer and inner shelf zones, respectively.

The krill *Euphausia superba* was present in most (86 %) of the samples from oceanic and ice covered neritic waters. Maximum density was measured at station 45 (278/1000 m$^3$) in oceanic, ice-free waters east of Peter I Island. However, abundance was extremely low in the region west of Peter I Island. Cluster analysis on dissimilarity of length frequency distributions separated two distinct groups at a distance level of 0.7. Group 1 was represented by stations located on the southern shelf and around the shelf break (Fig.6a). These samples included a higher proportion of age group 1+ specimens (23.1 %) and the modal size of adults was about 45 mm. Group 2 consisted only of oceanic stations. In this cluster krill age class 1+ was scarse and adult krill dominated the offshore waters. Furthermore, this group showed a shift to larger adult animals with a modal size of 50 mm (Fig. 6b).

The overall length frequency distribution (Fig. 6c) shows the relatively low abundance of age group 1+ specimens in the region. The recruitment index was $R_1 = 0.076$ ($S_E$ = 0.011). Mean length of one year recruits was 23.6 ± 2.20 mm. Juveniles made up 9.4 % of the stock, subadults 47.8 %, and adults 42.8 %. Most of the adult females (36.6 %) belonged to the prespawning stage 3A (adult without spermatophores). Since gravid (stage 3D) and recently spent females (stage 3E) were absent (Fig. 6d), one can conclude that the krill stock was still in an early process of spawning, which is confirmed by the absence of any surface larval stages during the study period.

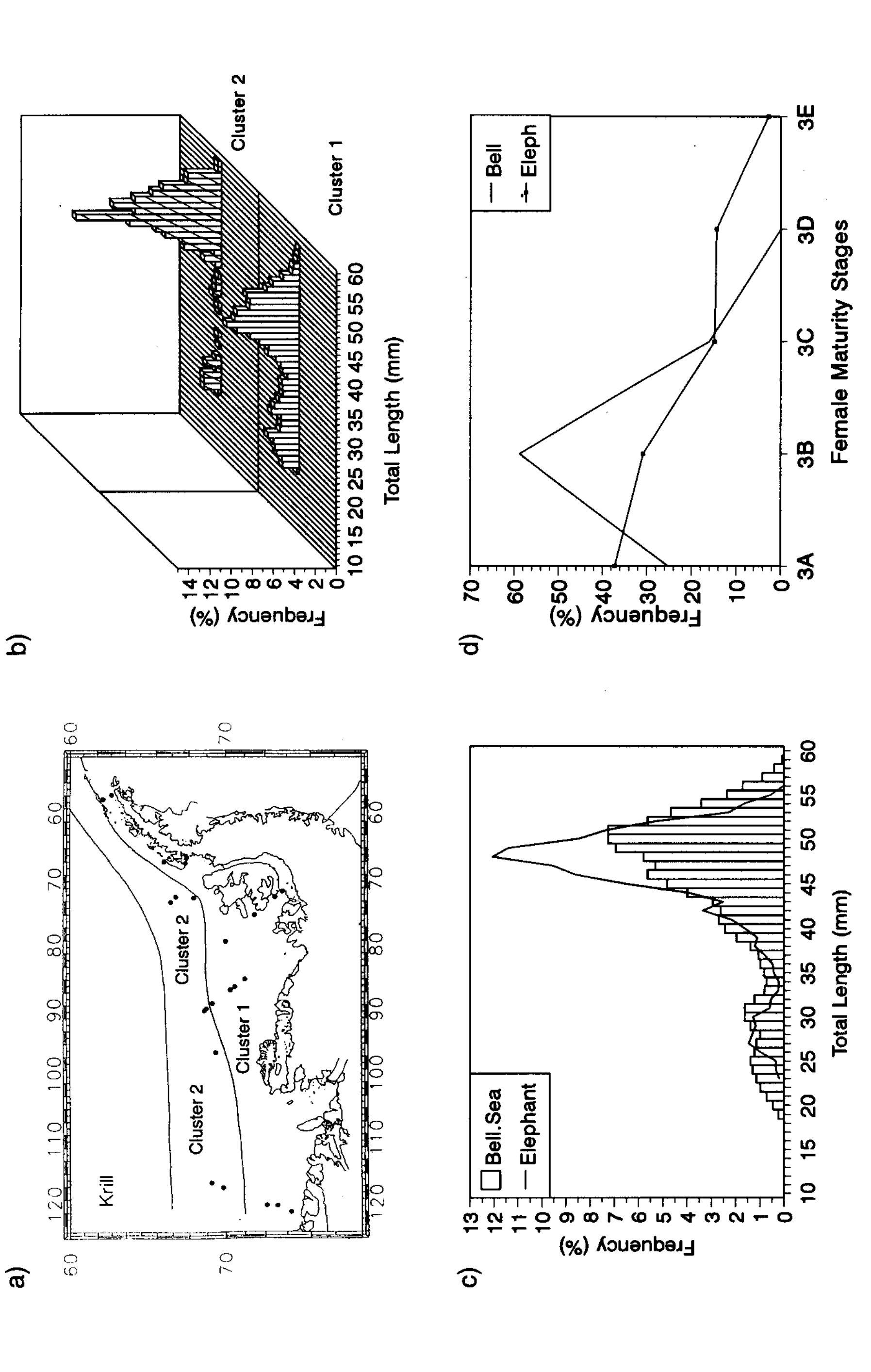



*Figure 6:* a) Spatial distribution of krill *Euphausia superba* length clusters in the Bellingshausen Sea; b) Krill length frequency distribution for different clusters; c) overall krill length frequency distribution in the Bellingshausen Sea and around Elephant Island; d) relative frequency of adult female maturity stages in the Bellingshausen Sea and around Elephant Island (data from Elephant Island after Anonymous 1995).

## Discussion

Mean species richness of zooplankton was similar in the Bellingshausen Sea and in the northern oceanic Weddell Sea (Siegel *et al.* 1992), although the total number of species was obviously higher in the Bellingshausen Sea. The lower number of zooplankton species in the Weddell Sea area may be explained by the early spring situation when many species still live in deeper water layers and have not started their seasonal vertical migration (Mackintosh 1937, Voronina 1973). This is supported by the observations from the northern Weddell Sea, when deeper water layers (down to 200 m) are included in the analysis (see Table 2). Furthermore, summer data from the eastern and southern Weddell Sea showed that the species richness was almost as high as in the Bellingshausen Sea (Boysen-Ennen and Piatkowski 1988).

Zooplankton diversity indices were again very similar between the two regions. Only the transitional zone (marginal pack-ice zone of the northern Weddell Sea) showed higher diversities, because dominance of single species was less pronounced in this zone. On the other hand, studies carried out along the Antarctic Peninsula in the seasonal pack-ice zone indicated a generally lower species diversity index (mean $H' = 0.350$ to 1.649) than for the Bellingshausen community ($H' = 1.997$). The oceanic and shelf areas of the Peninsula region are known for high dominance of krill, *Thysanoessa macrura* or salps (Piatkowski 1989; Siegel and Piatkowski 1990), which results in a lower diversity index.

Ice cover has been shown to have a strong effect on the occurrence of species (Siegel *et al.* 1992). Species abundances decreased rapidly when entering the pack-ice of the northern Weddell Sea and species that were rare in oceanic open waters disappeared under the closed pack-ice. Poor food resources in the water column under the ice probably prevent most species from colonizing these waters, because they are generally not capable of utilizing the ice algae, the only sufficient food resource.

The oceanic closed pack-ice zone supports only poor resources, with ice algae in late winter and spring. With the exception of krill only very few zooplankton species seem to be able to utilize this resource (there may be other species, but we have no information on the species level about their ability to use or depend on this resource), and thus krill is becoming the dominating element in the community. However, despite the described relative diversity of this community, abundances are generally low, because species cannot sustain high numbers and biomass.

Results from other investigations on zooplankton biomass are listed in Table 5. Comparisons are difficult, because of different size fractions of the studied zooplankton, different gear sizes and different vertical extent of sampling. Some investigators included the mesopelagic zooplankton in their calculations, a community which was found to have a higher diversity than the epipelagic one (Hardy and Gunther 1935; Siegel and Piatkowski 1990), but probably has a lower standing stock. Some studies excluded salps and euphausiids from their biomass estimates, because of the pronounced net avoidance of larger zooplankton species to small plankton nets. Both approaches reduce the biomass estimates for the epipelagic plankton quite substantially, so that these results must be considered as minimum zooplankton biomass estimates.

*Table 5:* List of zooplankton biomass data from Antarctic waters. Results in brackets are transformed data by Boysen-Ennen *et al.* (1991). Figures indicated with asterisks are median values, while others are means.

| Region | Latitude | Depth | Dry weight g/m | Wet weight g/m | Wet weight g/1000 m³ | Dominant species | Reference |
|---|---|---|---|---|---|---|---|
| Southern Ocean | 55 – 70 | 0 -1000 | 2.1 | (19.5) | (19.5) | Copepoda | Foxton (1956 |
| Indian Ocean | 50 – 70 | 0 – 100 | (0.9) | | 73.6 | Copepoda | Voronina and Naumov (1968) |
| Lützow-Holm Bay (Shelf) | 69 | 0 – 660 | (1.1) | | 1.5-25.5 | Copepoda | Fukuchi et al. (1985) |
| Prydz Bay | 60 – 68 | 0 – 200 | (2.4) | | 59.7 | - | Hosie et al. (1988) |
| Prydz Bay | 60 – 68 | 0 – 200 | | | 27 | - | Hosie and Stolp (1989) |
| Mc Murdo (Ross Sea) | 78 | 0 – 800 | 0.2 – 2.3 | | (1.5-34.4) | Copepoda/ *E. crystallo-rophias/ Limacina helicina* | Hopkins (1987) |
| Ross Sea | 78 | 0 – 300 | | | 2.5 | - | Foster (1987, 1989) |
| Scotia Sea | 57 – 61 | 0 – 200 | 0.9 | 4.6 | 24 | *E. superba* | Lancraft et al. (1989) |
| Scotia Sea | 60 – 61 | 0 – 200 | | | 82.8 | Salps/ *E. superba* | Sicinski et al. (1991) |
| N. Weddell Sea (oceanic) | 64 – 67 | 0 – 1000 | 1.1 – 1.3 | | 8.8-10.4 | Copepoda | Hopkins and Torres (1988) |
| N. Weddell Sea | 65 – 70 | 0 – 200 | (0.8) | | 30.2 | Copepoda | El Sayed and Taguchi (1981) |
| N. Weddell Sea (ocean. open waters) | 58 – 60 | 0 – 60 | 1.5 | 9.0 | 149.7* | Salps/ Copepoda | Siegel et al. (1992) |
| N. Weddell Sea (ocean.marg.ice zone) | 60 | 0 – 300 | 0.45 | 2.7 | 9.1* | Salps/ Euphausiacea | Siegel et al. (1992) |
| N. Weddell Sea (ocean.closed pack ice) | 60 – 63 | 0 – 60 | 0.45 | 2.2 | 37.3* | *E. superba* | Siegel et al. (1992) |
| N. Weddell Sea | 64 – 66 | 0 – 200 | 1.2 | 20 | (100) | *E. superba* | Lancraft et al. (1989) |
| E. Weddell Sea (oceanic) | 66 – 73 | 0 – 300 | 2.8 | 20.9 | 70.9 | Euphausiacea/ Copepoda | Boysen-Ennen et al (1991) |
| NE Weddell Sea (shelf) | 70 – 74 | 0 – 300 | 3.4 | 23.6 | 78.1 | *E.crystalloro-phias/* Copepoda | Boysen-Ennen et al. (1991) |
| SE Weddell Sea (shelf) | 75 – 78 | 0 – 300 | 1.2 | 8.7 | 28.7 | *E.crystalloro-phias/* Copepoda/ *Limacina helicina* | Boysen-Ennen et al. (1991) |
| S Weddell Sea (shelf) | 75 – 77 | 0 – 200 | (1.6) | (2.0) | 99.8 | - | El Sayed and Taguchi (1981) |
| Antarctic Peninsula | 64 | 0 – 1000 | 3.1 | | (28.8) | Copepoda | Hopkins (1985) |
| Pacific Sector | 50 – 70 | 0 – 1000 | 2.7 | | (21.6) | Copepoda | Hopkins (1971) |
| Bellingshausen Sea (oceanic) | 67 – 73 | 0 – 200 | 0.1* 2.0 | 0.6* 10.7 | 3.1* 56.8 | Chaetognatha/ Copepoda | present study |
| (neritic) | 67 – 73 | 0 – 200 | 0.2* 1.3 | 1.2* 6.9 | 6.0* 36.8 | Chaetognatha/ *E. superba* | present study |

Comparing our results with those obtained by similar net types and in similar depth ranges (*e.g.* Hosie *et al.* 1988; Hosie and Stolp 1989; Lancraft *et al.* 1989; Boysen-Ennen *et al.* 1991; Sicinski *et al.* 1991; Siegel *et al.* 1992) we can see that the Bellingshausen Sea zooplankton biomass is in the lower range of the estimates. A few lower values were only recorded from the southern shelf of the Weddell Sea and the Prydz Bay, areas which are also influenced by extremely prolonged seasonal ice cover. Median biomass values demonstrate that zooplankton standing stock in oceanic areas of the Bellingshausen Sea was even lower than under the seasonal pack-ice of the northern Weddell Sea. Since most of the investigations were carried out during mid austral summer, one can conclude that the southern Weddell Sea, Prydz Bay, Bellingshausen Sea and probably Ross Sea sustain only a low zooplankton biomass with probably low production rates.

Most studies carried out in high latitudes recorded copepods as the dominant components of the oceanic zooplankton biomass or *Euphausia crystallorophias* for the neritic areas. We can confirm the numerical dominance of copepods for the oceanic as well as the neritic Bellingshausen Sea. However, it is interesting to note, that chaetognaths, especially *Eukrohnia hamata* and *Sagitta gazellae* substantially contribute to the numerical dominance of species. Mackintosh (1934) noted that the copepod *Rhincalanus gigas* was the dominant species, with *Calanoides acutus* ranking second. In other years, however, the latter was more abundant, and in some years chaetognaths were very abundant. During our study we observed a situation similar to the alternative described by Mackintosh (1934) where *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* outnumbered *Rhincalanus gigas.* From the numerical dominance the composition resembles the oceanic community described by Hosie and Cochran (1994) for the Prydz Bay region. Regarding the dominance in biomass (wet weight) we found a slightly different situation. In the oceanic region chaetognaths dominated the zooplankton, while chaetognaths and krill *Euphausia superba* were the dominant components in shelf waters. Neither copepods nor *Euphausia crystallorophias* were of major relevance to the biomass of the neritic zooplankton.

According to Mackintosh (1934) chaetognaths are typical warm water species sometimes found in colder water, while most of the copepods mentioned belong to widespread species. Due to this dominance of warmwater species and because of the low biomass of high latitude neritic species (*e.g. E. crystallorophias* and *Pleuragramma antarcticum*) we suspect that the interannual difference in the composition of the dominant species is caused by variability in ice conditions and that in the Bellingshausen Sea the summer 1993/94 or the preceding winter was warmer than during other years.

The tunicate *Salpa thompsoni* shows a high degree of interannual variation in biomass and abundance. Mean abundance estimates for the Antarctic Peninsula area and different years range from 40 specimens/1000 $m^3$ for the season 1990/91 (Nishikawa *et al.* 1995) to 5010 specimens/1000 $m^3$ in 1989/90 (Park and Wormuth 1993) with maximum densities exceeding 25 000 salps/1000 $m^3$ (Siegel unpubl. data). The season 1993/94 was another successful salp year: Loeb and Siegel (1995) recorded a mean density of 931 salps/1000 $m^3$ (median 582 salps/1000 $m^3$) for the Elephant Island area. For the same period we observed very low salp densities in the Bellingshausen Sea with 1.3 to 7 specimens/1000 $m^3$ (median 0.1 to 0.4 specimens/1000 $m^3$).

Regional differences were not only observed for salp abundances, but also for the spatial distribution of salp size groups. A more northern group consisted of larger salps which were found under the influence of West Wind Drift waters, while distinctly smaller salps occurred in southern waters of the East Wind Drift (the region of the 'Belgica' drift). During the same period the large, ubiquitous salp concentrations in the South Shetland Island area were of similar size to those found in the Bransfield Strait and the northern ranges of the Bellingshausen Sea. Size classes even larger than 60 mm were measured around the South Shetlands, which were missing in our samples (Anonymous 1995). A spatial separation of size groups in other years was already reported by Huntley *et al.* (1989). These authors concluded that the larger size groups (around Elephant Island) were advected from upstream areas along the Antarctic Peninsula where smaller salps were found. This seems meaningful for the Elephant Island/ South Shetland area, with a continuous flow from the southwest. However, for the Bellingshausen Sea with the two different current systems, we suspect that salps on the southern shelf were advected from the oceanic region and trapped under unfavourable conditions. Sufficient food supply leads to the rapid development of large numbers of aggregate forms. Increase in size of aggregate forms and continual release of chains by solitary salps result in a mixed size distribution and rapid multiplication in early spring (Foxton 1966). This strong salp recruitment obviously occured in the West Wind Drift waters during the 1993/94 season. On the other hand long and dense ice cover and consequently low phytoplankton concentrations in late winter/early spring inhibit rapid salp growth and recruitment (Siegel and Loeb 1995). This situation generally occurs in regions such as the southern Weddell Sea or the Bellingshausen Sea. As a result salp length is small, reproduction is low and therefore also abundance is low in the East Wind Drift zone, even in years when salps show a mass development in regions under the influence of the West Wind Drift.

According to Mackintosh (1934) abundance of euphausiids was generally low in the Bellingshausen Sea. From other parts of the Southern Ocean we know that high latitude shelf areas are dominated by *Euphausia crystallorophias* as one of the main indicator species, *e.g.* in the southern Weddell Sea (Fevolden 1980; Siegel 1982; Boysen Ennen and Piatkowski 1988) or the Prydz Bay area (Hosie and Cochran 1994). A mean density of 54 specimens/1000 $m^3$ was reported for the Weddell Sea by Boysen-Ennen and Piatkowski (1988), although this value should be treated with caution, because the mean was calculated from positive hauls only and zero values were deleted, thereby overestimating the abundance to an unknown degree. Our results from the Bellingshausen Sea are probably in the same range (mean 39.8 individuals/1000 $m^3$ and median 2.1 individuals/1000 $m^3$).

During our study we did not encounter larval stages of *Euphausia crystallorophias* and adult stages were still in the process of spawning. Investigations carried out in the Indian Ocean sector over many years indicate the peak spawning season for this species during late November/December with few exceptions of late spawning in January (Pakhomov and Perissinotto 1994). Fevolden (1980) found furcilia stages in the Weddell Sea from mid February onwards. In February/March Boysen-Ennen and Piatkowski (1988) sampled rather high densities of larvae in the Weddell Sea (1927 specimens/1000 $m^3$) with highest concentrations in the upper 50 m water column. Since these authors used the same net equipment as in the present study, our results can hardly be explained by methodological biases. On the other hand results obtained for the recruitment index for age group 1+, year-class 1992/93, show a very successful spawning for this euphausiid stock in the preceding year. Pakhomov and Perissinotto (1994) suggested that spawning success of *Euphausia crystallorophias* may strongly depend on the timing of ice breakout and formation of polynias above the continental shelf. This hypothesis should be considered for this species in more detail by future studies, because it has great relevance for the krill *Euphausia superba* (see below).

Krill is almost completely absent on the shelf of the southern Weddell Sea (Fevolden 1980; Siegel 1982; Boysen-Ennen and Piatkowski 1988), and in the neritic waters of the Ross Sea (Marr 1962), but seems to occur regularly on the shelf of the ice covered Bellingshausen Sea. Mackintosh (1973) defined various krill stocks around the Antarctic on the basis of regional differences in krill densities. He also defined a Bellingshausen stock for the area between 72° and 97° W, but pointed out that this does not imply that krill within the different stocks are isolated from the rest. Marr (1962) and Lubimova *et al.* (1982) concluded from their studies that areas of high krill density occur around 90° W and south of 65°/66° S latitude. A recent UK hydroacoustic survey indicated that the northern distribution limit of krill in this area is probably around 66° to 67° S (Murray *et al.* in press). These authors estimated mean biomass of 19.6 and 42 g/m$^2$ for two consecutive surveys in November and December 1992. Hewitt and Demer (1994) summarized biomass estimates from hydroacoustic surveys in the Elephant Island area which is thought to be an area of high krill concentrations. They listed results which range from 8.4 to 134.5 g/m$^2$, most values between 24 and 78 g/m$^2$. Biomass estimates from RMT net samples in the Antarctic Peninsula region range from 4.2 to 13.9 g/m$^2$ (Siegel 1986, 1992). From the present study we calculated a mean biomass of 2.0 g/m$^2$ for the entire area. From the comparison it can be concluded that krill biomass in the Bellingshausen Sea is in the lower range of the values, generally found in the Antarctic Peninsula and Elephant Island region.

Krill size classes were spatially separated with larger size groups preferably in offshore water. This confirms the description of Makarov (1979) and Lubimova *et al.* (1982), who found the large mature specimens predominately between 66° and 68° S in the northern periphery of the krill distribution range, gradually extending to the north in the eastern part in the vicinity of the Antarctic Peninsula. This spatial succession of krill size/age groups was also described for other areas, *e.g.* the Peninsula region and the southern Scotia Sea/northern Weddell Sea (Siegel 1988; Siegel *et al.* 1990). The overall length frequency distribution showed a dominance of length classes > 40 mm indicating a poor availability of age groups 1+ and 2+. The same situation was found around Elephant Island (Anonymous 1995), with larger krill beyond the continental shelf break, and overall dominance of krill > 40 mm. Larger sized length classes were slightly underestimated, because the study did not cover the areas close to the northern distribution range adaeqately, where larger specimens dominate. The recruitment index for age group 1+ in the Bellingshausen Sea was calculated as $R_1 = 0.076$, the mean index from two surveys off Elephant in the same summer season was $R_1 = 0.064$ (Siegel and Loeb 1995). This is in very close conformity and shows that not only the actual krill stock composition but also the recruitment of year class 1992/93 was very similar over a wide spatial scale in the Southern Ocean.

It was shown by Siegel and Loeb (1995) that krill recruitment strongly depends on the extent, duration and concentration of ice coverage during winter. Long and wide ice cover favours krill spawning success and larval survival, while weak ice conditions negatively affect krill recruitment. In this respect it is interesting to note, that sea ice conditions between the Bellingshausen Sea and the Antarctic Peninsula region are closely positively linked over the years, while at the same time other regions show an inverse trend in ice conditions to the area under consideration (Stammerjohn and Smith in press). This would support the similarities within the krill stock composition between the two regions.

Earlier studies reported that krill spawning in the Bellingshausen Sea occurs mostly in January and February and that during this period 53 to 98 % of the females were of gravid or spent maturity stages (data of four years published by Spiridonov 1995). In the present study the proportion of gravid stages reached only 7.6 % and spent females were not observed. Furthermore no krill larvae were caught in the surface water during the present investigation. From this it can be concluded that spawning was rather late in the Bellingshausen Sea in 1994, even later than off Elephant Island (see also Fig. 6d). However, the krill maturation process around Elephant Island was already interpreted as little advanced and as too late in the season to support a successful spawning and later recruitment of the year class 1993/94 (Siegel and Loeb 1995). The same conclusion can be drawn for the Bellingshausen Sea stock.

The recruitment indices for krill and for the other euphausiid species showed opposite trends. *Euphausia superba* had a low recruitment value in the Bellingshausen Sea in 1994, while *Euphausia crystallorophias* and the omnivorous *Thysanoessa macrura* had rather high values. It is not known, which environmental or biological parameters control spawning and recruitment of these two species. However, if ice conditions regulate reproduction timing and offspring success, then ice conditions must act in quite a different way than they do for *Euphausia superba.*

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