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Zooplankton biomass in the ice-covered Weddell Sea, Antarctica *

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Abstract. Zooplankton was sampled by a Rectangular Midwater Trawl (RMT 1 + 8) in Weddell Sea surface waters (0 to 300 m) between 66 and 78°S during austral summer (February–March 1983). Sixty-nine taxa including different developmental stages were considered and divided into 16 size classes between <1 and >39.5 mm length. Biomass was determined by taxon and size class for three different meso- and macroplankton communities in the oceanic region, on the northeastern shelf and on the southern shelf of the Weddell Sea. The highest biomass of 11.2 mg DW m^{-3} (3.4 g DW m^{-2}) was found in the northeastern shelf community (70 to 74°S), where juvenile and adult *Euphausia crystallorophias* accounted for 3.7 mg DW m^{-3} (1.1 g DW m^{-2}). Although not quantitatively sampled, early copepodite stages (CI to CIII) of *Calanoides acutus* and *Calanus propinquus* ranked second with 2.7 mg DW m^{-3} (0.8 g DW m^{-2}). Biomass in the northeastern shelf community was concentrated in the size ranges 1 to 4 mm and 19.5 to 39.5 mm. The oceanic community of the central Weddell Sea was dominated by copepods smaller than 5 mm, which made up half of the total oceanic biomass. The tunicate *Salpa thompsoni* (7.0 to 8.5 mm) was the dominant single species with 1.6 mg DW m^{-3} (0.5 g DW m^{-2}). Euphausiids, mainly juvenile and adult krill *Euphausia superba*, comprised 1.2 mg DW m^{-3} (0.4 g DW m^{-2}). Total standing stock in the oceanic community was 9.4 mg DW m^{-3} (2.8 g DW m^{-2}). Lowest biomass values were found in the southern shelf community (south of 75°S) with 4.0 mg DW m^{-3} (1.2 g DW m^{-2}), concentrated in the 1 to 4 mm and 14.5 to 34.5 mm size classes. Abundant species were the pteropod *Limacina helicina* (1 to 2 mm; 0.7 mg DW m^{-3}; 0.2 g DW m^{-2}) and *E. crystallorophias* (24.5 to 39.5 mm; 0.9 mg DW m^{-3}; 0.3 g DW m^{-2}). The data reveal that it is essential to distinguish among subsystems in the Southern Ocean. This leads to a better understanding of the structure and function of those pelagic food webs which represent alternatives to the paradigmatic krill-centered system.

Introduction

Although the surface waters of the Antarctic are considered a relatively uniform biogeographic region (Hedgpeth 1969), the Southern Ocean is well known for its latitudinal zonation. Hempel (1985) describes three very different large-scale subsystems, the ice-free West Wind Drift dominated by copepods, the seasonal pack-ice zone with krill *Euphausia superba* as the main component, and the permanent pack-ice zone where copepods and the ice krill *Euphausia crystallorophias* are the major plankton elements. Quantitative zooplankton investigations in these regions have often been biased towards small or sluggish taxa due to the use of small vertical nets, which can be avoided by larger plankton. On the other hand, large krill nets do not catch the mesoplankton and these nets are usually employed in areas of high krill density. In the South, sampling is severely hampered by pack-ice, thus excluding most of the permanently ice-covered parts of the Southern Ocean from investigations. Therefore, only rough estimates of zooplankton biomass are available, particularly in the Antarctic sea ice zone.

Recently, zooplankton biomass has been studied in more detail in an area west of the Antarctic Peninsula (Croker Passage), the northwestern Weddell Sea, and the southern Ross Sea (Hopkins 1985a, 1987, Hopkins and Torres 1988). These investigations show significant differences between these areas, both in species composition and size-related biomass distribution. High Antarctic areas like the Weddell Sea (65 to 78°S) are mostly within the permanent pack-ice zone. The zooplankton distribution in this region has been described by Boysen-Ennen and Piatkowski (1988). Based on multivariate data analyses, these authors distinguished three zooplankton communities in the seasonally and permanently ice-covered parts of the Weddell Sea: an oceanic community, a northeast-

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Table 1. Data on zooplankton samples (taken with a Rectangular Midwater Trawl, RMT) from the Weddell Sea (February–March 1983) used in this study

Sample no.	Date (1983)	Lat. (°S)	Long. (°W)	Bottom depth (m)	Haul depth (m)	Vol. filtered (m^3)		Biomass (mg DW m^{-3})
						RMT1	RMT8	
Oceanic community								
1	6 Feb	70°50.5′	13° 40.7′	2550	180–0	1581	24 003	9.9
2	25	72°58.1′	20° 05.3′	1200	300–0	1918	23 423	16.1
3	25	72°36.0′	18° 39.3′	1900	350–0	1736	20 955	9.7
4	4 Mar	70°58.2′	13°44.0′	2300	300–0	1901	25 051	8.9
5	4	71°11.4′	13°33.1′	1600	300–0	1709	21 475	3.5
6	5	71°20.0′	21°37.0′	4400	210–0	1809	27 964	7.5
7	7	67°57.3′	27°12.4′	4700	302–0	2215	32 133	19.7
8	8	67°39.4′	33°42.6′	4600	298–0	2027	28 372	11.0
9	9	67°02.7′	40°56.2′	4500	303–0	2222	30 105	4.1
10	9	66°23.3′	50°52.0′	3200	300–0	1934	28 526	4.0
Mean ± SD								9.4 ± 5.0
Northeastern shelf community								
1	6 Feb	71°29.4′	13°16.6′	235	185–0	1400	21 260	1.8
2	24	74°11.3′	24°35.5′	545	327–0	1947	24 730	7.2
3	24	74°11.5′	24°36.1′	547	308–0	1751	21 551	14.4
4	24	74°08.4′	24°24.5′	525	305–0	1693	20 124	8.2
5	26	72°24.7′	16°21.0′	300	285–0	1628	22 198	17.0
6	26	72°09.1′	15°11.6′	200	188–0	1298	17 883	29.0
7	1 Mar	70°29.9′	7°52.7′	280	240–0	1604	18 927	1.1
Mean ± SD								11.2 ± 9.1
Southern shelf community								
1	12 Feb	75°33.9′	30°40.0′	450	305–0	2072	27 494	2.4
2	12	75°57.4′	28°42.0′	400	292–0	2158	27 827	1.4
3	13	77°17.6′	35°13.7′	655	312–0	2049	27 355	10.9
4	14	77°24.3′	38°26.6′	1033	304–0	2001	27 313	2.6
5	16	77°21.5′	40°53.6′	700	303–0	1953	27 364	5.2
6	16	77°13.5′	41°05.0′	660	265–0	1093	13 358	3.6
7	16	77°15.1′	41°33.8′	660	300–0	1409	20 564	7.4
8	17	77°28.7′	41°19.0′	710	350–0	1417	24 061	4.8
9	17	77°26.1′	41°31.2	670	298–0	1500	19 379	2.9
10	21	77°38.6′	38°25.0′	1155	353–0	2189	27 112	2.0
11	21	77°43.9′	36°21.7′	945	325–0	2343	29 016	4.0
12	22	76°55.4′	32°54.5′	359	303–0	2260	29 521	2.4
13	22	76°34.7′	30°46.6′	391	278–0	2122	27 764	2.5
14	23	75°36.8′	27°16.6′	269	215–0	1745	21 659	3.4
15	23	75°09.8′	24°41.8′	620	305–0	1852	24 044	5.0
Mean ± SD								4.0 ± 2.4

ern shelf community, and a southern shelf community. The analyses revealed significant differences in species composition and abundance among these communities. To find out how these differences in abundance are reflected in terms of biomass, we analyzed the biomass distribution according to species and size composition for each of the three Weddell Sea communities, which all are of a non-krill-dominated type, and we discuss implications for higher trophic levels. The data presented here are the first comprehensive zooplankton biomass analyses from the southern Weddell Sea.

Material and methods

Since 1983 we have been able to use Rectangular Midwater Trawls (RMT 1+8) on R.V. "Polarstern" to sample zooplankton in the ice-covered parts of the Weddell Sea. These nets collect a broad size range and minimize bias due to sampling. The nets were towed in leads in the pack-ice and in the southern coastal polynya (from the Russian: stretch of open water in an ice-covered area). All zooplankton abundance data are based on 32 standardized RMT 1+8 hauls (mesh size 320 and 4500 μm; mouth opening 1 and 8 m^2; Baker et al. 1973) from the upper 300 m in February/March 1983 (Table 1). Twenty-two stations were located on the shelf while ten stations were from oceanic waters (Fig. 1, Table 1). The procedures for collecting, sorting, identifying and evaluating the samples are summarized by Boysen-Ennen (1987) and Piatkowski (1987).

Zooplankton material for dry weight determinations was collected in January/February 1985 in the southern Weddell Sea by Bongo and RMT nets (Hagen 1988). Specimens were sorted, rinsed in filtered seawater, blotted, measured and deep-frozen at −80 °C, then freeze-dried to constant weight for 48 h and immediately weighed on a micro-balance (±0.02 mg). (These samples were further analyzed for biochemical composition.)

Size measurements were carried out on specimens fixed in 4% formaldehyde from the 1983 cruise. A stereo microscope was used

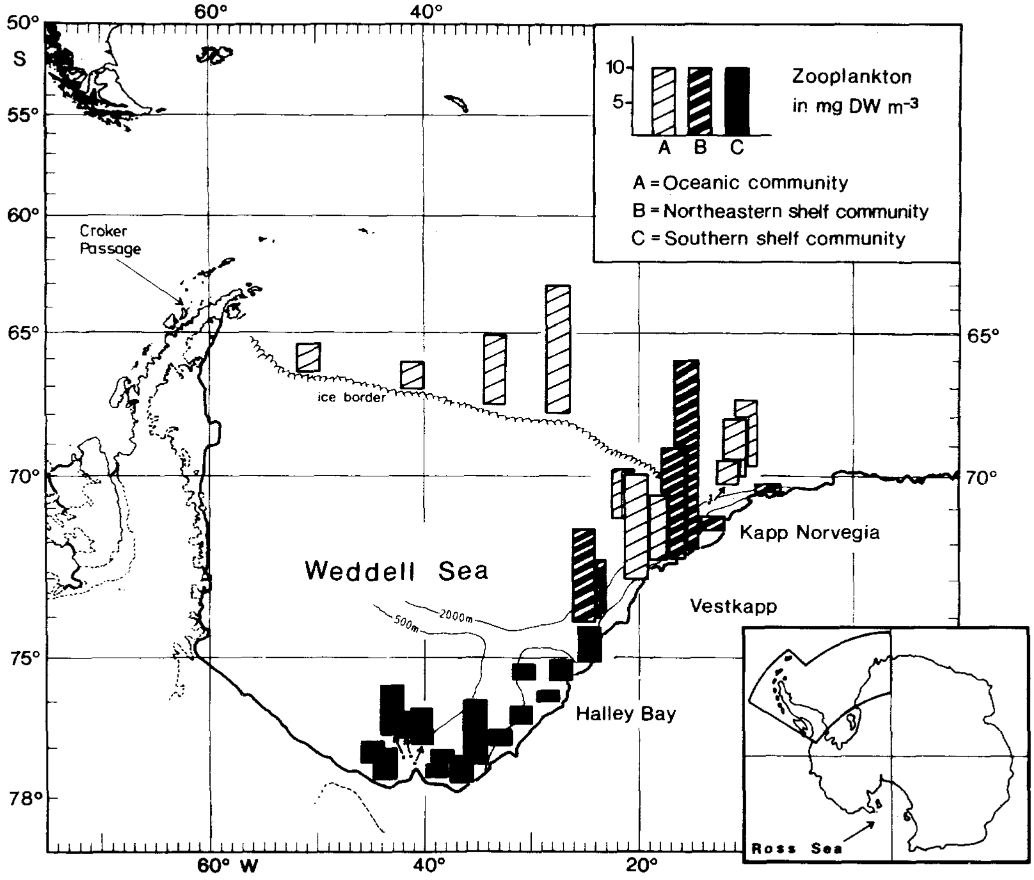

Fig. 1. Zooplankton biomass in the Weddell Sea (see Table 1 for exact biomass data)

to measure specimens <7.5 mm (precision ±0.05 mm). Precision for larger specimens was ±0.5 mm. Length data for *Euphausia superba* were supplied by V. Siegel (personal communication).

Length-weight relationships for each species were calculated using the dry weight data from Hagen (1988), which include the major biomass species of the Weddell Sea. For ostracods we used data from specimens collected in the southern Weddell Sea during October/November 1986 published by Mizdalski (1988). Dry weight data were not available for the less abundant species, which altogether comprised less than 5% of the zooplankton biomass (see Table 2). For these species length-weight relationships from morphologically similar species in our collection were applied. Ctenophores and the scyphomedusae *Atolla wyvillei* were excluded from our calculations.

Length-frequency distributions were produced for 69 taxa, separately for each of the three zooplankton communities defined by Boysen-Ennen and Piatkowski (1988). Biomass was then determined for each size class using the length-weight regression curves. Finally, data for each size group, taxon and sampling station were summed for biomass considerations.

Zooplankton biomass (mg m^{-3}) was standardized as standing stock (g m^{-2}) to allow for comparison with biomass estimates from other sources and sampling depths. Published data were separated into mesoplankton biomass and macroplankton biomass (according to size ranges given by the authors), net types, and mesh sizes.

Results

Geographical distribution of zooplankton biomass

Zooplankton biomass at the various sampling sites in the Weddell Sea range between 1 and 29 mg DW m^{-3} (mean 7.2; Table 1, Fig. 1). On stations in the oceanic community, biomass values are between 3.5 and 19.7 mg DW m^{-3} (mean 9.4; Table 1). Zooplankton biomass in this community is mainly composed of copepods (48.8%; Table 2; Fig. 2). The most important species are *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei*, but *Rhincalanus gigas*, *Euchaeta antarctica* and *Euchirella rostromagna* also contribute significantly to the copepod biomass. *Salpa thompsoni* (17.5%) and *Euphausia superba* (9.5%) show a patchy distribution with local mass occurrences in the oceanic Weddell Sea. The siphonophores *Dimophyes arctica* and *Diphyes antarctica* as well as small chaetognaths are characteristic taxa with considerable biomass in this community (Table 2, Fig. 2). Due to the extremely narrow shelf north of 74°S, the oceanic community approaches the continental ice shelf over the troughs near Kapp Norvegia, Vestkapp and Halley Bay (Fig. 1).

At shallower stations, biomass values of the northeastern shelf community are between 1.1 and 29.0 mg DW m^{-3} (mean 11.2; Table 1). Major components in this community are the different stages of *Calanoides acutus* and *Calanus propinquus* (47.2%), and *Euphausia crystallorophias* (32.4%). Biomass of *Salpa thompsoni* comprises 4.5% and of *E. superba* 3.6% (Table 2, Fig. 2).

In the southern shelf community standing stock varies between 1.4 and 10.9 mg DW m^{-3} (mean 4.0; Table 1). It is thus the community with the lowest biomass. Apart from the copepods (18.2%), the zooplankton is mainly

Table 2. Mean biomass (mg DW 1000 m^{-3}) with confidence levels (CL = ±95%) and percentage (%) of species (and life history stages) in each of the three subsystems of the Weddell Sea (n = number of stations)

Species	Oceanic (n=10)			Northeastern (n=7)			Southern (n=15)		
	Mean	±CL	%	Mean	±CL	%	Mean	±CL	%
Coelenterata	833.5	574.5	8.9	67.2	106.1	0.6	249.5	147.7	6.2
Calycopsis borchgrevinki	37.7	20.4	0.4	1.2	3.0	<0.1	0.0	0.0	0.0
Dimophyes arctica[a]	521.2	333.0	5.6	0.8	1.4	<0.1	158.1	94.8	3.9
Diphyes antarctica	211.5	100.5	2.3	47.1	58.0	0.4	76.6	28.0	1.9
Pyrostephos vanhoeffeni	37.9	85.7	0.4	18.1	44.2	0.2	14.8	24.9	0.4
Vogtia serrata[a]	25.2	34.8	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Mollusca	165.1	146.3	1.8	50.5	84.4	0.4	806.4	530.2	20.1
Marseniopsis sp.	38.8	65.4	0.4	43.2	69.1	0.4	108.2	36.7	2.7
Capulus subcompressus[a]	0.0	0.0	0.0	0.7	1.1	<0.1	18.0	9.8	0.4
Clione limacina	25.0	29.6	0.3	4.6	8.9	<0.1	14.3	7.8	0.4
Limacina helicina	10.1	10.7	0.1	0.1	0.6	<0.1	665.9	476.0	16.6
Clio pyramidata	91.2	40.6	1.0	1.9	4.7	<0.1	0.0	0.0	0.0
Polychaeta	107.9	122.8	1.2	20.6	25.5	0.2	8.9	6.7	0.2
Pelagobia longicirrata[a]	2.7	2.1	<0.1	2.9	2.7	<0.1	2.2	1.0	<0.1
Maupasia coeca[a]	0.0	0.0	0.0	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Rhynchonereella bongraini[a]	19.8	10.8	0.2	0.6	1.1	<0.1	<0.1	<0.1	<0.1
Vanadis antarctica	13.3	19.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Tomopteris carpenteri[a]	34.4	40.7	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Tomopteris spp.	23.9	34.9	0.3	2.3	5.2	<0.1	0.2	0.2	<0.1
Travisiopsis levinsini[a]	6.4	3.1	<0.1	0.3	0.5	<0.1	0.2	0.2	<0.1
Typhloscolex mülleri[a]	3.3	4.2	<0.1	0.9	1.5	<0.1	1.3	1.3	<0.1
Bylgides pelagica[a]	4.1	7.5	<0.1	10.3	10.5	<0.1	3.1	2.9	<0.1
Spionid larvae[a]	<0.1	0.1	<0.1	3.3	4.1	<0.1	1.9	1.1	<0.1
Ostracoda									
Conchoecia spp.	62.2	43.7	0.7	4.4	4.5	<0.1	20.3	9.6	0.5
Copepoda	4544.1	3889.1	48.8	6300.6	5869.9	55.7	729.6	382.1	18.2
Calanus propinquus CIV–adult	987.4	822.0	10.6	1087.9	1366.2	9.6	129.5	91.8	3.2
Calanoides acutus CIV–adult	1051.0	757.3	11.3	1605.7	1021.7	14.2	223.8	106.4	5.6
Calanidae CI–CIII	773.1	851.3	8.3	2647.4	2678.3	23.4	63.2	39.0	1.6
Rhincalanus gigas	267.0	280.1	2.9	9.3	16.1	<0.1	1.8	2.9	<0.1
Clausocalanus ssp.[a]	0.1	0.2	<0.1	0.5	0.6	<0.1	0.2	0.1	<0.1
Ctenocalanus citer[a]	18.5	16.4	0.2	20.5	7.5	0.2	8.4	2.4	0.2
Aetideopsis spp.[a]	0.0	0.0	0.0	0.0	0.0	0.0	6.9	7.8	0.2
Gaidius sp.[a]	0.6	1.0	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
Euchirella rostromagna[a]	179.4	206.0	1.9	8.9	8.3	<0.1	0.0	0.0	0.0
Euchaeta antarctica (incl. Euchaetidae CI–CIII)	286.8	231.9	3.1	297.2	274.5	2.6	80.5	55.1	2.0
Scolecithricella minor[a]	2.9	1.0	<0.1	0.1	0.2	<0.1	0.5	0.2	<0.1
Racovitzanus antarcticus[a]	8.3	5.6	<0.1	0.2	0.4	<0.1	0.3	0.4	<0.1
Stephos longipes[a]	2.9	1.0	<0.1	0.1	0.2	<0.1	0.6	0.3	<0.1
Metridia gerlachei	944.1	684.6	10.1	619.5	491.7	5.4	213.0	74.3	5.3
Heterorhabdus sp.[a]	8.0	4.4	<0.1	0.5	0.5	<0.1	0.1	0.2	<0.1
Haloptilus sp.[a]	4.0	12.2	<0.1	0.0	0.0	0.0	<0.1	0.4	<0.1
Oithona spp.[a]	0.8	0.9	<0.1	2.5	3.3	<0.1	0.7	0.5	<0.1
Oncaea spp.[a]	9.2	13.4	0.1	0.3	0.4	<0.1	0.1	0.1	<0.1
Euphausiacea	1167.9	1678.0	12.5	4120.9	6409.5	36.4	926.7	584.9	23.1
Euphausia superba	885.4	1254.8	9.5	402.3	310.1	3.6	8.5	6.0	0.2
Euphausia crystallorophias	91.8	146.1	1.0	3667.1	5987.2	32.4	910.3	573.0	22.7
Thysanoessa macrura	190.7	271.1	2.0	51.5	112.2	0.5	7.9	6.1	0.2
Decapoda	58.9	75.9	0.6	5.1	6.3	<0.1	10.6	5.4	0.3
Notocrangon antarcticus[a]	0.8	1.9	<0.1	3.3	3.4	<0.1	9.8	8.5	0.2
Chorismus antarcticus[a]	0.1	0.3	<0.1	1.8	2.9	<0.1	0.8	0.9	<0.1
Acanthephyra pelagica	56.8	72.6	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Hymenodora gracilis[a]	1.2	1.1	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
Amphipoda	103.1	108.5	1.1	6.6	11.6	<0.1	162.1	117.4	4.0
Orchomene plebs, O. rossi	0.3	1.1	<0.1	1.8	1.6	<0.1	19.7	8.1	0.5
Epimeriella macronyx	0.0	0.0	0.0	1.3	3.1	<0.1	29.8	24.0	0.7
Eusirus propeperdentatus	0.0	0.0	0.0	0.0	0.0	0.0	99.9	71.6	2.5
Eusirus microps	0.0	0.0	0.0	0.0	0.0	0.0	7.6	6.6	0.2

Table 2 (continued)

Species	Oceanic ($n=10$)			Northeastern ($n=7$)			Southern ($n=15$)		
	Mean	±CL	%	Mean	±CL	%	Mean	±CL	%
Vibilia antarctica	14.3	32.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Cyllopus lucasii, C. magellanicus	10.6	9.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Hyperiella dilatata	11.1	15.8	0.1	0.7	0.7	<0.1	2.1	2.5	<0.1
Hyperiella macronyx	1.2	1.1	<0.1	0.0	0.0	0.0	0.6	0.6	<0.1
Hyperoche spp.[a]	3.7	3.9	<0.1	0.0	0.0	0.0	2.4	4.0	<0.1
Primno macropa	61.9	45.2	0.7	2.8	4.3	<0.1	0.0	0.0	0.0
Chaetognatha	582.4	314.7	6.3	208.0	177.4	1.8	176.8	98.7	4.4
Sagitta gazellae	123.1	41.7	1.3	59.2	44.5	0.5	104.4	44.7	2.6
Sagitta marri[a]	0.8	0.4	<0.1	<0.1	<0.1	<0.1	0.0	0.0	0.0
Eukrohnia hamata	30.5	15.9	0.3	11.4	9.1	0.1	4.3	2.7	0.1
Eukrohnia bathypelagica[a]	0.3	0.1	<0.1	0.0	0.0	0.0	0.0	0.0	0.0
Chaetognatha (RMT 1)	427.7	256.5	4.6	137.4	123.9	1.2	68.1	51.3	1.7
Tunicata									
Salpa thompsoni	1631.3	3201.6	17.5	507.5	802.0	4.5	876.6	1297.8	21.8
Pisces (postlarvae)	59.9	61.8	0.6	23.5	26.5	0.2	45.5	37.4	1.1
Pleuragramma antarcticum	16.3	24.4	0.2	14.5	9.6	0.1	36.1	20.6	0.9
Trematomus scotti[a]	0.0	0.0	0.0	0.3	0.3	<0.1	<0.1	<0.1	<0.1
Aethotaxis mitopteryx[a]	<0.1	<0.1	<0.1	5.5	13.1	<0.1	7.9	15.0	0.2
Prionodraco evansi[a]	0.1	0.3	<0.1	0.7	1.0	<0.1	0.2	0.2	<0.1
Dacodraco hunteri[a]	0.0	0.0	0.0	0.4	0.3	<0.1	0.2	0.6	<0.1
Pagetopsis sp.[a]	0.0	0.0	0.0	2.1	2.1	<0.1	1.1	1.1	<0.1
Notolepis coatsi[a]	43.5	37.2	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Total	9316	10211	100	11315	13524	100	4013	3219	100

[a] Dry weight data for length-weight relationships derived from similar species in our collection

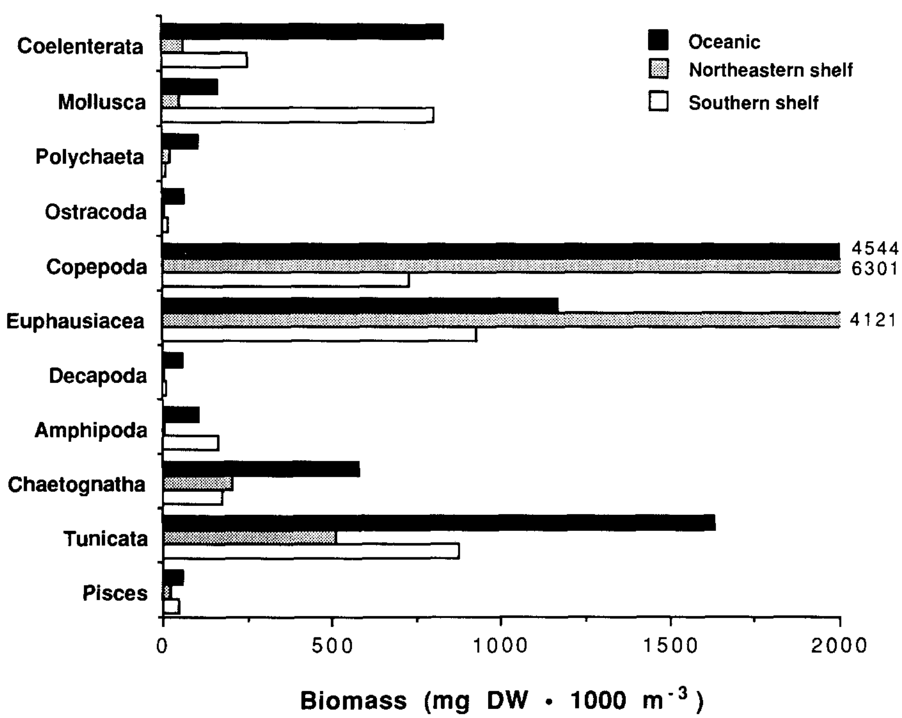

Fig. 2. Mean biomass of major taxonomic groups in Weddell Sea zooplankton communities (see Table 2 for confidence levels)

composed of shelf species, e.g. *Euphausia crystallorophias* (22.7%) and *Limacina helicina* (16.6%). *Salpa thompsoni* (21.8%) is also an important component, although its occurrence is very patchy. Low in biomass (2.5%) but characteristic for this community is the gammaridean amphipod *Eusirus propeperdentatus*. *Euphausia superba* is virtually absent in this plankton community (Table 2, Fig. 2).

In spite of the pronounced variability in each of the three communities, the differences in total biomass be-

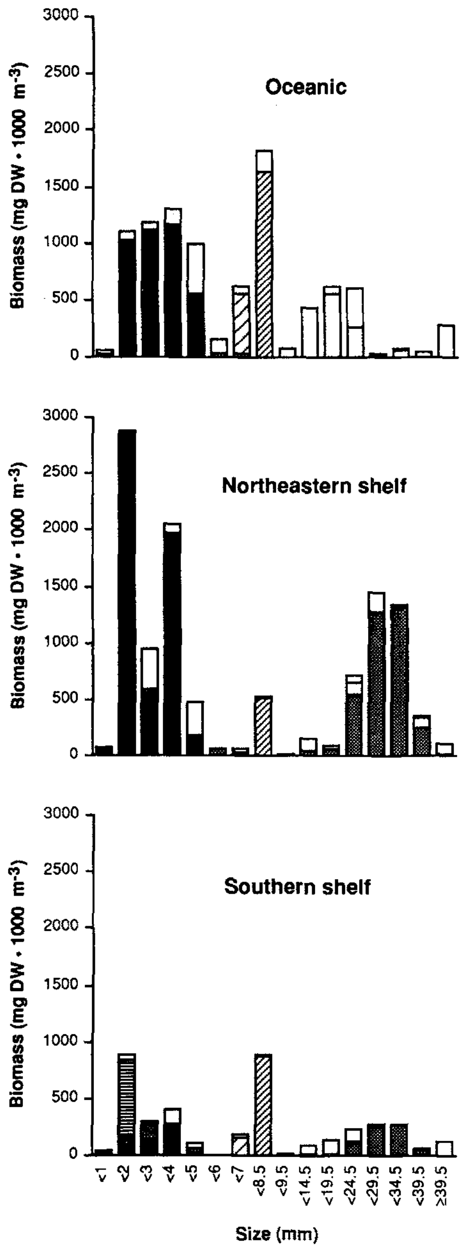

Fig. 3. Biomass by size groups in each of the three Weddell Sea zooplankton communities (taxa exceeding 5% of the biomass in one of the three communities are indicated). ■ *Calanus, Calanoides, Metridia*; □ *Limacina helicina*; □ *Dimophyes arctica*; ▨ *Salpha thompsoni*; ▩ *Euphausia superba*; ▦ *Euphausia crystallorophias*; □ other plankton

tween the southern and the oceanic community are significant, as indicated by the 95% confidence levels and Mann-Whitney *U*-test ($p < 0.01$). A comparison of the communities based on the biomass values of all occurring taxa shows that the biomass composition of the oceanic community differs significantly, both from the northeastern shelf ($n = 69$ pairs, $p < 0.01$, Wilcoxon signed rank test) and the southern shelf ($n = 69$ pairs, $p < 0.01$, Wilcoxon signed rank test). On the other hand, there is no difference in biomass by taxa between the northeastern shelf and southern shelf ($n = 69$, $p = 0.31$, Wilcoxon signed rank test). These tests demonstrate pronounced differences in zooplankton biomass composition between oceanic and neritic areas of the Weddell Sea, whereas from northeast to southwest along the coast the differences in the zooplankton communities are less strongly developed.

Size distribution and composition of zooplankton biomass

The division into biomass size classes revealed a pattern of three pronounced biomass maxima in the communities (Fig. 3). The first biomass maximum is in the 1.0 to 4.9 mm size classes, dominated by the copepods *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei*, both in the oceanic and the northeastern shelf community. In the southern shelf community the 1 to 2 mm large *Limacina helicina* is by far the most important single species in terms of biomass in the 1.0 to 4.9 mm size range. The second biomass maximum at 6.0 to 8.5 mm is due to medium-sized specimens of *Salpa thompsoni* and the siphonophore *Dimophyes arctica* (Fig. 3). Except for these gelatinous species, the 5 to 10 mm size range is characterized by low biomass. Excluding the salps, mesoplankton biomass (<14.5 mm) accounts for 6.6 (61%), 5.7 (75%) and 1.9 (62%) mg DW m^{-3}, in the northeastern, the oceanic, and the southern community, respectively.

The third biomass maximum is in the 14.5 to 39.5 mm size range. It is two to four times higher in the northeastern shelf community than in the oceanic or southern shelf community (Fig. 3). The most important species of the shelf communities is *Euphausia crystallorophias*. In the northeastern shelf community only small amounts of *E. superba* add to the macroplankton biomass, whereas it is a dominant component in the oceanic region. Other important components of the oceanic macroplankton are the chaetognath *Sagitta gazellae*, the siphonophore *Diphyes antarctica* and the euphausiid *Thysanoessa macrura*. Excluding the salps, the macroplankton fraction (14.5 to >39.5 mm) accounts for 4.1 (38%), 1.8 (24%) and 1.1 (35%) mg DW m^{-3} in the northeastern, the oceanic, and the southern community, respectively.

Discussion

Mesoplankton

Mesoplankton (<14.5 mm) biomass in the Southern Ocean is generally between 0.8 and 3.6 g DW m^{-2} (range of mean values; Table 3). High values were measured for instance in Croker Passage near the Antarctic Peninsula (Hopkins 1985 b) and low values in the oceanic northern Weddell Sea (El-Sayed and Taguchi 1981). Mesoplankton biomass in the investigated communities of the Weddell Sea (0.9 to 2.3 g DW m^{-2}) is thus on the same order of magnitude as biomass in other parts of the Southern Ocean. The present data reveal a decrease of mesoplankton biomass from north to south, in spite of the change from an oceanic (central Weddell Sea) to a neritic (eastern

Table 3. Summary of literature values of Antarctic mesoplankton biomass estimates from net catches. WS: Weddell Sea; original data are underlined; conversion ratio DW:WW = 1:8 for copepod-dominated plankton (Hagen 1988)

Region	Latitude (°S)	Period, or months	Depth (m)	DW ($g\,m^{-2}$)	WW ($g\,m^{-2}$)	DW ($mg\,m^{-3}$)	WW ($mg\,m^{-3}$)	Dominant taxa	Source
Pacific Sector	50–70	annual	0–1000	2.6–2.7	20.8–21.6	2.6–2.7	20.8–21.6	Copepoda	Hopkins (1971)
Pacific, Indian Sector	50–70	1–4	0–100	0.9	7.4	9.2	73.6	Copepoda	Voronina and Naumov (1968)
Southern Ocean	55–70	annual	0–1000	2.4–3.2	19.5–25.9	2.4–3.2	19.5–25.9	Copepoda	Foxton (1956; Table 5)
Antarctic Peninsula	64	3–4	0–1000	3.6	28.8	3.6	28.8	Copepoda	Hopkins (1985a)
Oceanic WS	64–67	3	0–1000	1.1–1.3	8.8–10.4	1.1–1.3	8.8–10.4	Copepoda	Hopkins and Torres (1988)
Lützow-Holm Bay	69	5–12	0–660	1.1	9	1.7	13.5	Copepoda	Fukuchi et al. (1985)
Northern WS	65–70	summer	0–200	0.8	6	3.8	30	Copepoda	El-Sayed and Taguchi (1981)
Oceanic WS	66–73	1–3	0–300	2.3	18.4	7.8	62.4	Copepoda	Present study
NE WS shelf	70–74	1–2	0–300	2.2	17.6	7.2	57.6	Copepoda	Present study
Southern WS shelf	75–77	3	0–200	1.6	20	12.5	100	–	El-Sayed and Taguchi (1981)
Southern WS shelf	75–78	1–2	0–300	0.9	7.0	2.9	23.2	Copepoda, *Limacina helicina*	Present study
McMurdo Sound	78	2	0–800	1.5–3.4	12.0–27.2	1.8–4.3	14.4–34.4	Copepoda, *Limacina helicina*	Hopkins (1987)

Table 4. Summary of literature values of Antarctic macroplankton and micronekton biomass estimates from trawled net catches excluding mesopelagic fish. WS: Weddell Sea; original data are underlined; conversion ratio DW:WW = 1:5 for krill-dominated plankton, 1:10 for fish (Hagen 1988)

Region	Latitude (°S)	Month	Depth (m)	DW ($g\,m^{-2}$)	WW ($g\,m^{-2}$)	DW ($mg\,m^{-3}$)	WW ($mg\,m^{-3}$)	Dominant taxa	Source
Scotia Sea	57–61	11–12	0–200	0.9	4.6	4.5	24	*Euphausia superba*	Lancraft et al. (1989)
Prydz Bay	60–68	11–1	0–200	2.4	11.9	11.9	59.7	–	Hosie et al. (1988)
Northern WS	64–66	3	0–200	1.2	20.0	6.0	100	Coelenterata, *E. superba*	Lancraft et al. (1989)
Oceanic WS	66–73	1–3	0–300	0.5	2.5	1.8	8.5	Euphausiacea	Present study
NE WS shelf	70–74	1–2	0–300	1.2	6.0	4.1	20.5	*E. crystallorophias*	Present study
Southern WS shelf	75–78	1–2	0–300	0.3	1.7	1.1	5.5	*E. crystallorophias*	Present study
McMurdo Sound	78	2	0–800	0.2	1.1	0.3	1.5	*E. crystallorophias*	Hopkins (1987)
McMurdo Sound	78	2	0–800	0.8	8.2	1.0	10.0	*Pleuragramma antarcticum*	Hopkins (1987)

and southern shelf) habitat. This latitudinal decrease continues the large-scale trend detected by Foxton (1956) for Southern Ocean mesoplankton between 55 and 70°S. Both biomass and species composition in the eastern and southern Weddell Sea closely resemble those from the southern Ross Sea (Hopkins 1987): In the mesoplankton size fraction considered (> 320 μm), calanoid copepods clearly dominate the biomass. Only in high Antarctic shelf regions are copepods partly replaced by smaller pteropods (*Limacina helicina*).

In the size distribution of mesoplankton biomass in the Weddell Sea *Calanoides acutus*, *Calanus propinquus* and *Metridia gerlachei* contribute most to the first biomass maximum between 1 and 5 mm. In Croker Passage and the western Weddell Sea this biomass peak is concentrated in the 4 to 5 mm fraction (Hopkins 1985a, Hopkins and Torres 1988). This difference is probably explained by the later sampling in Croker Passage and the western Weddell Sea, where plankton was collected in late March and April and the copepods had grown and reached larger body lengths. Hence, with regard to its amount and composition, the copepod biomass maximum is a very consistent feature of the Antarctic zooplankton. The second mesoplankton biomass peak in the Weddell Sea caused by *Salpa thompsoni* (7.0 to 8.5 mm) is lacking in the size distributions published by Hopkins (1985a) and Hopkins and Torres (1988). In contrast to copepods, salps are a highly variable component of the Antarctic zooplankton (Everson 1984, Piatkowski 1985).

Macroplankton

Published data on macroplankton biomass in the Southern Ocean are on the order of 0.2 to 2.4 $g\,DW\,m^{-2}$ (Table 4), excluding studies which focussed only on krill. Macroplankton biomass is lower than mesoplankton biomass in all latitudes and also decreases from lower to higher latitudes. Our estimates for the macroplankton biomass of the Weddell Sea fall in the lower range of published data (Table 4). Both the oceanic region and the southern shelf are characterized by extremely low macroplankton biomasses of 0.5 and 0.3 g DW m^{-2}, respectively. Besides krill, major components of the oceanic macroplankton biomass are coelenterates, chaetognaths, and the euphausiid *Thysanoessa macrura* (Table 2). Biomass on the northeastern shelf (1.2 g DW m^{-2}) is dominated by the ice krill *Euphausia crystallorophias* and a small portion of *E. superba*, whereas on the southern shelf only *E. crystallorophias* attains any importance in terms of macroplankton biomass. This finding is consistent with records from other high Antarctic systems, e.g. the southern Ross Sea, where *E. crystallorophias* is also the most abundant macroplankton species (Hopkins 1987) (Table 4).

Krill (*Euphausia superba*) is often considered the most important zooplankton species of the Southern Ocean. For instance, in Croker Passage krill biomass outnumbered that of other zooplankton by an order of magnitude (Hopkins 1985b). This ratio, however, does not reflect the overall share of krill in the Southern Ocean zooplankton. As a result of the intense international "BIOMASS" studies, average densities of krill in its principal distribution areas in the Atlantic sector are now estimated to be on the order of 1 to 2 g DW m^{-2} (Siegel 1986a). Thus, krill biomass is of the same order of magnitude as mesoplankton biomass, even in areas of main krill occurrence, e.g. in the waters around the Antarctic Peninsula. Obviously, the overall contribution of krill to Southern Ocean zooplankton has been overestimated in the past.

Food web implications

Taking into account the higher production : biomass ratio of copepods (4.5: Voronina et al. 1981) over krill (1.0: Everson 1977, Siegel 1986b), copepods contribute most to the total zooplankton production of the Southern Ocean. Based on the biomass values shown in Tables 3 and 4, mesoplankton production in the Atlantic sector (Antarctic Peninsula, Scotia Sea, oceanic Weddell Sea, northeastern and southern Weddell Sea shelf) exceeds macroplankton production by a factor of 8 to 14. However, copepods are normally not considerd a major food resource of large predators in the Antarctic Ocean (Everson 1977). This comparatively high mesoplankton production is transferred up the food chain via additional trophic levels. In the oceanic parts of the Southern Ocean, this trophic link is provided by mesopelagic fishes (e.g. Myctophidae; Rowedder 1979). These species, however, are absent from shallower waters over the high Antarctic shelves (DeWitt 1970; Hubold and Ekau 1987), where the holopelagic notothenioid fish *Pleuragramma antarcticum* dominates. *P. antarcticum* feeds on copepods throughout its life cycle. Older specimens take *Euphausia crystallorophias* and krill in addition to copepods (Moreno et al. 1986, Hubold and Ekau 1990). The species is thus adapted to make full use of both biomass peaks in the size distribution of zooplankton. This trophic flexibility may explain the relatively large biomass of *P. antarcticum*, which is the most abundant fish species of the Weddell Sea shelf (Hubold and Ekau 1987). Due to its high abundance and unique trophic position as planktivorous species, *P. antarcticum* is a key link between small zooplankton and large consumers in the neritic food webs of the Antarctic Ocean (Takashi and Nemoto 1984, Eastman 1985, Green and Williams 1986, Plötz 1986).

The zooplankton biomass distribution in non-krill-dominated Antarctic systems implies a more diverse food web, with fishes or other medium-sized species (e.g. squids, decapods) as links between zooplankton and top predators. These systems differ from the "typical" Antarctic food chain, where krill is directly utilized by top predators due to its high abundance and large size. Both krill-dominated and copepod-fish-dominated food webs of the Antarctic sea ice zone will need to be more thoroughly investigated to reach a better understanding of the different Antarctic marine ecosystems and provide a more solid basis for future ecosystem modelling.

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