

MACRO- AND MEGAPLANKTONIC CNIDARIANS COLLECTED IN THE EASTERN PART OF THE WEDDELL GYRE DURING SUMMER 1979

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The species composition, abundance and spatial distribution of macroplanktonic cnidarians in the eastern part of the Weddell Gyre are described from a series of nekton samples collected over three depth ranges between 0 and 2000 m. On average, cnidarians contributed 52.6% to the biovolume of these samples, although the range was high (5.0–93.1%). In total 23 species of siphonophores and 20 species of medusae were identified; a number that is very high in comparison with previous studies. There was a high diversity at bathypelagic depths, with 38 species being collected below 1000 m. The most abundant siphonophores were *Dimophyes arctica* (up to 45 nectophores per 10^4 m^3) and *Heteropyramis crystallina* (up to 22 nectophores per 10^4 m^3). The most abundant medusa was *Pantachogon haeckeli* (up to 30 specimens per 10^4 m^3). Medusae were most abundant at mesopelagic depths, reaching 46 specimens per 10^4 m^3 in the 500–1000 m depth range. Smaller calyphorophoran siphonophores were concentrated in the top 500 m of the water column, with total numbers averaging 107 per 10^4 m^3 . The number of larger calyphorophorans increased with depth, being most abundant in the 1000–2000 m depth range. Although many species had a widespread geographical distribution within the sampling area, the hydrographical conditions appeared to be affecting the distribution of some.

INTRODUCTION

Studies on the macrozooplankton communities of the Southern Ocean started around the turn of the century, but most of these were non-quantitative. More recently, quantitative studies of the Southern Ocean have increased, with the objectives of establishing zoogeographic communities associated with the various water masses and to identify indicator species. These studies show that, in general, an oceanic and a neritic community can be distinguished (e.g. Siegel & Piatkowski, 1990). Basically, the oceanic macrozooplankton community shows a circumpolar distribution (Baker, 1954), but it is clear that the distribution of certain groups, for instance krill and salps, is very patchy, particularly during summer. In the oceanic region the composition and abundance of the macrozooplankton community can also be greatly affected by the seasonal changes in the ice cover (Ainley *et al.*, 1986).

In the top 500 m during spring and summer, copepods, krill and salps usually overwhelmingly predominate. However, Boysen-Ennen *et al.* (1991) found that cnidarians

had the fourth highest biomass in the upper 300 m of the Weddell Sea, while Hopkins *et al.* (1993) found that, in the upper 1000 m of the Weddell–Scotia Confluence region, the biomass of krill was matched by that of midwater fish and of gelatinous megaplankton. In autumn and winter, as the ice edge moves north and reaches its maximum extent, the oceanic populations of the main filter feeders modify their life strategies (Smith & Schnack-Schiel, 1990). The krill migrate to neritic areas, while the solitary stage of salps, and a diapause stage for many copepods, sink down to mesopelagic depths. During this period, there is a notable increase in carnivores, particularly cnidarians and ctenophores (Lancraft *et al.*, 1991).

The present paper describes the species composition, distribution and abundance of macrozooplankton cnidarians in the African sector of the Southern Ocean during summer 1979. The physics and biology of this area are poorly understood, but the eastern end of the Weddell Gyre is located between 20 and 30°E in this area (Deacon, 1979; Orsi *et al.*, 1993). Marr (1962) had noted that very few krill had been found in this region, in marked contrast to their richness in the Weddell Drift. The rationale for RRS 'Discovery' Cruise 100 was to carry out a closely integrated physical and biological programme in order to investigate this feature further. The water column was sampled down to 2000 m in order to encompass the bathypelagic communities that have rarely been investigated in the Southern Ocean. The data obtained vindicate Marr's (1962) observations as very few krill were collected, the biological collections consisting predominantly of gelatinous organisms.

MATERIALS AND METHODS

The samples were collected during RRS 'Discovery' Cruise 100 (January–March 1979) to the African sector of the Southern Ocean. The positions of the stations relevant to the present paper are shown in Figure 1. The biological samples were collected using an

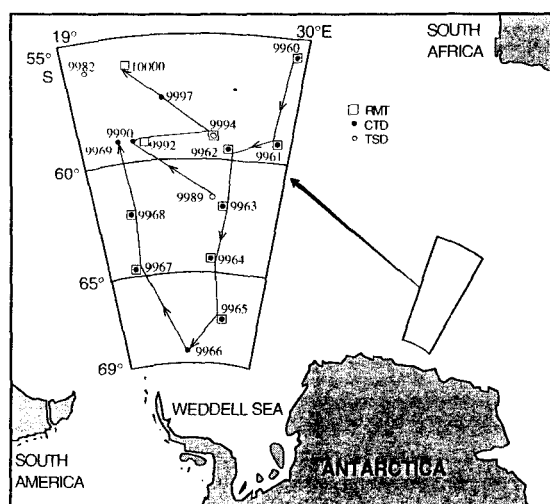


Figure 1. Positions of relevant stations, both hydrographical and biological, occupied during RRS 'Discovery' Cruise 100.

opening-closing RMT 1+8M multi-net system (Roe & Shale, 1979) that was towed obliquely down through the water column by continuously paying out the warp, while maintaining the net speed at ~ 2 kt (1 m s^{-1}). The depth ranges sampled were approximately 0–500, 500–1000, and 1000–2000 m (see Table 1). The volume of water filtered was calculated according to the formulae in Roe *et al.* (1980). However, Pommeranz *et al.* (1982) have pointed out that there may be some inaccuracies in these measurements, particularly when paying out or hauling in. Although their data do not apply to the multi-net system, we calculate that the possible error is in the region of $\sim 6\%$, which we consider not to be of importance. The samples were fixed in 5% borax buffered formalin and are preserved in Steedman's fluid.

Table 1. Station data for the oblique RMT8 hauls made during RRS 'Discovery' Cruise 100.

Station	Date 1979	Position		Depth range (m)	Time (GMT)	Volume filtered (m ³)
9960#3	10/2	55°59.5'S	29°56.9'E	0-510	1211-1239	12004
9960#4	10/2	55°59.4'S	29°54.6'E	510-990	1239-1316	16444
9960#5	10/2	55°59.4'S	29°51.6'E	990-2000	1316-1439	37044
9961#1	11/2	58°52.1'S	29°00.5'E	0-500	1950-2030	17535
9961#2	11/2	58°54.0'S	28°59.4'E	500-1000	2030-2114	21797
9961#3	11/2	58°56.5'S	28°58.1'E	1000-2000	2114-2250	45170
9962#1	12/2	58°59.1'S	26°11.3'E	0-490	1743-1824	18741
9962#2	12/2	58°59.6'S	26°07.9'E	490-1000	1824-1907	21015
9962#3	12/2	59°00.0'S	26°03.9'E	1000-2005	1907-2045	46803
9963#3	14/2	61°59.1'S	26°06.7'E	0-500	2141-2229	23270
9963#4	14/2	61°58.4'S	26°10.5'E	500-995	2229-2316	22344
9963#5	14/2	61°57.2'S	26°14.4'E	995-2010	2316-0053	45293
9964#1	15/2	64°18.0'S	25°48.4'E	0-500	2014-2056	23100
9964#2	15/2	64°19.9'S	25°47.3'E	500-990	2056-2151	30250
9964#3	15/2	64°22.5'S	25°45.9'E	990-2010	2151-2315	46200
9965#1	16/2	66°51.8'S	25°52.4'E	0-510	1814-1900	22585
9965#2	16/2	66°52.9'S	25°55.4'E	510-995	1900-1938	18492
9965#3	16/2	66°53.8'S	25°58.1'E	995-2000	1938-2110	42563
9967#2	19/2	64°56.1'S	21°34.1'E	0-495	2306-2354	24392
9967#3	19/2	64°55.8'S	21°34.8'E	495-995	2354-0029	17479
9967#4	20/2	64°54.7'S	21°34.2'E	995-2005	0029-0221	53463
9968#1	20/2	62°11.1'S	20°59.3'E	0-500	1911-1956	24750
9968#2	20/2	62°09.3'S	20°58.5'E	500-980	1956-2046	27500
9968#3	20/2	62°06.7'S	20°57.5'E	980-1990	2046-2214	48400
9989#1	15/3	61°48.5'S	26°00.6'E	0-500	1606-1639	15380
9989#2	15/3	61°47.0'S	26°00.3'E	500-1000	1639-1727	24257
9989#3	15/3	61°44.7'S	26°00.3'E	1000-2000	1727-2017	93500
9992#1	17/3	59°08.2'S	22°11.0'E	0-500	1122-1204	20787
9992#2	17/3	59°09.3'S	22°14.3'E	500-1000	1204-1245	20951
9992#3	17/3	59°10.8'S	22°18.6'E	1000-2000	1245-1413	41663
9994#2	18/3	58°59.9'S	25°47.0'E	10-500	1105-1144	18437
9994#3	18/3	59°01.8'S	25°48.0'E	500-1000	1144-1238	29389
9994#4	18/3	59°04.2'S	25°44.1'E	1000-2010	1238-1402	40011
10000#2	23/3	55°35.2'S	21°56.6'E	20-500	2034-2129	30382
10000#3	23/3	55°35.5'S	21°51.6'E	500-1000	2129-2209	21433
10000#4	23/3	55°35.6'S	21°47.9'E	1000-1800	2209-2315	30820

The medusae and siphonophores, both asexual and sexual stages, from the RMT 8 samples have been identified; and the total biovolume (displacement volume) of each group measured, without taking into account the probable shrinkage of these gelatinous animals during preservation. Thus any calculation of the percentage contribution of cnidarians to the total biovolume of the catch almost certainly represents an underestimate. The data for the specific populations were normalized to 10,000 m³ of water filtered. In the case of a few siphonophore species this can raise problems (see Pugh, 1984). For the purposes of this study, any species of physonect (those with a pneumatophore and several nectophores or swimming bells) was normalized on the assumption that each animal possessed twenty nectophores. Thus, any number of nectophores between 1 and 20 was assumed to represent one animal. Usually, the number of pneumatophores present was in agreement with this assumption. For the calycophoran species, which were by far the most abundant siphonophores, problems arose for only two of the commoner species. Specimens of *Rosacea plicata* (see Tables 2 & 3 for authorities) are comprised of an apposed pair of identical nectophores; so the number of nectophores found was rounded up to an even number and divided by two. The numbers of bracts and gonophores of this species were not included in the analyses as they remain attached to the stem. In the case of *Vogtia serrata*, and other rarer *Vogtia* species, the number of nectophores present on each animal is approximately 8–15. Since these are of variable size, and the smallest are likely to be lost through the meshes of the net, we have taken a value of ten per animal in order to normalize the data.

At most of the stations where the nets were deployed, the hydrography of the water column was investigated by means of CTD casts. Additional CTD and TSD casts, made at various times during the cruise, have also been used to enhance these data (Figure 1).

RESULTS AND DISCUSSION

The sampling programme during RRS 'Discovery' Cruise 100 basically can be split into three transects. The first, southbound during the first leg of the cruise, encompassed stations 9960 (55°59'S 30°E) to 9965 (Figure 1), with additional CTD data available from station 9966 (68°28'S 24°E). During this transect there was a 3° longitudinal change, westwards, between stations 9961 and 9962 so that the physical structure of the water column at these two stations was quite different (see below), despite their being approximately on the same latitude. The second transect, northbound during the first leg of the cruise, included only two biological stations (9967 and 9968), which were ~4–5° to the west of their corresponding stations (9964 and 9963) on the first transect (Figure 1). Additional CTD data were available for stations 9966 and 9969 (59°06'S 20°06'E). The temperature structure of the water column to 2000 m for these first two transects will be shown separately (Figures 2 & 3A) but for ease of comparison the biological data are combined (see Tables 2 & 3).

The third transect of relevant biological stations (9989, 9992, 9994, and 10000) was run a month or so after the first two transects, northbound during the second leg of the cruise. Again, as during the first transect, there was a change in longitude (~4°) between

Table 2. Distribution of siphonophores (numbers per $10^4 m^3$) in the oblique RMT8 hauls made during RRS 'Discovery' Cruise 100. Data for transects 1 (Stn 9960–9965) and 2 (Stn 9967–9968) combined. Data for each species presented in depth order. See Table 1 for Station data.

Species	9960	9961	9962	9963	9968	9964	9967	9965	10000	9994	9992	9989
<i>Marrus</i>	0.83	0.57	-	-	0.40	-	-	-	0.33	-	-	-
<i>antarcticus</i>	1.22	-	-	2.24	0.73	0.33	0.57	1.08	-	1.70	-	-
Totton 1954	0.54	0.66	0.21	0.44	-	-	0.37	-	0.65	1.00	-	-
<i>Rosacea</i>	10.00	41.63	0.54	10.74	0.81	0.87	0.41	-	-	1.09	1.93	-
<i>plicata</i>	0.61	-	-	-	-	-	-	-	-	-	-	-
s. Bigelow 1911	0.27	-	-	-	-	-	-	-	0.16	-	-	-
<i>Nectopyramis</i>	-	-	-	-	-	0.43	-	0.44	-	0.54	-	-
<i>natans</i>	0.61	0.46	0.48	-	-	-	-	-	-	-	-	-
(Bigelow 1911)	-	-	0.43	0.66	0.21	0.22	0.37	0.23	0.32	-	-	0.11
<i>Vogtia</i>	4.08	5.08	12.54	11.04	4.36	3.03	7.75	3.37	5.30	8.24	8.18	9.10
<i>serrata</i>	1.64	0.37	8.47	6.53	6.26	2.15	0.46	0.97	5.37	4.22	5.30	0.54
(Moser, 1925)	0.43	2.04	0.06	0.07	0.15	0.04	-	-	-	-	0.14	-
<i>Diphyes</i>	0.83	1.14	10.67	4.73	12.12	14.72	12.30	14.179.87	15.19	7.70	6.50	-
<i>antarctica</i>	-	0.46	-	-	0.73	-	-	2.16	0.47	0.68	0.48	0.41
Moser 1925	-	-	-	-	0.41	-	-	0.47	1.30	1.00	0.48	0.11
	4.17	17.11	50.69	17.19	11.31	2.60	22.14	14.17	3.62	39.59	45.22	37.06
	0.61	0.92	2.86	1.34	1.09	0.99	-	0.54	2.33	1.02	-	-
	-	-	-	0.22	0.21	0.87	0.94	0.23	3.57	0.50	0.24	-
<i>Lensia</i>	-	1.14	0.53	0.43	0.81	0.43	-	1.77	-	-	0.48	1.95
<i>achilles</i>	2.43	1.38	1.43	1.34	0.73	0.33	2.86	3.24	-	0.34	0.48	-
Totton 1941	0.81	0.44	-	0.88	-	0.65	1.68	0.23	-	0.50	0.48	-
<i>Lensia</i>	3.33	0.57	1.07	3.01	1.62	2.16	0.82	0.44	-	2.17	-	0.65
<i>havock</i>	-	0.92	10.94	9.85	7.27	3.97	6.29	7.57	0.47	4.42	2.86	-
Totton 1941	0.81	3.10	-	0.22	1.24	0.43	-	0.23	0.65	0.25	-	-
<i>Muggiaea</i>	-	-	4.27	5.16	7.68	10.82	28.29	24.35	-	4.34	3.85	6.50
<i>bargmannae</i>	-	-	-	-	0.73	-	4.58	1.08	-	0.34	-	-
Totton 1954	-	0.22	0.23	0.22	0.21	-	0.19	1.17	-	0.25	-	-
<i>Dimophyes</i>	17.49	21.67	45.36	40.40	18.59	16.88	29.93	9.30	11.52	61.83	41.85	35.11
<i>arctica</i>	-	2.75	2.38	3.13	2.55	0.33	0.57	0.54	2.33	1.36	1.43	-
(Chun 1897)	0.54	0.44	1.71	1.32	1.24	0.65	1.31	0.70	4.87	3.00	2.16	-
	0.83	-	6.40	-	-	-	-	-	-	-	-	2.60
	1.22	-	-	0.45	-	-	-	-	-	-	-	-
	-	-	0.21	0.22	-	-	0.19	-	0.65	-	-	-
<i>Clausophyes</i>	2.50	1.71	-	0.43	-	-	-	-	-	-	1.44	-
<i>moserae</i>	-	6.88	-	0.90	-	0.33	-	0.54	-	0.34	-	-
(K. & E. 1860)	10.80	0.22	1.92	0.44	0.41	0.43	-	-	0.65	2.00	2.16	-
<i>Clausophyes</i>	-	-	-	-	0.40	-	0.41	-	-	-	-	-
<i>galeata</i>	-	-	-	0.45	0.36	-	-	-	-	-	-	-
L. & v.R. 1908	-	-	0.43	0.66	1.24	0.43	-	0.23	-	-	-	0.43
<i>Chuniphyes</i>	-	0.57	-	0.43	0.81	0.43	0.82	1.77	-	0.54	1.92	3.90
<i>moserae</i>	-	5.96	0.48	0.90	1.45	0.66	1.14	-	-	0.34	1.91	0.82
L. & v.R. 1908	0.27	-	5.13	3.75	6.82	2.81	8.04	4.46	6.49	4.50	9.60	2.35
<i>Crystallophyes</i>	0.83	9.12	4.80	3.01	3.23	0.43	2.87	6.64	-	4.88	14.43	7.15
<i>amygdalina</i>	0.61	-	-	-	0.36	0.33	-	1.08	-	-	-	-
Moser 1925	-	0.44	-	-	-	-	0.75	-	-	0.25	0.48	-
<i>Heteropyramis</i>	22.49	13.69	12.27	17.19	3.64	2.60	4.10	7.08	-	15.73	26.94	13.65
<i>crystallina</i>	1.82	0.46	14.28	8.95	13.45	6.28	6.29	18.39	-	16.33	11.46	-
(Moser 1925)	11.61	3.10	3.85	3.75	2.07	2.16	1.31	2.82	2.60	5.50	3.60	-
	24.16	10.84	6.40	3.01	-	0.43	0.82	-	-	3.25	17.32	1.30
	8.51	6.42	-	0.90	0.36	0.66	-	2.70	-	1.02	0.95	-
	3.78	0.44	-	1.32	1.03	0.87	0.75	-	1.30	2.25	2.16	-

Unboldened: asexual, polygastric stage (number of nectophores, or greater of anterior & posterior nectophores if both present). Bold: sexual stage, (number of eudoxids, greater of bracts or gonophores). See text for details of italicized numbers. Authorities: K. & E., Keferstein & Ehlers; L. & v.R., Lens & van Riemsdijk.

Table 3. Distribution of medusae (numbers per 10^4 m^3) in the oblique RMT8 hauls made during RRS 'Discovery' Cruise 100. See Table 2 for further details.

Species	9960	9961	9962	9963	9968	9964	9967	9965	10000	9994	9992	9989
<i>Euphysora</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>gigantea</i>	-	-	-	-	-	-	-	-	-	-	-	-
Kramp 1957	0.27	-	0.21	0.66	0.41	-	0.19	-	-	-	0.48	-
<i>Pandea</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>rubra</i>	-	-	-	0.45	0.36	0.66	0.57	-	-	-	-	-
Bigelow 1913	-	-	0.21	-	-	-	-	-	-	-	-	-
<i>Calyropsis</i>	-	8.55	0.53	-	3.23	3.90	-	2.66	2.63	4.88	1.92	3.25
<i>borchgrevinkii</i>	-	0.46	5.71	4.92	2.91	1.98	-	-	1.87	0.34	1.91	1.24
(Browne 1910)	-	0.22	-	-	0.41	-	-	-	0.65	-	-	-
<i>Chromatonema</i>	-	-	0.53	-	-	0.43	-	-	-	-	-	-
<i>rubrum</i>	-	0.92	0.48	-	-	-	-	-	-	-	-	-
Fewkes 1882	0.54	-	0.43	-	0.41	-	0.56	-	-	0.25	0.48	-
<i>Pantachogon</i>	2.50	0.57	-	-	-	-	0.41	-	-	0.54	-	-
<i>haeckeli</i>	29.80	0.46	14.75	4.03	3.27	0.99	6.29	2.70	-	8.17	12.89	-
Maas 1893	10.80	8.41	0.85	0.22	-	0.22	-	0.23	0.32	-	0.24	-
<i>Crossota</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>brunea</i>	6.08	-	0.48	0.45	-	-	-	0.54	-	-	0.95	-
Vanhöffen 1902	1.08	1.11	0.21	-	0.41	-	-	0.47	0.32	-	-	0.21
<i>Halicreas</i>	-	0.57	-	0.43	-	-	-	0.44	-	-	-	-
<i>minimum</i>	0.61	2.29	0.48	0.45	-	0.33	0.57	-	0.47	0.34	0.95	0.41
Fewkes 1882	1.89	-	1.07	1.55	1.03	1.52	0.94	0.94	0.32	1.75	1.44	-
<i>Haliscera</i>	-	3.99	11.74	3.87	-	-	-	0.44	-	11.93	12.99	18.21
<i>conica</i>	-	-	-	0.45	-	-	4.00	1.08	-	2.38	-	-
Vanhöffen 1902	-	1.77	-	1.10	-	-	-	-	-	-	-	-
<i>Botrynema</i>	-	2.28	0.53	-	-	2.16	-	-	-	-	1.44	-
<i>brucei</i>	-	6.88	-	0.45	-	0.33	0.57	0.54	-	-	0.48	-
Browne 1908	1.62	-	2.14	4.42	1.24	3.25	3.93	3.52	0.32	3.25	4.56	2.57
<i>Cunina</i>	-	-	-	-	-	-	0.82	-	-	0.54	-	-
<i>duplicata</i>	-	1.38	0.95	-	0.36	0.66	1.14	-	-	0.34	-	-
Eschscholtz 1829	-	-	0.43	0.66	0.83	-	-	-	0.97	0.50	0.24	-
<i>Aegina</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>citrea</i>	0.61	-	0.48	-	0.36	-	-	0.54	-	-	-	-
Eschscholtz 1829	-	-	-	0.44	0.21	-	0.19	-	-	0.25	-	0.11
<i>Narcomedusan</i>	-	1.14	0.53	-	0.81	0.43	-	-	-	4.34	4.33	1.30
sp.	-	-	-	-	-	-	-	-	-	0.34	-	-
<i>Atolla</i>	0.83	0.57	-	-	0.40	1.30	1.64	1.77	-	-	-	0.65
<i>wyvillei</i>	7.91	2.29	3.81	3.13	1.82	0.66	0.57	0.54	0.47	0.68	3.82	1.24
Haeckel 1880	5.40	1.11	1.71	1.77	0.41	0.65	-	0.23	0.32	1.50	1.20	0.32
<i>Periphylla</i>	0.83	-	0.53	0.43	-	2.16	1.23	0.44	-	-	-	-
<i>periphylla</i>	1.22	0.92	0.95	1.34	0.36	0.33	1.14	1.08	1.87	0.34	-	1.65
(Péron & Lesueur 1810)	-	0.22	0.43	-	0.41	0.43	1.31	0.47	0.65	1.00	0.96	-

stations 9992 and 9994 (Figure 1), but this time eastwards. Unfortunately, contemporaneous CTD casts were not made at these stations (see Figure 3B), although station 9990 (59°07'S 21°58'E) lay very close to station 9992. However, TSD data (kindly supplied by Dr Barry Heywood, British Antarctic Survey) are available for two of them (stations 9989 and 9994). Another CTD cast was made at station 9997 (57°29'S 23°02'E), approximately midway between stations 9994 and 10000. In an attempt to complete the picture,

we have used CTD data from station 9982 (56°03'S 19°50'E) to approximate the hydrography at station 10000. None the less, it must be noted that the former station lay 2° to the west of the latter, and was occupied eleven days earlier.

Hydrography

The hydrography of the Weddell Gyre has been discussed in detail in two recent papers (Orsi *et al.*, 1993; Gouretski & Danilov, 1993), and so we will summarize only the hydrographic changes that occurred along the three main transects, as defined above. Throughout the transects three main water masses were found. These are, according to Hellmer *et al.* (1985): (1) Antarctic Surface Water (AASW: $-1 \leq T^{\circ}\text{C} \leq +2$; $33.4 \leq S \leq 34.2$), which occupied the superficial layers, forming a mixed layer as a result of summer warming of Winter Water. (2) Winter Water (WW: $-1.75 \leq T^{\circ}\text{C} \leq -1$; $34.2 \leq S \leq 34.5$). This was present immediately below the mixed layer, and extended down to a maximum depth of ~200 m. (3) Circumpolar Deep Water (CDW: $0.0 \leq T^{\circ}\text{C} \leq +2.0$; $34.66 \leq S \leq 34.74$). This was the major water mass present within the sampling range, and is thought to have been advected poleward, by the Weddell Gyre, from the Antarctic Circumpolar Current (ACC) (Gouretski & Danilov, 1993). Below ~500 m this water became progressively cooler to the south.

The temperature structure of the water column (0–2000 m) during the first transect of stations is shown in Figure 2. The most northerly station (9960) was located south of the Antarctic Polar Front (APF), which is defined by the presence of the 2°C isotherm at 200 m depth. The physical structure of the water column at this and the subsequent station

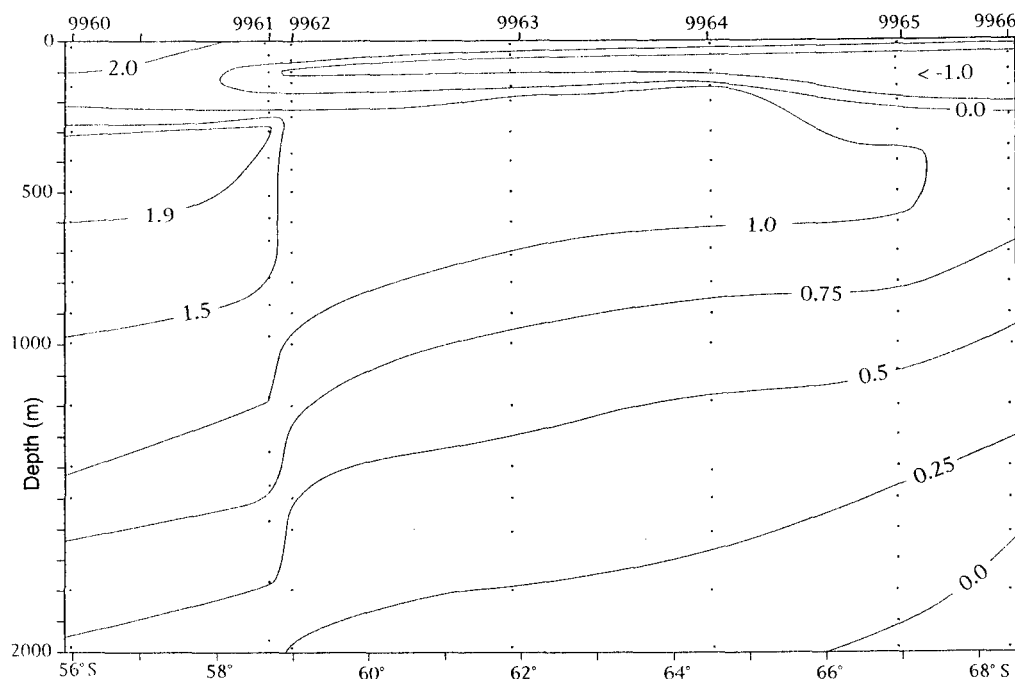


Figure 2. Temperature structure of the water column (0–2000 m) during the first transect.

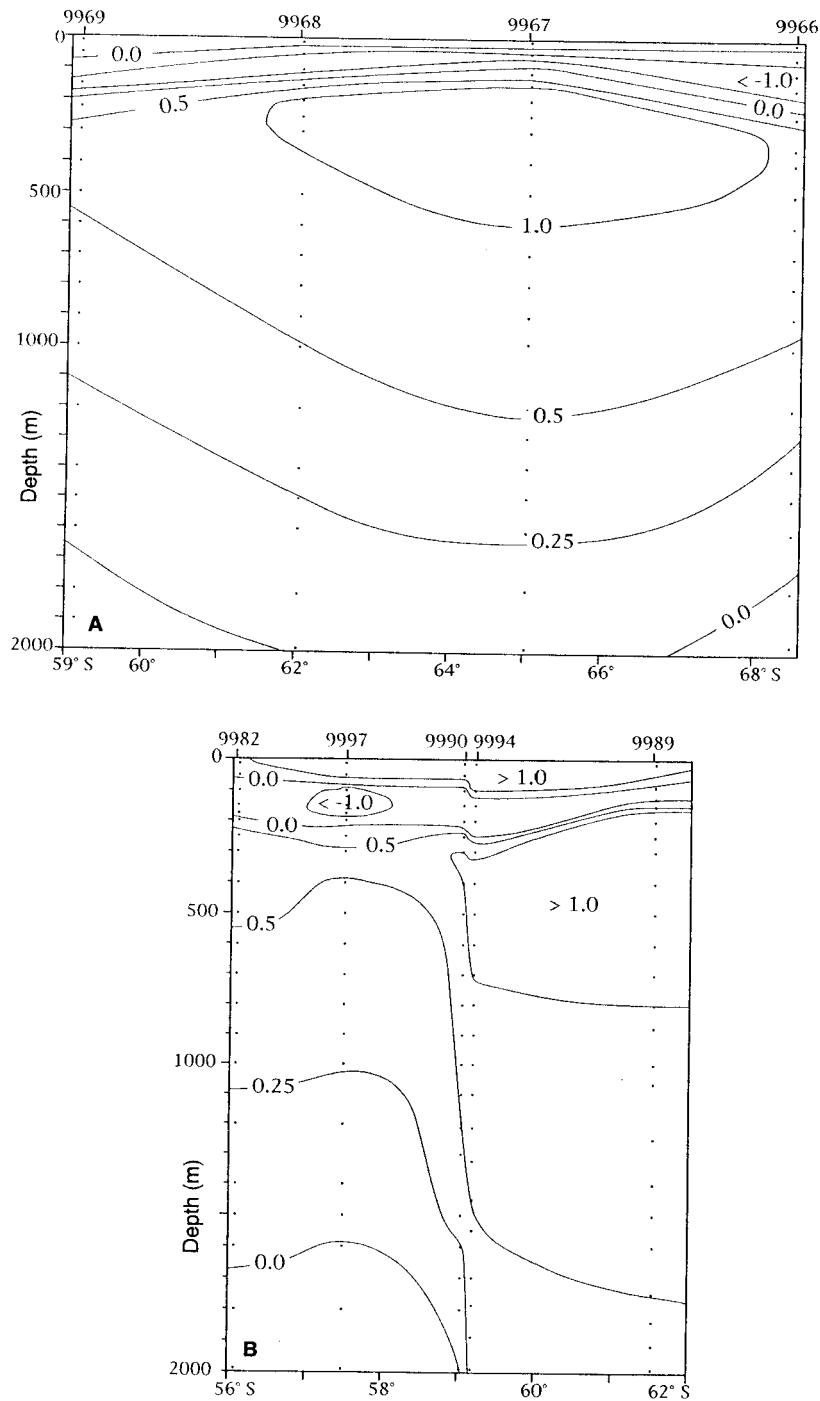


Figure 3. Temperature structure of the water column (0–2000 m) during (A) the second, and (B) the third transect.

(9961) is typical of ACC waters. The marked change between stations 9961 and 9962, resulting from the 3° longitudinal change in position, represents the transition between the warmer waters of the ACC into the Weddell Gyre itself. The remaining, more southerly, stations have a physical structure typical of the Weddell warm regime, indicating the advection of warm CDW waters into the eastern part of the gyre.

During the second transect (Figure 3A) the same basic water masses were present but, although CTD casts were made as far north as 56°S, there was no sign of any effect of the Polar Front during this more westerly transect. Most of the stations lay within the Weddell warm regime, including the two at which biological samples were collected, but the transition toward the Weddell cold regime is indicated by the shoaling of the isotherms below 500 m at station 9969.

The hydrography of the third transect (Figure 3B) was quite different from the previous two. A prior series of CTD casts made, approximately down 20°E, indicated that the Polar Front had retreated to the north of 51°S, and the northern boundary of the Weddell Sea Gyre, the Weddell Front (Gouretski & Danilov, 1993), was located at ~52–53°S. The core of the Weddell cold regime was located at ~58–59°S, being defined by the doming isolines, as well as by the lowest temperatures and salinities of the CDW. At this latitude, Antarctic bottom water ($T \leq 0.0^{\circ}\text{C}$; $34.6 \leq S \leq 34.75$) rose above 2000 m depth. The Weddell warm regime was located south of 59°S.

Species composition

In total 43 species of planktonic cnidarians (23 siphonophores and 20 medusae) were collected. The siphonophores consisted of five physonects and 18 calyphores (Table 2 & Appendix 1). The most abundant siphonophores were the calyphores *Dimophyes arctica*, *Heteropyramis crystallina*, *Diphyes antarctica*, *Muggiaea bargmannae* and *Rosacea plicata*. Of the physonect species, only *Marrus antarcticus* and *Pyrostephos vanhoeffeni* were easily identifiable at the specific level, and the colonies of *Bargmannia* sp. and *Moseria* sp. probably belong to new species. A physonect colony that may belong to a new genus was also collected. Siphonophores were more abundant than medusae in 90% of the samples. Their densities were always highest in the top 500 m (107.4 ± 43.4 specimens per 10^4 m^3) and diminished with depth (25.8 ± 12.3 and 15.8 ± 7.2 per 10^4 m^3 in the 500–1000 and 1000–2000 m depth ranges respectively).

Of the 20 medusan species collected, four were Anthomedusae, eight Trachymedusae, three Narcomedusae, and five Scyphomedusae (Table 3 & Appendix 1). All the species have been recorded previously in the Southern Ocean, with the probable exception of one unidentified narcomedusan. Although *Pantachogon haeckeli* and *Haliscera conica* were numerically the most abundant medusan species, it is difficult to equate their impact on the ecosystem with that of the less abundant, but larger, specimens of *Periphylla periphylla* and *Atolla wyvillei*. None the less, the densities of medusae were highest in the 500–1000 m depth range (15.6 ± 11.9 animals per 10^4 m^3), with 11.1 ± 7.9 and 8.1 ± 5.1 animals per 10^4 m^3 in the 0–500 m and 1000–2000 m depth ranges respectively.

Despite the extent of the depth ranges sampled, clear depth distributional patterns emerge for many species. These can be summarized as broadly epipelagic (0–500 m),

mesopelagic (500–1000 m) and bathypelagic (1000–2000 m), although several species have broader depth distributions. In addition the prevailing hydrographical conditions are seen to affect the geographical distribution of some species.

Epipelagic species

The species that show the strongest tendency towards an epipelagic distribution are mainly calycophoran siphonophores. *Dimophyes arctica* (maximum height anterior nectophore 8 mm) was the most abundant siphonophore and occurred at all the stations, with a maximum of 62 nectophores per 10^4 m^3 (Table 2, Figure 4). Nevertheless it was most abundant between ~ 59 and 62°S , with lowest numbers at the most southerly station. The asexual stage was considerably more abundant than the sexual one, whose eudoxids were distributed erratically throughout the water column. *Dimophyes arctica* has a widespread distribution in the world's oceans, from the Arctic to the Antarctic, but generally is more abundant at higher latitudes. Maximum densities of this species, in the North Atlantic, are usually found in the top 600 m of the water column, but at higher latitudes a deep population can also be found in the 1000–2000 m depth range (Pugh, unpublished data). This species can tolerate a wide temperature range (-1.13 to 22.05°C ; Totton, 1954), but shows higher abundances at the lower end of this range.

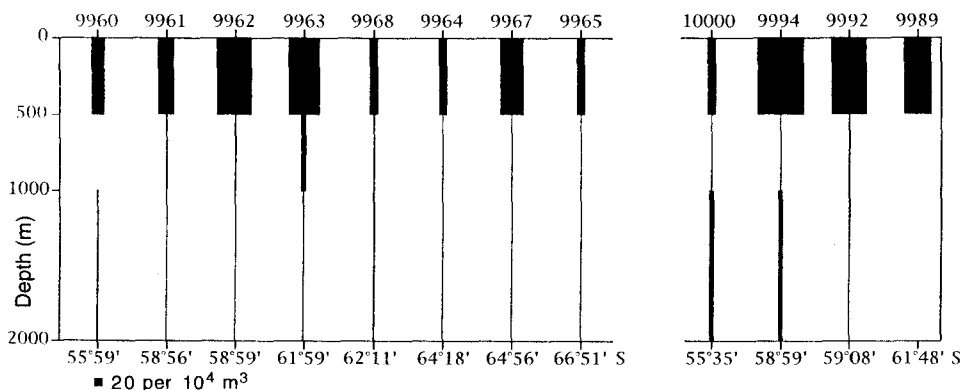


Figure 4. Depth and latitudinal distribution of *Dimophyes arctica* along the three transects (1 & 2 combined).

Crystallophyes amygdalina (anterior nectophores up to 9 mm in height) had a similar, but slightly more erratic, distribution (Table 2), with up to 14 posterior nectophores per 10^4 m^3 present in the top 500 m. It was not found in the Weddell cold regime (station 10000). The relatively few published records (e.g. Totton, 1954) for this species indicate that it has a widespread distribution. However, it is more commonly found at higher latitudes, including the Arctic (Pagès, unpublished data). It occurs throughout the water column, down to a depth of 3000 m, but previously it had been found mainly at meso- and bathypelagic depths.

Muggiaea bargmannae (maximum nectophore height 8 mm) showed a distinct latitudinal change in its abundance (Figure 5, Table 2). It was found almost exclusively within

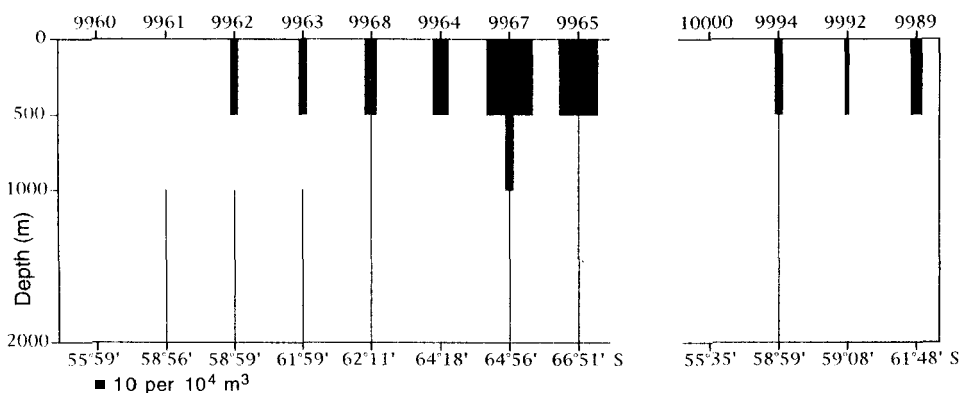


Figure 5. Depth and latitudinal distribution of *Muggiaea bargmannae* along the three transects (1 & 2 combined).

the Weddell warm regime, and showed a steady increase in numbers towards the south. No eudoxids were collected, possibly because they were too small to be retained by the 4.5-mm mesh of the RMT8. This species appears to be the only siphonophore to have a bipolar distribution, although several other species are largely confined to higher latitudes. Totton (1954) found it to occur, in the Southern Hemisphere, only to the south of the Antarctic Convergence, while Stepanjants (1967) recorded it, in the Northern Hemisphere, from Okhotsk, Bering, Kurile and Kamchatka waters, in the -1.45 to 4°C temperature range. Margulis (1978) made further observations of the species in the region of the Arctic Front off Greenland. There appear to be no records for the occurrence of this species between 40°N and 35°S , and even some of the records from lower latitudes should be treated with caution, as their exact geographical position or the prevailing hydrographical conditions are uncertain.

Diphyes antarctica (anterior nectophores up to 26 mm in height), although present at all the stations sampled (Table 2), was most abundant within the Weddell Gyre, and only low numbers of the nectophores were found in the warmer waters affected by the Antarctic Circumpolar Current. This species is endemic to the Southern Ocean and the few scattered data indicate that it has a circumpolar distribution (Baker, 1954). Since *D. antarctica* is probably one of the key species in the Antarctic food web, it is imperative that further studies on its ecology and distribution are made.

The distribution of *Rosacea plicata* (definitive nectophore up to 18 mm in length) also appears to be influenced by the prevailing hydrographical conditions. It was most abundant in the north-eastern part of the sampling area (Figure 6), with up to 10.5 definitive nectophores per 10^4 m^3 being present. There was a notable decrease in the numbers of definitive nectophores toward the west and south. The overall distributional pattern appears to be linked to the south-westward intrusion of northerly waters across the Antarctic Circumpolar Current, and thence into the Weddell Gyre close to its north-eastern boundary (see Orsi *et al.*, 1993; Gouretski & Danilov, 1993). It is interesting to note that larval nectophores, whose numbers are included in Table 2 but not shown in Figure 6, were found only at stations 9960 and 9961, indicating that the

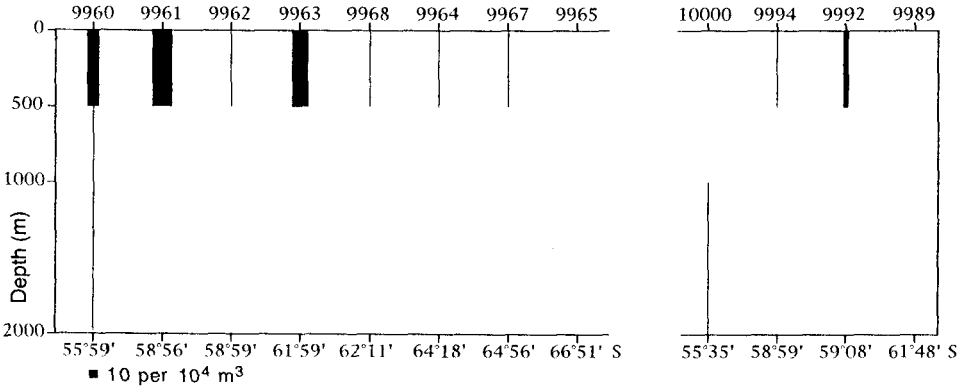


Figure 6. Depth and latitudinal distribution of *Rosacea plicata* along the three transects (1 & 2 combined).

population was reproductively active there. This would be consistent with previous data which indicate that the species has a widespread distribution in the world's oceans, except for polar waters. In the north-east Atlantic (Pugh, 1986) this species reaches maximum numbers between 40 and 50°N, mainly within the 200–500 m depth range.

The only medusa to have a consistently epipelagic distribution was an unidentified narcomedusan species (maximum diameter 20 mm). Although only rarely caught, it was absent from both the more northerly and southerly stations (Table 3). It is probable that the specimens belong to a new species but, because of their poor state of preservation, this remains uncertain.

Epi- and mesopelagic species

The species included in this category were generally commonest in the 0–500 m depth range, but occasionally had a relatively large deeper population. *Calycopsis borchgrevinki* (maximum diameter 22 mm) and *Haliscera conica* (maximum diameter 17 mm) are

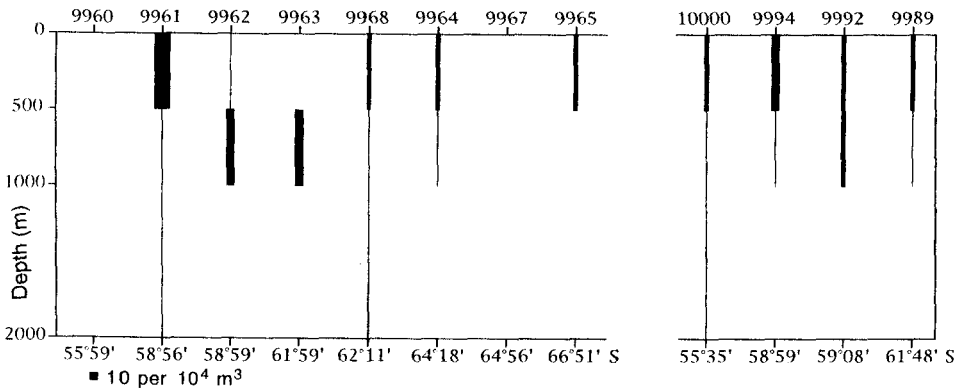


Figure 7. Depth and latitudinal distribution of *Calycopsis borchgrevinki* along the three transects (1 & 2 combined).

examples of this category. *C. borchgrevinki* was absent from the most northerly station (Figure 7), and, somewhat surprisingly, from one of the more southerly ones. However, it was most abundant at station 9961, where the warmer waters from the Antarctic Circumpolar Current occurred. Despite its ease of recognition there are scant data concerning its abundance and distribution; and its polyp stage remains unknown. These data indicate that it is an Antarctic and Subantarctic species with a circumpolar distribution, and the most northerly record is for a specimen caught at the surface near Marion Island (48°38'S 38°04'E) (Moore, 1984). The population of *H. conica* was mainly concentrated in the central part of the sampling area, between 59 and 62°S, and was absent at the most northerly stations. The epi/mesopelagic depth distribution found in the Southern Ocean contrasts with its generally bathypelagic distribution in other areas. It has been found in the Mediterranean, in the Atlantic Ocean, from the Azores to Antarctica, and in southern parts of the Indian and Pacific Oceans (Kramp, 1959).

Vogtia serrata (nectophores up to 17 mm in height) reached maximum abundances of 12.5 colonies per 10^4 m^3 in the 0–500 m depth range (Table 2), based on the normalization of ten nectophores per colony, but had a widespread distribution apparently unaffected by changes in the hydrographical conditions. Previous data for this species in the Southern Ocean deal only with its biomass (Boysen-Ennen *et al.*, 1991). Elsewhere it has a widespread distribution throughout the world's oceans, with the exception of the Arctic. In the North Atlantic it has been found at all depths from the surface to 5425 m, but its peak of abundance lies in the 300–600 m depth range (Pugh, 1991; unpublished data). Pugh (1991) also concluded that the depth distribution of hippopodiid siphonophores, to which this species belongs, is directly related to that of their preferred prey, ostracods.

Mesopelagic species

Lensia havock (anterior nectophore up to 16 mm in height) was mainly found in the 500–1000 m depth zone (Figure 8), and it was most abundant within the Weddell warm regime, with the notable exception of station 9989. Lowest abundances were found at

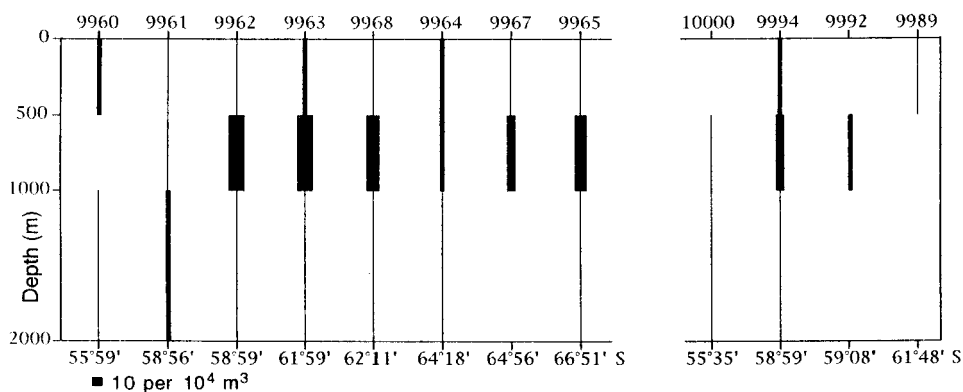


Figure 8. Depth and latitudinal distribution of *Lensia havock* along the three transects (1 & 2 combined).

the lower latitude stations, where its depth distribution was more erratic. This is in agreement with the scant number of published records (Pugh, 1974). It has been collected in all the world's oceans, except the Arctic. Other data for the North Atlantic Ocean (Pugh, unpublished data) indicate that it lives almost exclusively within the 400–1500 m depth range, with a few records from deeper depths. Thus the occurrences above 500 m and below 1000 m can largely be considered to be due to small-scale extensions of its mainly mesopelagic depth range.

The depth distribution of *Lensia achilles* (anterior nectophore up to 14 mm in height) was similar to that of *L. havock*, although it was less abundant (Table 2). It had a fairly even latitudinal distribution during the first two transects, but was less abundant during the third one, and was not found in the waters of the Weddell cold regime. It is widely distributed in the world's oceans, but has not been recorded from the Arctic. Although previous records are few, other data from the North Atlantic Ocean (Pugh, unpublished data) indicate that it is the fourth most abundant *Lensia* species with a widespread depth distribution, from the surface to 5415 m. Maximum densities were found at 53 and 60°N, with the bulk of the population occurring in the 400–800 m depth range. The present data are in accord with this.

Heteropyramis crystallina (nectophore up to 6 mm in height) is included in this group, despite its somewhat erratic depth distribution (Table 2), as other data (Pagès & Pugh, unpublished data) indicate that it is mainly a mesopelagic species. Both asexual and sexual stages were abundant, but nectophores predominated. During the first two transects the bulk of the population was found in the top 500 m in the more northerly waters affected by the Antarctic Circumpolar Current, but was mainly at mesopelagic depths in the Weddell warm regime. Its depth distribution during the third transect was more erratic, but it was present only in low numbers in the Weddell cold regime. In the Southern Hemisphere *H. crystallina* has been found mainly at latitudes south of 40°S. In the Northern Hemisphere it appears to be known only from the Atlantic, again mainly at latitudes higher than 40°N, but not in the Arctic Ocean. However, it is not a truly bipolar species as specimens have occasionally been collected between 40°N and 40°S. The taxonomic status of this species is currently under review, but here we recognize it as a separate species within the genus *Heteropyramis*.

Although the abundance of *Pandea rubra* (up to 100 mm in diameter) was low (Table 3), it occurred mainly in the 500–1000 m depth range in the central part of the sampling area, and only once was found below 1000 m. However, no specimens were found during the third transect. Previous records for this species are scattered throughout the oceans, with the exception of the Arctic, and mainly in deep waters.

Meso- and bathypelagic species

Pantachogon haeckeli (up to 12 mm in diameter) is a good example for this category. It was the most abundant medusan species, and the bulk of the population generally was found in the 500–1000 m depth range (Figure 9). However, at the northerly stations it had a more widespread depth distribution. The hydrographical conditions appear to be playing a part in determining its distribution as it was most abundant, with up to 30

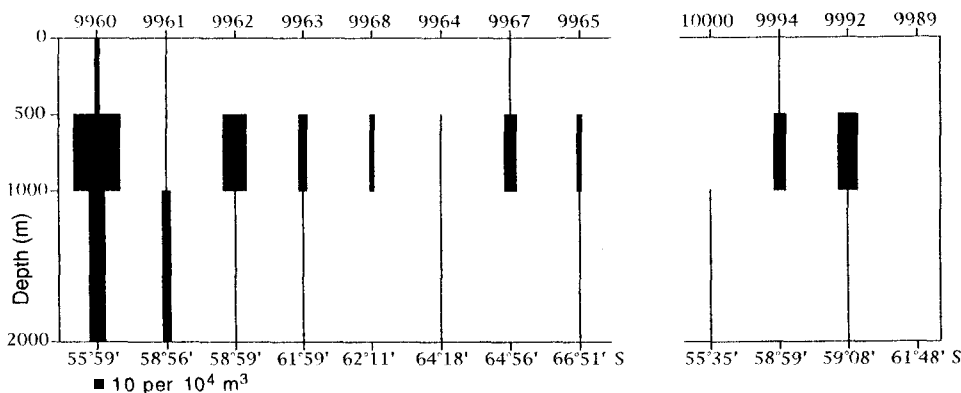


Figure 9. Depth and latitudinal distribution of *Pantachogon haeckeli* along the three transects (1 & 2 combined).

specimens per 10^4 m^3 , at the station closest to the Polar Front. South of $\sim 59^\circ\text{S}$, and in the Weddell cold regime, numbers were relatively low. The present data are in accord with previous studies (e.g. Thurston, 1977) that have shown it to be an abundant mesopelagic hydromedusan in the North Atlantic. Probably it is also present in the Pacific and Indian Oceans, but their mesopelagic medusan populations are poorly known.

Clausophyes moserae (height of anterior nectophore up to 10 mm, posterior nectophore up to 12 mm) had a similar distribution (Table 2). Maximum numbers (~ 11 nectophores per 10^4 m^3) were found at the northerly stations whose hydrography was influenced by the Antarctic Circumpolar Current. It was present only in low numbers in the Weddell Gyre itself. Margulis (1988) pointed out that this species has long been confused with another, *C. ovata* (Keferstein & Ehlers, 1860). Although she considered it to be a subspecies of *C. galeata* Lens & van Riemsdijk, 1908, Pugh & Pagès (1993) considered that there were sufficient reasons to establish *C. moserae* as a distinct species. Since most of the previous records for *C. ovata* actually refer to *C. moserae* it is possible to establish that the species has a widespread geographical distribution, particularly in the Atlantic Ocean. In the North Atlantic (Pugh, unpublished data) it is a very common siphonophore, occurring throughout the water column to a depth of 5430 m, but particularly abundant in the 500–1500 m depth range.

Although *Chuniphyes moserae* (anterior nectophore up to 43 mm in height) had a similar depth distribution to that of *Clausophyes moserae*, being most abundant in the 1000–2000 m depth range (Table 2), it tended to be more abundant at the stations within the Weddell Gyre. This species was originally described from the Antarctic (Totton, 1954), and there are few other records (e.g. Stepanjants, 1967) from widely dispersed areas. This lack of data is probably a result of the scant sampling at the bathypelagic depths at which this species mainly lives (Pugh, unpublished data).

The medusae *Crossota brunnea* (31 mm maximum diameter) and *Aegina citrea* (22 mm maximum diameter) were present throughout most of the sampling area in low numbers (Table 3). Their distribution was erratic, showing no obvious trends, except that the former tended to be less common at higher latitudes. They were only collected at depths

below 500 m. Another scarce species, *Haliceas minimum* (37 mm maximum diameter), had a similar depth distribution. However, it was also found occasionally in the 0–500 m depth range (Table 3) at some stations in the eastern part of the sampling area. *Crossota brunnea* has been found mainly in the Southern Hemisphere at similar depths, and the most northerly record is for a specimen caught at 8°26'N 15°11'W (Kramp, 1959). Both *A. citrea* and *H. minimum* are known to have widespread distributions in the three great oceans, the former mainly at epi- and mesopelagic, the latter at meso- and bathypelagic depths.

Bathypelagic species

Euphysora gigantea (up to 18 mm in diameter) was collected only below 1000 m. However, it was relatively rare and had an erratic distribution throughout the sampling area (Table 3). The few previous records for this species indicate that it occurs, at depth, in the Atlantic region of the Antarctic, with a more or less scattered northward distribution (Kramp, 1959). However, there is one other record from Baja California (600–475 m) (Alvariño, 1976). The single specimen of *Halitrephes maasi* (55 mm in diameter) collected at station 9994 (1000–2010 m) is the southernmost record for this species. Normally it has a bathypelagic distribution throughout the tropical and subtropical regions of the three great oceans (Kramp, 1959), although Larson *et al.* (1991) have made *in situ* observations of it at mesopelagic depths.

Botrynuma brucei (up to 30 mm in diameter) was found at all stations (Figure 10), but was rarest in the Weddell cold regime. Although its highest abundance (~7 specimens per 10^4 m^3) occurred in the 500–1000 m depth range, it was most frequently found between 1000 and 2000 m. This species has a widespread distribution at meso- and bathypelagic depths in all the oceans except the Arctic.

Rarer species

Atolla wyvillei (maximum diameter 78 mm) and *Periphylla periphylla* (maximum diameter 230 mm) were present in low abundances (up to 8 and 2 specimens per 10^4 m^3 ,

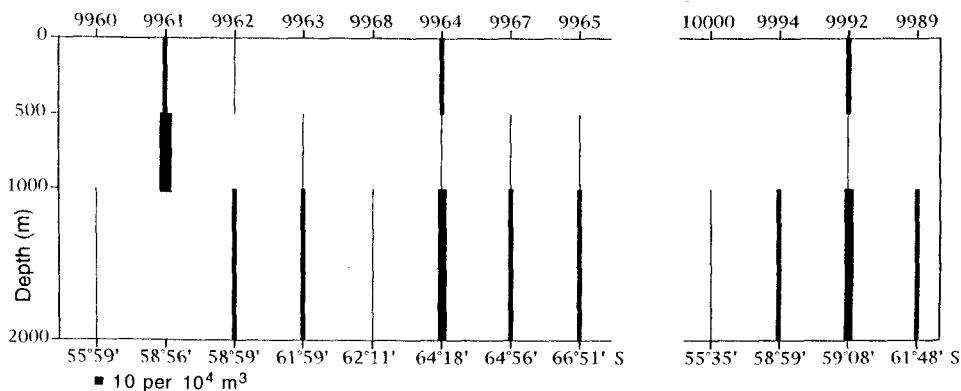


Figure 10. Depth and latitudinal distribution of *Botrynuma brucei* along the three transects (1 & 2 combined).

respectively) at all stations and almost all samples (Table 3). However, the relatively large size of the specimens meant that they contributed greatly to the total biovolume. Both were most frequently found in the 500–1000 m depth range. The two specimens of *Atolla gigantea* (maximum diameter 110 mm) are the first new records for this species since Larson (1986) established it as valid. It is known only at meso- and bathypelagic depths, from the Gulf of Panama and in all sectors of the Southern Ocean. The rarity *A. chuni* in our samples, as compared with previous data (Larson, 1986), may be the result of the prevailing hydrographical conditions as it occurred only at the stations closest to the Polar Front.

The geographical and depth distributions of *Nectadamas diomedae* and *Nectopyramis natans* were summarized recently by Pugh (1992). His data indicated that in the North Atlantic both species, but particularly *N. natans*, generally are found at lower latitudes. The presence of the latter species in the Southern Ocean is, therefore, somewhat surprising, and our data (Table 2) greatly enhance our knowledge of the distribution of this rare species. In Table 2, the numbers for the asexual stage of *N. natans* refer to larval nectophores, except for station 9962#3 where one definitive and one larval nectophore were present. At stations 9963#5 and 9967#4, both larval (two and one) nectophores and eudoxids (one and one, respectively) were present.

The new records for *Clausophyes galeata* (Table 2) similarly contribute greatly to our limited knowledge about this species. It was present only in the central part of the sampling area, between 59 and ~65°S, at all depths, but mainly between 1000 and 2000 m. Its presence in the upper 500 m was restricted to the western part. It has been collected in the three great oceans, and in the Antarctic, but records are scarce. The few records from the North Pacific cover a large area, including Japan and the Philippines (Bigelow, 1913), Kamchatka (Stepanjants, 1967), and the north-east China Sea (Zhang & Zhang, 1980). In the Southern Hemisphere it has been recorded only once (Totton, 1954), off the Antarctic ice edge in the Australian basin. However, recent RRS 'Discovery' collections have revealed several specimens at 41°N 21°W and 47°N 19°W (Pugh, unpublished data), all at depths greater than 3976 m and relatively close to the sea bed.

In summary, of the 43 cnidarian species identified only a few have a geographical distribution restricted to the Southern Ocean. Most of these endemic species, that is *Diphyes antarctica*, the probably new narcomedusan species, and *Calycopsis borchgrevinki*, are mainly epipelagic in their depth distribution. However, the endemic physonect siphonophore, *Pyrostephos vanhoeffeni*, has a more widespread depth distribution. In addition, our two deeper records for the endemic medusan, *Ptychogena antarctica*, extend its known range, as previously it has been found only inshore and close to the surface.

The distribution of several of the epipelagic species was clearly affected by the prevailing hydrographical conditions, although the most abundant siphonophore, *Dimophyes arctica*, had a widespread distribution throughout the sampling area. Three species, *Diphyes antarctica*, *Muggiaea bargmannae* and *Crystallophyes amygdalina*, were largely confined to the Weddell warm regime, and *M. bargmannae* showed a marked increase in numbers at the more southerly stations. In contrast, the endemic medusan,

Calycopsis borchgrevinki, although present at most of the Weddell Gyre stations, reached maximum numbers at the station (9961) affected by the Antarctic Circumpolar Current. However, it was absent from the station (9960) to the south of the Antarctic Polar Front. Finally, the other common epipelagic siphonophore, *Rosacea plicata*, was most abundant in ACC waters, where it was reproductively active. *Muggiaea bargmannae* is presently the only known siphonophore with a bipolar distribution, while the other non-endemic species have widespread distributions throughout the world's oceans. All these, however, tend to reach maximum abundances at higher latitudes, but it is interesting to note that, whereas *D. arctica* and *C. amygdalina* have been found in the Arctic Ocean, *R. plicata* has not.

Three other siphonophore species, *Vogtia serrata*, *Lensia achilles* and *Heteropyramis crystallina*, which live at upper mesopelagic depths, also have a similar widespread distribution in the world's oceans, but with maximum abundances at higher latitudes. None of them has been recorded in the Arctic Ocean. All were found throughout the study area, with the exception of *L. achilles* which was not found in the Weddell cold regime. However, the distribution of other, deeper-living, mesopelagic species did appear to be affected by the hydrographical conditions. *Pantachogon haeckeli* and *Clausophyes moserae* were most abundant in the waters affected by the ACC or at the northern end of the Weddell warm regime; whereas *Lensia havock* and *Haliscera conica* were most frequently found within the Weddell warm regime itself. Again all these species have widespread geographical distributions, except for the Arctic. It is probable that most of these common mesopelagic cnidarians, and some more bathypelagic ones like *Botrynema brucei* and *Chuniphyes moserae*, have been advected into the Southern Ocean by warm Atlantic deep water. None the less, it is apparent that the Southern Ocean is acting as a source for some of the deeper-living species that are transported to lower latitudes by the Antarctic bottom water. This appears to be the case for the medusae *Euphysora gigantea*, *Crossota brunnea*, *Atolla chuni* and *A. gigantea*, and the siphonophore *Marrus antarcticus*.

CONCLUSIONS

The number of cnidarian species identified from the 12 stations sampled was very high in comparison with that recorded in earlier works concerned with Antarctic zooplankton communities, although specialist works (Alvarinho *et al.*, 1990, ~80 siphonophore species; Kramp, 1959 and Larson, 1986, ~85 medusa species) list more. The present high diversity in the Weddell Gyre region cannot be attributed wholly to the fact that the depth range sampled was greater than that in most previous studies, as only six relatively rare species were found exclusively below 1000 m. None the less, since we caught only four of the 12 known scyphomedusan species that occur south of the Polar Front (Larson, 1986), it is evident that the population of planktonic cnidarians in the Southern Ocean is even more diverse, and its impact on the ecosystem has yet to be fully understood.

Although many of the cnidarian species tended to have either an epi-, meso- or

bathypelagic depth distribution, they also occurred frequently at other depths. Such a widespread vertical distribution is probably a reflection of the narrow range of temperatures (-1.77 to $+1.99^{\circ}\text{C}$) found within the 0–2000 m depth range. The coldest temperatures ($<0^{\circ}\text{C}$) were restricted to the top 200 m and it is probable that, with a finer depth scale of net sampling in the upper 500 m, where all the water masses were present, more structure would be found. However, the greatest number of cnidarian species (34) in our study was found in the 500–1000 m depth range. This suggests that several species are adapted to living at mesopelagic depths rather than throughout a particular water mass, as the almost isothermal Circumpolar deep water extended from ~200 m to below the maximum sampling depth. This is in accordance with studies on the depth distribution of cnidarians in other areas of the world's oceans. In addition, 38 species (20 siphonophores and 18 medusae) were collected below 1000 m, indicating a high diversity at bathypelagic depths.

Although the specific densities were low at all stations and depths, this is the normal pattern for macroplanktonic cnidarians in oceanic waters (Biggs *et al.*, 1981; Pugh, unpublished data). None the less, these highly predacious carnivores can still have a great impact on the ecosystem (Alldredge, 1984). The smaller calycophoran siphonophores were concentrated in the upper 500 m of the water column, where total numbers averaged $\sim 110/10^4 \text{ m}^3$ and peaked at $170/10^4 \text{ m}^3$. The numbers of larger calycophores increased with depth, being most abundant in the 1000–2000 m depth range.

Typically, medusae were most abundant at mesopelagic depths and, in the 500–1000 m depth range, densities reached $46/10^4 \text{ m}^3$, averaging $\sim 15/10^4 \text{ m}^3$. It is, of course, probable that the abundances of both siphonophores and medusae are higher, as nets are not the ideal method for collecting gelatinous organisms, and many fragile species are destroyed or reduced to unidentifiable fragments. None the less, the lower abundance of medusae belies the fact that their displacement volume was usually considerably higher than that of the siphonophores. For instance, at station 9964#1, a single specimen of *Periphylla periphylla* contributed 4000 ml to a total catch biovolume of 4470 ml. On average, cnidarians contributed 52.6% to the biovolume of the samples, although the range was high (5.0–93.1%). In the majority of cases, siphonophores made up <5% of this volume, but in the 0–500 m depth range they frequently contributed more (up to 50%). In the 1000–2000 m depth range, cnidarians on average contributed ~60% to the total biovolume. This suggests, taking into account the fact that these gelatinous organisms shrink considerably during preservation, that they must be having a considerable impact on the ecosystem at such depths. However, very little is known about planktonic communities at depths greater than 1000 m in the Southern Ocean. The other main contributors to the biovolume of the catches were chaetognaths, fish and decapods, except at station 10000, where salps were predominant at all depths. Occasionally small quantities of krill were collected, thereby considerably reducing the percentage contribution of cnidarians to the total biovolume.

The significance of the proportionally high biovolume of the cnidarians, particularly the medusae, is further enhanced by the fact that these animals have large 'encounter

zones' (Madin, 1988), thereby further increasing their impact. The importance of the concept, that it is more important to consider the spatial scale within which an animal moves, feeds and responds rather than to consider its absolute abundance, has been discussed luminously by Swanberg *et al.* (1990). Thus, if one is to consider the impact of an individual organism, it is more important to consider m^3 per organism than organisms per m^3 . This concept is largely ignored by modellers, as, indeed, are gelatinous plankton themselves. For instance, Hopkins *et al.* (1993) barely touched on the role that gelatinous organisms play in the trophic ecology of the Scotia Sea zooplankton community despite the fact that they were the second most diverse group, after copepods. We still have a long way to go before we can understand the Antarctic ecosystem, and the roles that gelatinous organisms play.

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Appendix 1. *Rare cnidarian species in collections.*

Medusae

- Ptychogena antarctica* Browne 1907 – 1 each at stations 9967#3 and 9992#3.
- Haliscera bigelowi* Kramp 1947 – 1 at station 9992#2.
- Halitrephes maasi* Bigelow 1909 – 1 at station 9994#4.
- Atolla chuni* Vanhöffen 1902 – 1 each at stations 9960#5 and 10000#4.
- Atolla gigantea* Maas 1897 – 1 each at stations 9965#1 and 10000#4.
- Tetraplatia volitans* Busch 1851 – 4 at station 9960#5, 1 at station 9994#3.

Siphonophorae

- Physonect* sp. – 72 n., 261 b. at station 9964#1; 1 p. at station 9965#3.
- Moseria* sp. – 4 n. at station 9962#2.
- Pyrostephos vanhoeffeni* Moser 1925 – 9, 11, 19, 28, 6 and 20 n. at stations 9960#4, 9964#2, 9967#2, 9992#2, 9994#2 and 9994#4 respectively.
- Bargmannia* sp. – 28 n. at station 9960#4.
- Nectadamas diomedae* (Bigelow 1911) – 1 e. each at stations 9961#2 and 9963#5.
- Vogtia spinosa* Keferstein & Ehlers 1861 – 2 n. at station 9992#3.
- Lensia hostile* Totton 1941 – 2, 1 and 1 an. at stations 9961#2, 9965#3 and 9968#2 respectively.
- Lensia reticulata* Totton 1954 – 1 an. at station 9963#5.
- Chuniphyes multidentata* Lens & van Riemsdijk 1908 – 2 an, 2 pn. at station 9961#3.

an., anterior nectophore; b., bract; e., eudoxid; n., nectophore; p., pneumatophore; pn., posterior nectophore.