VERTICAL DISTRIBUTION AND ABUNDANCE OF PELAGIC CNIDARIANS IN THE EASTERN WEDDELL SEA, ANTARCTICA

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The species composition, abundance and vertical distribution of micronektonic cnidarians has been investigated in the upper 2800 m at Discovery Station 9969, located in the cold regime in the eastern Weddell Sea, Antarctica. In total 22 siphonophore and 20 medusan species were identified. Overall siphonophores were more abundant than medusae, but the latter usually contributed much more to the biovolume. On average, cnidarians contributed more than 50% to the total biovolume of each catch; and they contributed >70% to the combined total of all the samples. Despite the high water content of these animals, these large biovolumes meant that the cnidarians formed ~25% of the total carbon in each catch. The possible impact of these gelatinous cnidarian populations on the ecosystem is discussed.

The vertical distribution of some individual species showed that they occurred over relatively discrete depth ranges, implying that the usage of such general terms as epi-, meso- or bathypelagic could be misleading. Thus the three most common siphonophore species, *Diphyes antarctica*, *Dimophyes arctica* and *Muggiaea bargmannae*, each reached a peak abundance in a different depth range within the 0–500 m depth range, while a fourth, *Crystallophyes amygdalina*, was found almost exclusively between 400 and 600 m. Even deeper living species were found to occur within restricted depth ranges. Thus, with one exception in all cases, the medusae *Atolla wyvillei* and *Halicreas minimum*, and the siphonophore *Chuniphyes moserae* were found only in the 700–2200, 500–1800 and 1200–2800 m depth ranges respectively.

INTRODUCTION

In a previous paper (Pagès et al., 1994) we noted that there was a dearth of information on the ecological role of pelagic cnidarians in the Southern Ocean, and of their general exclusion from ecosystem models. This is despite the fact that, in the eastern Weddell Sea, they made up more than 50% of the micronekton biovolume. Although, as with all gelatinous organisms, their wet/dry weight ratio is high, and their carbon content is low, this does not mean that they have an insignificant impact on the ecosystem. Indeed, Larson (1986a) has suggested that there are positive advantages to having a high water content. The large encounter zones that the cnidarians exhibit, together with their almost insatiable appetite, further enhance the relative status of these animals.

Several of the more recent studies dealing with the zooplankton/micronekton populations of the Southern Ocean were reviewed in a previous paper (Pagès et al.,

1994). Since then, a few others have been published, for example, Pagès & Kurbjeweit (1994) have made detailed studies on the mesoplanktonic cnidarians collected from a transect of stations across the Weddell Sea. Although their samples were collected by much smaller nets (0·25 m²), with a considerably finer mesh size (100 μm), their data are of considerable relevance to the present paper. Hosie (1994) studied the macrozooplankton community in the Prydz Bay region, as part of the BIOMASS programme. That study was aimed at the biology of krill and 'to improve our knowledge of the other zooplankton, necessary for understanding all aspects of the Antarctic marine ecosystem'. Although detailed statistical analyses were carried out to characterize the various faunal assemblages, siphonophores were unfortunately treated as a whole, so that any specific distributions could not be assessed, and only a single medusan species was considered. Finally, Pakhomov et al. (1994) considered the macrozooplanton/micronekton communities in the vicinity of the Antarctic Polar and Subtropical Fronts. Tunicates dominated the former, and the overall contribution of cnidarians was low. However, in the region of the latter front, cnidarians contributed, on average, more than 25% to the total community abundance, and on occasions this percentage rose to more than 70%.

Although the depth ranges (~0–500, 500–1000, and 1000–2000 m) sampled during a previous study (Pagès et al., 1994) were rather extensive, our results indicated that the depth distribution of many cnidarian species could be broadly categorized as epi-, meso- or bathypelagic. Nonetheless, it was suggested that with a finer depth scale of sampling, particularly in the top 500 m, where the coldest waters and different water masses were to be found, more structure to the depth distribution of the species might become apparent. In order to investigate this point we have examined the material from Discovery Station 9969 (59°06′S 20°06′E), in the Weddell Sea, where the water column was sampled in 100, 150 or 200 m depth bands to a depth of 2800 m.

MATERIALS AND METHODS

During RRS 'Discovery' Cruise 100 to the African sector of the Southern Ocean, a series of 18 hauls was carried out (21–23 February, 1979) over discrete depth ranges from the surface to 2800 m using an opening-closing RMT 1+8M multi-net system at Station 9969 (59°06′S 20°06′E). The water depth at this station was ~5100 m. Hauls were made over approximately 100 m depth ranges in the top 1000 m of the water column; except that the 100–400 m depth range was covered by two hauls (100–250 m and 250– 400 m) so that the former of these encompassed the cold-water (minimum -1·18°C) zone. The hauls were of 1 h duration, except for the 0–100 m depth range where the nets were fished for only 30 min. Below 1000 m the hauls were of 2 h duration and covered approximately 200 m depth ranges. Cruise time constraints, in conjunction with the shortness of the nights, meant that a day and night series of hauls could not be carried out. However, to avoid any confusions that might arise from diel vertical migration all the hauls in the top 1000 m were carried out during the day. It is reasonable to expect, particularly at such high latitudes (Angel, 1985), that if any of the cnidarians present underwent a diel vertical migration then this would take place

within this depth range. The only possible exception might be *Periphylla periphylla*. Below 1000 m, the hauls were usually carried out at night in order to maximize the fishing effort within the limited time available. The volumes of water filtered were calculated from the flowmeter data using the standard formulae. Samples were fixed in 5% borax buffered formalin and later transferred into Steedman's preserving fluid.

The RMT8 (mesh size 4·5 mm) samples from 'Discovery' Station 9969 were sorted into major taxa and counted. Copepods were excluded from this analysis because they are not sampled quantitatively by this net. Indeed, Hubold et al. (1988) have shown that copepods are not sampled quantitatively by nets with a mesh size >500 μm. The medusae and siphonophores, both asexual and sexual stages, were identified; and the total biovolume (displacement volume) of all major taxonomic groups measured. No account was taken of the probable shrinkage, during preservation, of the gelatinous animals. All these data were normalized to 10^4 m^3 of water filtered. For a few siphonophore species it is necessary to normalize the abundance data further (see Pagès et al., 1994). In this respect, and for the present data, the numbers of *Rosacea plicata* were very low; while the population of *Vogtia serrata* included a large number of larval nectophores that were counted as individuals. The biovolume data were converted to carbon using data from Larson (1986a) for the cnidarians, and the corrected formula in Wiebe (1988) for the remainder of the catch. Larson's mean DW%WW and Carbon%DW, has been taken and a density of 1·025 assumed, to produce a factor of 0·0003649 to convert mls 10^{-4} m^3 to mg C m^{-3}. Allowing for the probable shrinkage of the cnidarians during preservation, it is likely that the calculated carbon value will be an underestimate. The cnidarian specimens are currently housed in the Southampton Oceanography Centre (SOC) collections.

RESULTS AND DISCUSSION

Hydrography

The hydrography of 'Discovery' Station 9969 (Figure 1) was discussed in a previous paper (Pagès et al., 1994) in relation to the more extensive sampling programme in the eastern part of the Weddell Gyre. This station was situated within the Weddell cold regime and was characterized by Antarctic surface water (see Gouretski & Danilov, 1993), with a temperature of >0·8°C extending down to ~100 m depth. This overlay a band (100–250 m) of cold winter water, where the temperature dropped to -1·18°C. The reverse thermocline then increased the temperature to ~0·6°C. Below this was a band of comparatively cold warm deep water, with the 0·5°C isotherm being relatively shallow (~520 m) and the 0·0°C isotherm being reached at ~1700 m. Antarctic bottom water was then found at the deeper depths. It is apparent that this station lay toward the easternmost boundary of the Weddell cold regime, as a station (Station 9990) a little over 100 km to the east appeared to lie in the transition between the warm and cold regimes (see Pagès et al., 1994). However, the boundary between the two regimes was not meridional as Station 9997, which was positioned ~250 km to the north-east, clearly also lay within the Weddell cold regime.
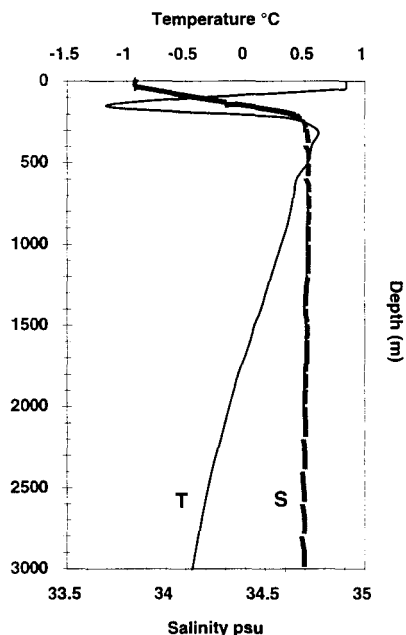
Figure 1. Profiles of temperature and salinity at 'Discovery' Station 9969.

General abundance, biovolume and biomass

The vertical distribution of the major micronektonic taxa collected at 'Discovery' Station 9969 is shown in Figure 2A, and those for siphonophores and medusae are shown in more detail in Figure 2B,C respectively. Cephalopods were only present in very low numbers, and have been excluded here. It can be seen that the highest numbers of micronekton were found in the top 700 m, with a maximum in the 400–500 m depth range, where a large number of euphausiids were found. Between 700 and 1800 m the micronekton numbers were at a fairly stable level, but below this there was a marked decline to very low numbers. Chaetognaths were numerically the predominant taxon throughout most of the water column, and averaged over 50% (range 26·5–72·9%) of the total numbers. In four hauls (between 1200 and 1800 m, and in the 2200–2400 m depth range) they were surpassed by small euphausiids, which were the second most abundant group, averaging ~25% of the total. Cnidarians averaged 15% of the total numbers. However, below 2000 m they were relatively more abundant, reaching over 40% of the total in the 2400–2600 m depth range. Siphonophores (Figure 2B) were more abundant than medusae (Figure 2C) in 77% of the samples, particularly those in the top 800 m. This is in accord with our previous data (Pagès et al., 1994). The highest concentrations of both siphonophores and medusae were found in the 250–500 m depth ranges, peaking at 133·3 and 53·8 specimens per 10^4 m^3 respectively, in the 400–500 m depth range. Below this depth, the numbers of siphonophores remained fairly high down to ~800 m. However, the numbers of medusae declined steadily to reach a relatively stable number (~8 specimens per 10^4 m^3) at depths below 800 m. Although the mainly epipelagic distribution of siphonophores is to be expected, the presence of
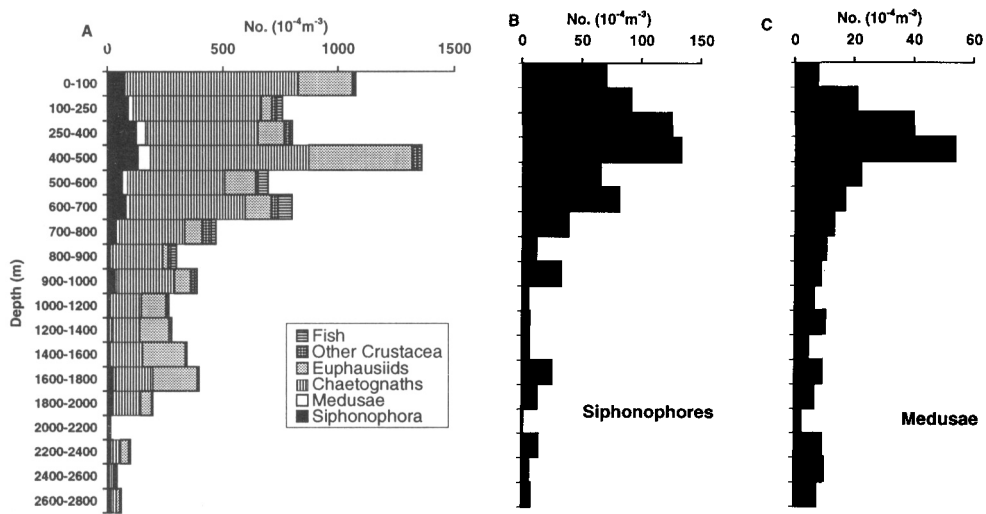
Figure 2. Vertical distribution of individuals (numbers per 10^4 m^3) of various taxa collected in the RMT8 samples at 'Discovery' Station 9969: (A) all sorted taxa; (B) siphonophores; and (C) medusae. Note: in this, and subsequent figures, the depth axis gives equal prominence to each haul, irrespective of its depth range.

peak numbers of medusae in the top 500 m contrasts with the general trend found for other data from the Southern Ocean, where they are usually most abundant in the 500–1000 m depth range (Pagès et al., 1996). This disparity was caused largely by the unexpectedly high numbers of the narcomedusan *Solmundella bitentaculata*, and also of *Haliscera conica*, in the 0–500 m hauls.

Although chaetognaths were numerically the dominant taxon in the samples, a completely different picture emerges when the vertical distribution of the biovolume of the various taxa is considered (Figure 3A,B). It should be noted that one very large squid, *Mesonychoteuthis hamiltoni*, with a mantle length of 117 cm, was caught in the 2000–2200 m depth range (see Rodhouse & Clarke, 1985). As the squid was almost certainly dead before collection, its presence in the sample was treated as a case of serendipity, and its volume has been ignored. Siphonophores, although usually more abundant than medusae, contributed less to the overall biovolume of each catch due to their smaller size. Their average contribution was 9·4 ±8·9% (range 0·6–31·8%) (Figure 3B). Nonetheless, siphonophores formed the largest component of the biovolume of the two shallowest samples. On the other hand, the medusae contributed, on average, 45·1 ±28·0% to the total, although the range (2·9–94·0%) was high. They were the largest contributor to the biovolume in 13 of the 18 hauls (Figure 3B). Collectively, the siphonophores and medusae contributed >50% to the biovolume of half of the individual hauls, and >70% to the grand total biovolume of all of the hauls. The very considerable contribution of medusae to three of the hauls was mainly due to the presence of large specimens of *Periphylla periphylla*, including a single specimen, in the 250–400 m depth
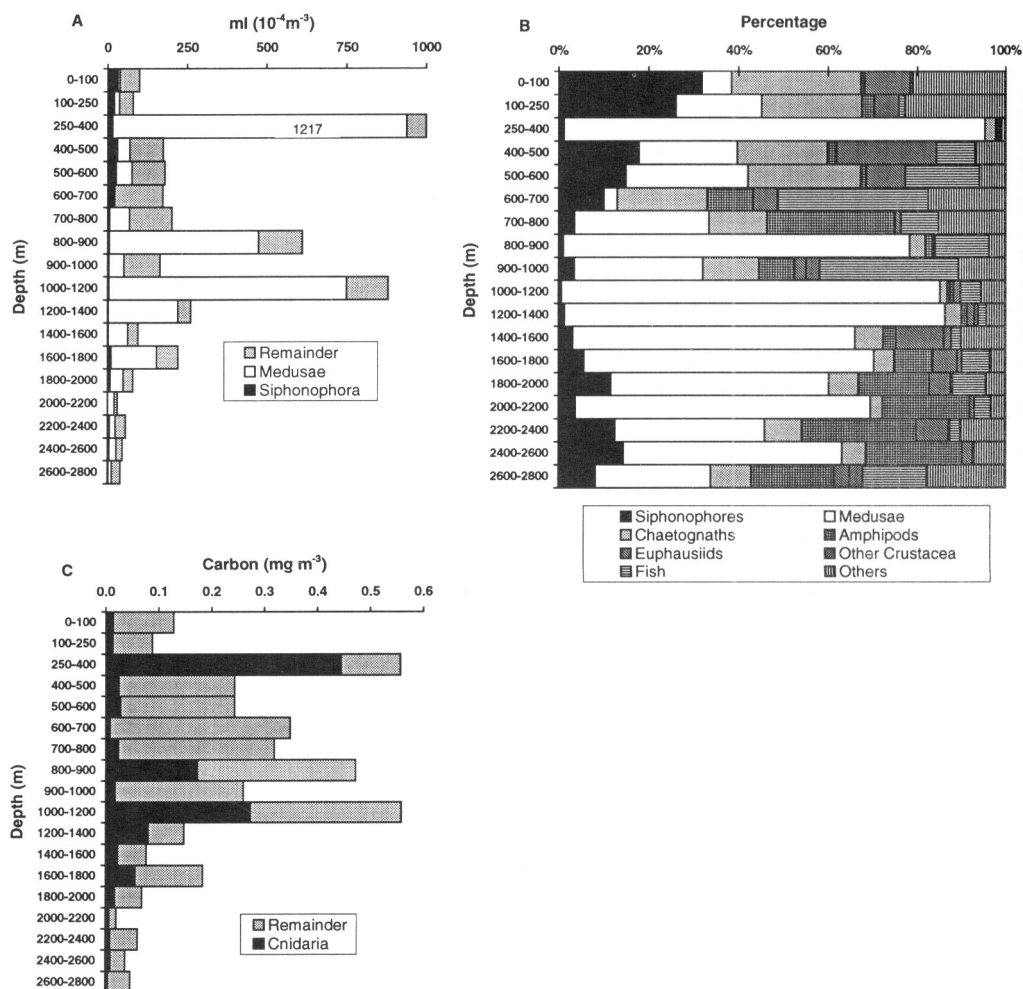
Figure 3. (A) The contribution of siphonophores and medusae (mls 10^{-4} m^3), and (B) the percentage contribution of the various taxa to the total biovolume of the catch from each depth range. (C) The contribution of cnidarian carbon to the total in each depth range.

range, that had a biovolume of 4000 ml. In the 1000–1200 m depth range a single specimen of the scyphomedusan *Deepstaria enigmatica* also made a substantial contribution (3800 ml). Chaetognaths, small euphausiids and fish tended to make up much of the remainder of the biovolume, particularly in the hauls from the top 1000 m of the water column. However, large gammarid amphipods occasionally made a substantial contribution, particularly at the deepest depths sampled. It is interesting to note that much of the residue of the hauls at these deeper depths was made up of carcasses of euphausiids, which may be a substantial source of food for the abyssal benthos (Sokolova, 1994).

The data for the carbon content of the micronekton (Figure 3C) show that the gelatinous organisms make a comparatively large contribution to the overall biomass

of the samples. This is despite the fact that no account was taken of the probable underestimation of their biovolume, due to the loss of parts during collection and to shrinkage during preservation. They averaged 25·3% of the total carbon, although the range (2·4–75·3%) was large. Nevertheless, in two depth ranges, where the biovolume was dominated by large medusan specimens, these animals contributed >50% to the total micronekton carbon.

Species composition

Both siphonophores and medusae were present in every depth range sampled. A total of 22 species of siphonophores and 20 of medusae were identified (Tables 1 & 2, respectively). The siphonophores consisted of the same five physonect species, and 16 of the 18 calycophorans that had been recorded during a previous study (Pagès et al., 1994), plus one additional species. For the medusae, 17 of the species were the same as those collected in our previous study. The patterns of vertical distribution of the main cnidarian species usually followed the general classification as adopted by Pagès et al. (1994), that is 'broadly' epipelagic (0–500 m), mesopelagic (500–1000 m) and bathypelagic (>1000 m), and will be discussed under the previous headings. However, with narrower depth ranges being sampled, such generic terms often become inappropriate, as the vertical distributions of many species either occupy only a part of one of these zones or span more than one of them. In addition, because the top 500 m was subdivided into four depth ranges, it is possible to reconsider the boundary between the epi- and mesopelagic zones. For the purposes of this paper this boundary is considered to lie in the region of 250–300m depth, below the permanent thermocline. This is accord with previous authors (see Mackie et al., 1987; Marshall, 1979). Thus the depth ranges from the three main zones coincide, approximately, with the three main water masses present.

'Epipelagic species'

The three species of calycophoran siphonophores most commonly found in these cool Antarctic waters were predominantly found in the 0–500 m depth zone. The hydrography within this depth range showed that there was a layer (~0–100 m) of relatively warm Antarctic surface water, formed from the winter water by summer heating. This overlay the cold remnant of the winter water, and beneath this there was a (reverse) thermocline, so that below ~250 m we enter the realm of the, in this case relatively cold, warm deep water. The latter we presently consider to lie in the mesopelagic zone.

Diphyes antarctica was the most abundant cnidarian species in the upper 250 m, with maximum numbers of the polygastric stage (34·6 nectophores per $10^4 m^3$) in the 0–100 m depth range (Figure 4), where the relatively warm Antarctic surface water was found. On the other hand, the eudoxid stage of this species peaked in the cold 100–250 m layer (56·0 gonophores per $10^4 m^3$) (Table 1). High densities of both stages occurred down to 500 m, and there was a long distributional tail down to 2800 m. The latter may be the result of surface contamination during the launch and recovery of the nets. However, Pagès & Kurbjeweit (1994) did not find any specimens of this species in their 0–50 m

Table 1. Vertical distribution of siphonophores (numbers per $10^4\,m^3$) in the RMT8 samples collected at 'Discovery' Station 9969.

	0-100	100-260	250-410	390-505	500-600	600-700	700-805	800-900	900-1000	1000-1205	1200-1400	1395-1600	1610-1800	1800-2000	2000-2200	2200-2400	2390-2600	2595-2800
Physonecta																		
Physonect sp.		0.29		0.36														0.15
Marrus antarcticus		1.03	0.30				1.21	1.52	1.21	1.02	0.89					0.15	0.15	0.15
Moseria sp.									0.30								0.15	0.15
Bargmannia sp.													0.17	0.15	0.16	0.76		
Pyrostephos vanhoeffeni										0.34								
Calycophora																		
Rosacea plicata			1.82							0.08			0.17					
Nectopyramis natans											0.30	0.32	0.30	0.45+0.30		0.15		0.15
Nectadamus diomedeae																		
Vogtia serrata	0.06	1.03	17.18	17.23	13.99	10.43	0.09	0.39	0.64	0.34	0.15	0.16	0.09	0.15		0.30	0.02	0.21
	2.42	6.45	43.03	36.67	8.58	4.17			0.61	0.17	0.03	0.11	0.17					0.30
Diphyes antarctica	34.55	25.22	7.58	0.72	0.32	0.96	0.91	0.30	0.30	0.17	0.15	0.48		0.15		0.30	0.15	0.15
	22.42	56.01	31.82	9.26	1.59	0.96	2.12		0.61	0.51		0.32	0.51			0.30	0.46	0.89
Lensia achilles							1.52	0.61										
Lensia havock			2.23			8.98	18.48	6.67	3.03	0.17	0.30	0.16	0.34			1.06	1.99	0.30
Lensia hostile													0.17	0.15		0.45	0.15	
Gilia reticulata					0.95	0.96	0.91		0.61				0.15			0.45	0.15	0.44
Muggiaea bargmannae	2.42	14.08	4.85	31.33	1.27	1.92	0.91						0.34			0.61	0.31	0.15
Dimophyes arctica	13.94	9.97	33.33	3.56	1.59	4.81	2.73	1.52	3.94	1.19	0.15	0.64	0.34	0.30		1.82	0.15	1.77
	3.03	32.85	27.27	7.12	2.54	5.13	2.73	0.30	1.52	0.17	0.30	0.32	0.34	0.33		0.30	0.15	0.44
Clausophyes moserae											0.74		0.30	0.30		0.45		0.89
Clausophyes galeata										0.85	0.15	0.64	2.57	1.81			0.15	
Clausophyes laetmata													0.60					
Chuniphyes moserae							0.30		0.30		1.48	2.90	18.99	8.45	0.98	6.52	2.60	1.77
													0.17					
Crystallophyes amygdalina			0.30								0.30		0.17					
Heteropyramis crystallina			26.70	8.90	29.59	43.96	6.67	1.21	19.39	1.02	1.18	0.64	0.68			1.36	0.46	1.03
	0.30		0.30	4.63	4.45	11.55	5.45	1.82	7.58	0.34	1.33		0.51			0.30	0.15	

Depth Range (m)

Not bold, asexual, polygastric stage (number of nectophores, or greater of anterior and posterior nectophores if both present); bold, sexual stage (number of eudoxids, greater of bracts or gonophores); italics, larval nectophores.

Table 2. Vertical distribution of medusae (numbers per $10^4\,m^3$) in the RMT8 samples collected at 'Discovery' Station 9969.

	Depth Range (m)																	
	0-100	100-260	250-410	390-505	500-600	600-700	700-805	800-900	900-1000	1000-1205	1200-1400	1395-1600	1610-1800	1800-2000	2000-2200	2200-2400	2390-2600	2595-2800
Euphysora gigantea									0·30		0·59	0·16						
Pandea rubrum							0·30	0·30										
Calycopsis borchgrevinki	1·82	1·47	0·91	7·48	9·86	0·32	0·30		0·30		0·44		0·17	0·15		0·15	0·15	0·15
Chromatonema rubrum									0·30	0·68	0·30			0·15	0·16		0·15	0·15
Leptomedusan sp.	4·24																	
Pantachogon haeckeli				0·71	1·27	6·74	10·00	5·15	3·33	0·17		0·16	0·17		0·16		0·15	0·15
Crossota brunnea									1·52	0·51								0·44
Halicreas minimum					0·64	0·64	0·61		0·30									
Haliscera conica	1·21	18·77	35·76	19·94	8·90	7·70	0·61	0·61		1·02	1·33	0·64	0·34					0·15
Botrynema brucei				0·36		0·96	0·61	0·30		0·17	2·36	1·45	5·64	5·89	1·79	8·79	8·25	6·21
Cunina duplicata									0·30	0·85	1·18	0·81	0·68					
Aegina citrea				1·42							0·15	0·32	0·17			0·30	0·46	0·44
Solmundella bitentaculata				22·07														
Narcomedusan sp.	0·61	0·59	3·03							0·34								
Atolla sp.											0·15	0·16						
Atolla wyvillei		0·29					0·30	2·73	2·73	2·72	3·69	0·64	0·17	0·30	0·16			
Atolla chuni												0·16						
Atolla gigantea								0·30			0·15	0·16		0·15	0·16		0·61	0·15
Periphylla periphylla			0·30	1·78	1·59	0·64	0·30	1·52			0·30	0·32	2·22	0·30	0·16	0·30	0·46	0·15
Deepstaria enigmatica										0·17								
Tetraplatia chuni										0·17								

hauls. The epipelagic depth distribution for this species is in basic agreement with those authors' results, as they found most nectophores in the 50–100 m depth range, while eudoxids peaked in the 100–200 m range. However, their mean abundance data are somewhat greater than those reported here. This is despite the fact that their smaller and finer meshed nets would not necessarily be expected to be more efficient at catching these relatively large animals. Nonetheless, the average number of specimens of *D. antarctica* collected in four hauls fished in the top 500 m (17 nectophores per $10^4\,m^3$) compares well with much of the data from a previous study (Pagès et al., 1994). It is apparent, with the finer-scale depth resolution of the present study, and in combination with the data of Pagès & Kurbjeweit (1994), that this species is largely found in the near-surface zone, above the permanent thermocline.

The nectophores of *Dimophyes arctica* were most abundant in the 250–400 m depth range (Figure 4), whereas eudoxid gonophores predominated in the 100–400 m range. The eudoxid bracts had a more widespread distribution, down to 800 m, but were much rarer than the gonophores, presumably having been lost through the meshes of the net. *Dimophyes arctica* was relatively abundant down to 1000 m, and was the only species of cnidarian to occur in all of the 18 depth ranges sampled, although surface contamination also may apply here. However, as was the case for *Diphyes antarctica*, Pagès & Kurbjeweit (1994) did not find this species in the 0–50 m depth range. These authors similarly found both the nectophores and the eudoxids to be most abundant in their 200–500 m depth range. Again their mean abundances were considerably higher than the present data, but in this case it probably is a reflection of the smaller mesh size of their nets as the animals are comparatively small. The mean (0–500 m) abundance of nectophores (15·2 per $10^4\,m^3$) is low in comparison with our previous data, although the numbers at Station 10000, which probably also lay in the Weddell cold regime, were similarly reduced. It appears from these data that *Dimophyes arctica*, at least in the Weddell Sea region, is an epi- and mainly upper mesopelagic species which, although present in more superficial waters, appears to have a preference for living in the warm deep water mass immediately below the permanent thermocline.
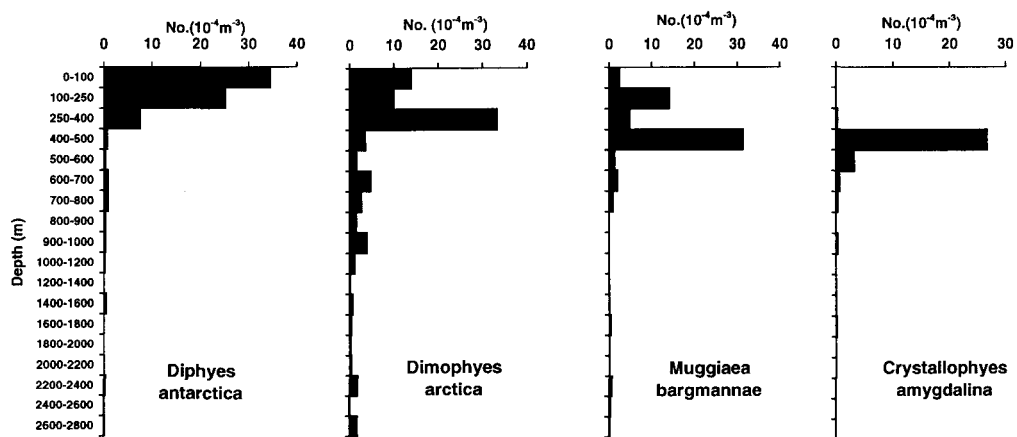

Figure 4. Vertical distribution of the nectophores (numbers per $10^4\,m^3$) of four 'epipelagic' siphonophore species at 'Discovery' Station 9969.

Muggiaea bargmannae, a species very similar to *D. arctica,* but with a bipolar distribution, was ranked third in abundance. The nectophores mostly occurred from the surface to 800 m, reaching a maximum in the 400–500 m depth range (31·3 nectophores per $10^4 m^3$) (Figure 4). No eudoxids were observed in the samples, probably because they were too small to be retained by the 4·5 mm mesh size of the RMT8. The average number of nectophores (13·2 per $10^4 m^3$) in the 0–500 m depth range is quite high in comparison with the data of Pagès et al. (1994), who found that there was a steady increase in numbers toward higher latitudes. However, the abundances are very low in comparison with Pagès & Kurbjeweit (1994), probably for the same size reasons as discussed for *D. arctica.* They found peak numbers of nectophores in the 100–200 m depth range, although numbers were still high in the 200–500 m depth range, where eudoxids reached their peak abundance. Thus for the data reported here, the peak abundance for each of these three common calycophoran species lay in a different depth zone, and there was a size-related depth distribution with the largest species occurring closest to the surface. *Diphyes antarcticus* clearly is mainly epipelagic species, while the depth distributions of *Dimophyes arctica* and *M. bargmannae* suggest that they occupy the boundary region between the epi- and upper mesopelagic zones.

There was one species, *Crystallophyes amygdalina,* that Pagès et al. (1994) unexpectedly had to consider as a 'broadly' epipelagic species as it occurred mostly in the 0–500 m depth range. However, in most other regions of the world's oceans it is usually found at meso- and occasionally bathypelagic depths. Some light has been shed on this apparent anomaly with the fishing of narrower depth horizons in the present study. These data (Figure 4) show that the bulk of the population (26·7 nectophores per $10^4 m^3$) was collected in the 400–500 m depth range, together with a small population in the 500–600 m range. It is apparent that this species is largely confined to a narrow depth range in the vicinity of 500 m depth and it is interesting to note that Pagès & Kurbjeweit (1994) found it only in their 200–500 m and 500–1000 m depth ranges, with higher numbers in the latter. Thus this species should be considered to have an upper mesopelagic distribution in the Weddell Sea. Nonetheless this distribution is shallower than that found at higher latitudes in the North Atlantic Ocean, where it occurs predominantly in the 600–900 m range (P.R.P., unpublished data).

'Epi- and mesopelagic species'

Pagès et al. (1994) included in this category those cnidarians that were most often found in the 0–500 m depth range, but occasionally had a significant deeper population. One of their examples was *Calycopsis borchgrevinki.* In the present study this species was found mostly in the top 600 m with, like *Crystallophyes amygdalina,* highest densities between 400 and 600 m (Table 2). However, some specimens were collected, usually individually, at deeper depths. It is unlikely that surface contamination could be a confusion factor here, because of the relatively large size of this species. Navas-Pereira & Vannucci (1994) considered that this species occurred throughout the water column, but their information was derived from open nets fished from as deep as 4392 m to the surface. It has never previously been recorded in discrete depth ranges as deep as 2390–2600 m, and this may indicate that this Antarctic anthomedusan has a more extensive vertical distribution than previously thought. The average numbers of

specimens in the 0–500 (2·9 per 10^4 m^3) and 500–1000 m (2·2 per 10^4 m^3) depth ranges were very similar to the values obtained at Station 10000 in a previous study, but in that study there were regional changes in its distribution. Our abundance and depth distribution data are also very similar to those of Pagès & Kurbjeweit (1994), who found it only in the 200–500 m depth range. Thus it appears that this species is largely an epi- and upper mesopelagic species.

In the present study, the hippopodiid siphonophore *Vogtia serrata* was most abundant in the 100–700 m depth range (Figure 5), although it was also present in most of the depth ranges sampled. Its peak abundance was found in the 250–400 m depth range (60 specimens per 10^4m^3), with a gradual decline in numbers below this. The population was dominated by larval nectophores, and this decline was largely due to a reduction in their numbers, while the numbers of polygastric stages remained relatively stable within the 250–700 m depth range. Thus this species has a mainly lower epipelagic and upper mesopelagic depth distribution. This vertical distribution agrees with that previously reported for these waters (Pagès et al., 1994), and for the North Atlantic (Pugh, 1974; 1991), where its small-scale vertical distribution also has been investigated. In addition, it has been found at epi- and mesopelagic depths in all of the three great oceans.
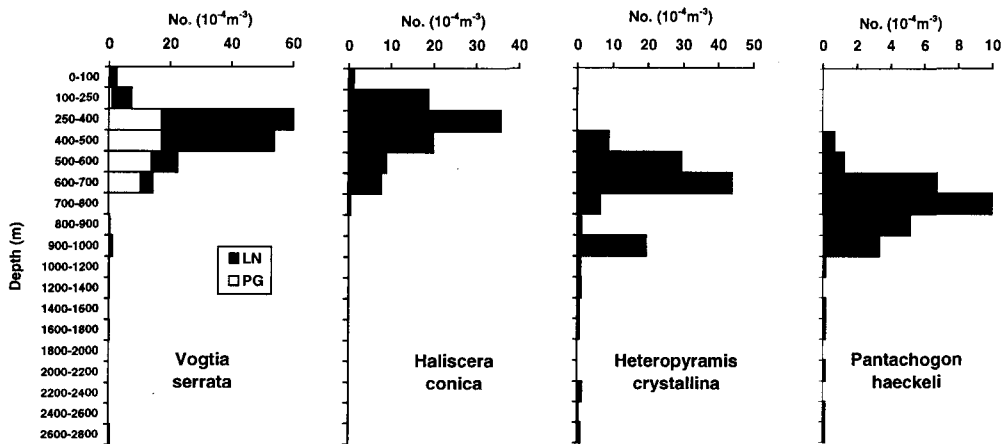

Figure 5. Vertical distribution of four 'epi- and mesopelagic' cnidarian species (numbers per $10^4 m^3$) at 'Discovery' Station 9969. For the siphonophore Vogtia serrata: LN, larval nectophore; PG, adult polygastric stage.

Another species that also showed a mainly lower epipelagic and upper mesopelagic depth distribution was the trachymedusan *Haliscera conica*. It was collected only in the upper 800 m (Figure 5). The bulk of the population (35·8 specimens per 10^4 m^3) was found in the 250–400 m depth range. The average (0–500 m) abundance (18·9 specimens per 10^4 m^3) is similar to that recorded in our previous study for the most adjacent stations, except that it was absent from Station 10000. However, at these stations it was rarely recorded below 500 m depth. As we noted, this relatively shallow depth

distribution is in marked contrast to that in other regions, where it is generally found at bathypelagic depths (e.g. Kramp, 1959). It was also thought to be a bathypelagic species in the Southern Ocean, but our studies reveal that, in the Weddell Sea at least, it has a very distinct epi- and mesopelagic distribution. Similarly, Pagès & Kurbjeweit (1994) found it to occur only in their 200–500 m and 500–1000 m depth ranges, but in considerably higher numbers.

'Mesopelagic species'

The species included in this category, were mostly collected in the 500–1000 m depth range, although some occurred sporadically, and in very low densities, below 1000 m. One such species was the clausophyid siphonophore *Heteropyramis crystallina*. The present data show that most of the specimens occurred between 400 and 1000 m, but with occasional specimens at deeper depths (Figure 5). Nevertheless, the core of the population lay within the 500–700 m depth range. A relatively narrow distribution such as this would be masked if sampling was carried out over a larger depth range, as was the case in a previous study. This is probably also the case for the data of Pagès & Kurbjeweit (1994) who found the bulk of the population of this species in their 1000–500 m sampling range. A similar situation pertains to the vertical distributions of *Pantachogon haeckeli* (Figure 5) and *Lensia havock* (Table 1), as both species were found almost exclusively in the 500–1000 m depth range. Again, the depth distribution patterns were not uniform and both species reached maximum abundance (10 and 18·4 specimens per 10^4 m^3 respectively) in the 700–800 m depth range. Previously we had considered *P. haeckeli* in the next category, because of regional differences in its occurrence below 1000 m. The other species that previously had been considered in this category, *Lensia achilles* (Table 1) and *Pandea rubrum* (Table 2), were only found in very low numbers in the present study.

One species that Pagès et al. (1994) did not find in the area was *Solmundella bitentaculata*. This showed a distinctive and peculiar depth distribution in that it occurred only in the 100–500 m depth range (Table 2). All the specimens were quite large (10 mm in bell diameter), and abundance was relatively high (22·07 specimens per 10^4 m^3). This depth distribution is of interest because, in the Weddell Sea and adjacent waters, usually only small specimens have been captured erratically throughout the water column and by fine mesh nets (Pagès & Kurbjeweit, 1994; F.P., unpublished data). The presence of adults is rarely reported and so the aggregation of so many adults within a single depth range is of considerable interest.

'Meso- and bathypelagic species'

This category is best exemplified by four medusan species. Two of these had limited depth distributions and occurred mainly in the mid part of the depth range sampled, while the other two had broader and discontinuous distributions. *Atolla wyvillei* occurred almost exclusively in the 700–2000 m depth range (Figure 6), with relatively high numbers between 800 and 1200 m. However, one small specimen was collected in the 100–250 m layer. Similarly, the trachymedusan *Halicreas minimum* occurred almost
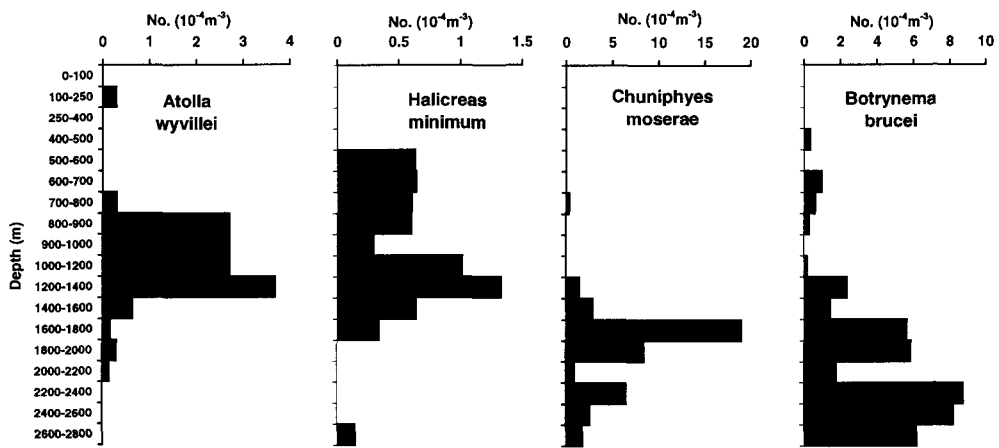
Figure 6. Vertical distribution of four 'meso- and bathypelagic' cnidarian species (numbers per $10^4\,m^3$) at 'Discovery' Station 9969.

exclusively in the 500–1800 m depth zone (Figure 6), with a solitary specimen being found in the deepest depth range sampled. This basic depth distribution is in accord with that reported by Navas-Pereira & Vannucci (1994) in a region south of the Polar Front. Neither species was found in the samples of Pagès & Kurbjeweit (1994).

Of the two species that showed a broad depth distribution, the scyphomedusan *Periphylla periphylla* was collected at all depths between 250 and 2800 m, with the exception of the 900–1000 m and 1000–1200 m depth ranges. As expected for such a large medusan, abundances were low (Table 2), but some medium and large specimens contributed greatly to the biovolume in the 250–400, 800–900 and 1000–1200 m depth ranges. The narcomedusan *Aegina citrea* was observed in three main depth ranges: 400–500, 1200–1800 and 2200–2800 m (Table 2). Although this species is known to live at meso- and bathypelagic depths in the three great oceans, the reasons for this discontinuous vertical distribution remain unclear. Its distribution does not seem to be related to that of its prey, which is other gelatinous organisms (Larson et al., 1989), since salps and ctenophores occurred in very low numbers and other medusan species were widely distributed.

Pagès et al. (1994) included some other species in this category, including *Clausophyes moserae* (Table 1) and *Crossota brunnea* (Table 2). Both these species were comparatively rare in the present study, but their depth distributions spanned the lower meso- and bathypelagic zones.

'Bathypelagic species'

Below 1000 m depth, only two species, the siphonophore *Chuniphyes moserae* and the trachymedusan *Botrynema brucei* were present in significant numbers, and both showed an extensive depth distribution. *Chuniphyes moserae* is generally considered to be a bathypelagic species, but it depth distribution was not uniform and it reached maximum

numbers (19 specimens per $10^4 \, m^3$) in the 1600–1800 m depth range (Figure 6). In a previous study we had considered this species in the preceding category , but this was because there were considerable regional differences in its depth distribution. However, at Station 10000, that also probably lay within the Weddell cold regime, it was exclusively found below 1000 m. *Botrynema brucei* primarily is a bathypelagic species, although some specimens were collected at shallower depths. However, below 1000 m depth it tended to increase progressively in abundance, with the exception of the 2000–2200 m depth range, to reach a peak concentration (8 specimens per $10^4 \, m^3$) in the 2200–2400 m depth range (Figure 6). Below this, its abundance was still relatively high and it is possible that the above trend may continue at deeper depths. This distributional trend is unusual amongst the cnidarian species collected, and probably means that *B. brucei* is the most abundant bathypelagic species at deeper depths in the Southern Ocean.

Several rarer species had fairly restricted depth distributions. For example, the large narcomedusan *Cunina duplicata* was collected only in the five depth ranges between 900 and 1800 m (Table 2). Although Pagès et al. (1994) found some specimens in the 0–500 m depth range, most other records, based on a stratified sampling programme (e.g. Pagès et al., 1996), indicate that it is a mesopelagic species. The rare prayid siphonophore *Nectadamas diomedeae* also occurred only in five contiguous depth ranges, between 1000 and 2000 m (Table 1). It is interesting to note that these specimens, together with the few previous records from the Southern Ocean (Pugh 1992), always refer to the eudoxid stage, and that the definitive nectophore has yet to be reported in Antarctic waters. A closely related, and similarly rare species, *Nectopyramis natans*, had a discontinuous distribution in the depth ranges between 1200 and 2600 m (Table 1). This is only the second time that this species has been recorded from the Southern Ocean. Pagès et al. (1994) found both stages in all three of the depth ranges they sampled, but mainly in the deepest (1000–2000 m) one.

One specimen of the giant scyphomedusan *Deepstaria enigmatica* (3800 ml in biovolume) was collected in the 1000–1205 m depth range. This is the fourth record for this species in the Southern Ocean, where it has been found in the proximity of the Antarctic Peninsula and on the other side of the continent (Larson, 1986b). However, these records could not set bounds to its depth distribution. The few non-Antarctic records (Gulf of Mexico and west coast of the USA) suggest that it is a cosmopolitan, but rare, species in deeper waters.

The calycophoran *Lensia hostile* occurred in very low numbers only in the three deepest depth ranges (2200–2800 m) (Table 1). Pagès et al. (1994) found two nectophores each in the 500–1000 m and 1000–2000 m depth ranges. This suggests that the species has a sporadic but quite wide meso- and bathypelagic distribution in the region. Some other species frequently found in the Southern Ocean (see Pagès et al., 1994, 1996), such as *Clausophyes moserae*, *Atolla gigantea*, *Chromatonema rubrum*, and *Crossota brunnea* were also observed in discontinuous depth ranges between 800 and 2800 m, thereby indicating a broad presence throughout the bathyal water column (Tables 1 & 2).

SUMMARY

One of the primary purposes of this paper was to consider whether the general categories for the depth distribution of animals in the ocean, that is epi-, meso-, and bathypelagic, are too broadly based to describe the vertical distributions of cnidarian species, even within a water column such as in the Weddell Sea where the overall temperature change is only ~2°C (-1·18–0·85°C). In a previous study (Pagès et al., 1994) it was suggested that such might be the case in what we called the 'broadly' epipelagic (0–500 m) depth range as different water masses were to be found therein. By sampling over smaller depth ranges, as in the present study, it was indeed found that these generic categories for depth distributions were masking finer scale specific distributions. In addition, it became evident that even depth horizons of ~100 m were too gross to resolve some of these distributions.

Although the three most abundant siphonophore species occurred throughout the 0–500 depth range, they showed considerable differences in their abundances in the various depth ranges sampled. Thus *Diphyes antarctica* was commonest at the shallowest depths above the permanent thermocline. Indeed Pagès & Kurbjeweit (1994) have shown that there may be an even finer resolution to this distribution, as they did not find any specimens in the 0–50 m depth range. Similarly, both sets of data indicate that *Dimophyes arctica* and *Muggiaea bargmannae* mainly occur in or below the permanent thermocline, and our slightly more detailed sampling effort showed that these two species reached peak abundances within different depth ranges.

An extreme case in point was shown by the very discrete depth distribution of *Crystallophyes amygdalina*. Virtually the entire population of this species was found in the 400–600 m depth range. Since 500 m is often used as the change over depth between nets in many large-scale sampling programmes, then the results would tend to indicate that this species has a widespread depth distribution. In this region at least, it is likely that the depth distribution of *C. amygdalina* is actually more discrete, lying close to a depth of 500 m. Another example of this feature is *Calycopsis borchgrevinki* whose main population also occurred in the 400–600 m depth range, although it was also present in some numbers at shallower depths.

Even the somewhat broader depth distributions of species, such as *Vogtia serrata* and *Haliscera conica*, indicate that they do not occur throughout the epi- and mesopelagic realms. Conversely, there are several species, such as *Pantachogon haeckeli* and *Lensia havock*, that reach peak abundances within discrete depth zones, although overall their depth distributions span the whole of the mesopelagic. This also applies to species, such as *Atolla wyvillei* and *Halicreas minimum*, whose distributions extended to deeper depths.

Thus it appears that caution should be applied when using the terms epi-, meso- and bathypelagic. Although these terms can be broadly used to categorize the depth distributions of groups of species, the depth distributions of many individual species are much more discrete and here the terminology can become meaningless. Indeed care must also be taken in defining what is meant by epi-, meso- or bathypelagic. These zones usually are defined as representing certain depth ranges; but the actual extent of these ranges can vary according to the author. This particularly applies to the depth

that marks the change-over from the epi- to the mesopelagic zone. This depth can be defined according to various parameters, such as temperature, or the depth of the permanent thermocline, the light regime, or simply by pressure (depth). The boundary between the meso- and bathypelagic realms is often defined by the maximum depth from which diel vertical migration occurs (Marshall, 1979). However, this will vary according to the size class and type of animal being considered, and is inevitably a compromise. On these bases, the extent of each of these pelagic zones should also vary with latitude and season. For instance, Mackie (1985), based on his observations from a submersible, equated the epipelagic zone with the top-mixed layer (0–50 m), and the boundary between the meso- and bathypelagic zones as the maximum observed depth from which diel migration occurred (~175 m).

Since many cnidarian species were found to have quite discrete depth distributions, the question arises as to what might be the controlling factors behind them. Navas-Pereira & Vannucci (1994) considered that, in the open Antarctic Ocean, temperature was a dominant factor in determining the distribution of medusae. It may be that the permanent thermocline, with the very cold winter water above, may be acting as a barrier to some species, but this is certainly not always the case. For instance there was a great similarity between the vertical distribution of the epipelagic species, *Diphyes antarctica*, in the present study and in that of Pagès & Kurbjeweit (1994). However, in the present study relatively warm superficial waters overlay the cold winter water, while in the other case the superficial waters, above the permanent thermocline, were uniformly cold. Below the permanent thermocline the temperature dropped by only ~1°C, and the transition from positive to negative temperatures did not appear to affect the vertical distribution of certain bathypelagic species. Thus most meso- and bathypelagic species live in relatively homogeneous water masses, consisting of warm deep water overlying Antarctic bottom water.

It is unlikely that the light regime will be playing a part in determining the depth distributions of individual cnidarian species, particularly those living in discrete depth bands below the permanent thermocline. Other factors that might be affecting their distributions are pressure *per se* and the depth distribution of their potential prey. Pressure is a probable candidate, but it cannot always be the determinant factor. For instance, in the Weddell Sea, we have found that the siphonophore *Crystallophyes amygdalina* occurred almost exclusively at a depth of ~500m. However, in the North Atlantic Ocean it is usually found in the 600–900 m depth range. A similar pattern emerges for the depth distribution of *Vogtia serrata.* Little is known about the feeding preferences of deeper-living cnidarians, and so it is uncertain whether such factors will be affecting their depth distribution. However, Pugh (1991) did show that there was a good correlation between the depth distribution of hippopodiid siphonophores, including *Vogtia serrata,* and that of their preferred prey, ostracods. However, few data are available on the depth distribution of ostracods in the Weddell Sea. It was also noted above that the depth distribution of *Aegina citrea* did not coincide with its potential prey, other gelatinous organisms.

Another significant outcome of this study was to indicate, once again, the important role that cnidarians play in the pelagic ecosystem of the Southern Ocean. Numerically, in the micronekton size ranges, they make up about 15% of the total. Their numbers

were exceeded only by chaetognaths (>50% of total) and euphausiids (~25%). Of course, macroplankton groups such as copepods are significantly more abundant, but they are not sampled quantitatively by the RMT8 net (Hubold et al., 1988). There are several papers on the distribution of copepods in the Weddell Sea (e.g. Boysen-Ennen & Piatowski, 1988). Both siphonophores, as expected, and, unexpectedly, medusae had peaks of numerical abundance in the top 500 m of the water column, with the total number of siphonophores being about 4·5 times that of the medusae. The unusual presence of adult *Solmundella bitentaculata* in the 400–500 m depth zone partially accounted for the high numbers of the latter.

In terms of biovolume a totally different picture emerges. Siphonophores, because of their generally smaller size, usually contributed far less to the total biovolume of each haul. On average, medusae contributed 45% to these individual totals but, because the range (3–94%) was considerable, they were not the major contributor in five of the hauls. This suggests considerable patchiness in their distributions. However, taking all the hauls into account, cnidarians contributed >70% to the total biovolume. It is often assumed that gelatinous organisms have little relevance to ecosystem models because their high (~96%) water content means that their dry weight and, more particularly, carbon content is relatively low. However, the data show that, because of the predominance of cnidarian biovolume in our catches, the calculated carbon values for these animals still form a substantial part of the total; averaging around 25% of the carbon of each haul and over 30% of the total carbon for all the hauls combined. Indeed, the biovolume and carbon content of such animals are often underestimated, as is almost certainly the case in the present study, due to loss of parts during collection and shrinkage after preservation.

Larson (1986a) reviewed the possibilities that there were selective advantages for animals to have a high water content in the pelagic marine environment. They would be close to neutral buoyancy, and by active sulphate exclusion, as has been demonstrated in cnidarians (Bidigare & Biggs, 1980), such could be achieved with little energy expenditure. Their low carbon content would indicate a lower metabolic rate, while allowing potential for rapid growth. Further, they will be able to prey upon non-gelatinous animals with the same carbon content, as they will be relatively larger, whilst remaining a poor food source for potential predators. This follows from the discussion of Purcell (1985) concerning the methods of predation employed by pelagic cnidarians and ctenophores. In this she, likewise, noted that the many scyphomedusans are much larger than their potential prey, and each specimen has the potential to capture and consume a considerable number of such items daily. The same also applies to the relatively smaller siphonophores because they have numerous stomachs to digest the prey. This contrasts with the relatively few prey items that a smaller predator can consume. For instance, Oresland (1991) found that the chaetognath *Eukrohnia hamata*, on average, preyed upon 0·3–0·7 copepods per day in the Gerlache Strait. Thus the greater abundance of these other predators does not necessarily mean that they have a greater impact on the prey population. As large medusae are relatively uncommon it is difficult to estimate their actual abundance when using data from net collections. Small mouthed, or fine meshed nets are unlikely to capture them. However,

they may be collected by larger, coarser meshed nets, but if they are not randomly distributed and an insufficiently large volume of water is filtered, then it is still difficult to assess their population density. The unusual occurrence of a large number of adult specimens of *Solmundella bitentaculata* in a single haul during the present study, whereas previous records for adult specimens in the same area are few, is indicative of this problem.

REFERENCES

Angel, M.V., 1985. Vertical migrations in the oceanic realm: possible causes and probable effects. *Contributions in Marine Science*, **27**, supplement, 45–79.

Bidigare, R.R. & Biggs, D.C., 1980. The role of sulfate exclusion in buoyancy maintenance by siphonophores and other oceanic gelatinous zooplankton. *Comparative Biochemistry and Physiology*, **66A**, 467–471.

Boysen-Ennen, E. & Piatowski, U., 1988. Meso- and macrozooplankton communities in the Weddell Sea, Antarctica. *Polar Biology*, **9**, 17–35.

Gouretski, V.V. & Danilov, A.I., 1993. Weddell Gyre: structure of the eastern boundary. *Deep-Sea Research*, **40**, 561–582.

Hosie, G.W., 1994. The macrozooplankton communities in the Prydz Bay region, Antarctica. In *Southern Ocean ecology* (ed. S. El-Sayed), pp. 93–123. Cambridge University Press.

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

Kramp, P.L., 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana-Report*, **46**, 1–283.

Larson, R.J., 1986a. Water content, organic content, and carbon and nitrogen composition of medusae from the northeast Pacific. *Journal of Experimental Marine Biology and Ecology*, **99**, 107–120.

Larson, R.J., 1986b. Pelagic Scyphomedusae (Scyphozoa: Coronatae and Semaeostomae) of the Southern Ocean. *Antarctic Research Series, National Research Council. Washington, DC*, **41**, 59–165.

Larson, R.J., Mills, C.E. & Harbison, G.R., 1989. *In situ* foraging and feeding behaviour of narcomedusae (Cnidaria: Hydrozoa). *Journal of the Marine Biological Association of the United Kingdom*, **69**, 785–794.

Mackie, G.O., Pugh, P.R. & Purcell, J.E., 1987. Siphonophore biology. *Advances in Marine Biology*, **24**, 97–262.

Marshall, N.B., 1979. *Developments in deep-sea biology*. Poole: Blanford Press.

Navas-Pereira, D. & Vannucci, M., 1994. Antarctic Hydromedusae and water masses. *Pesquisas Antártica Brasiliera*, **2**, 101–141.

Oresland, V., 1991. Feeding and predation impact of the chaetognath *Eukrohnia hamata* in Gerlache Strait, Antarctic Peninsula. *Marine Ecology Progress Series*, **63**, 201–209.

Pagès, F. & Kurbjeweit, F., 1994. Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica. *Polar Biology*, **14**, 243–251.

Pagès, F., Pugh, P.R. & Gili, J.-M., 1994. Macro- and megaplanktonic cnidarians collected in the eastern part of the Weddell Gyre during summer 1979. *Journal of the Marine Biological Association of the United Kingdom*, **74**, 873–894.

Pagès, F., White, M.G. & Rodhouse, P.G., 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in Summer 1994. *Marine Ecology Progress Series*, **41**, 139–147.

Pakhomov, E.A., Perissinotto R. & McQuaid, C.D., 1994. Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Marine Ecology Progress Series*, **111**, 155–169.

Pugh, P.R., 1974. The vertical distribution of the siphonophores collected during the SOND cruise, 1965. *Journal of the Marine Biological Association of the United Kingdom*, **54** 25–90.

Pugh, P.R., 1991. Co-occurrence of hippopodiid siphonophores and their potential prey. *Hydrobiologia*, **216/217**, 327–334.

Pugh, P.R., 1992. A revision of the sub-family Nectopyramidinae (Siphonophora, Prayidae). *Philosophical Transactions of the Royal Society of London* B, **335**, 281–322.

Purcell, J.E., 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bulletin of Marine Science*, **37**, 739–755.

Rodhouse, P.G. & Clarke, M.R., 1985. Growth and distribution of young *Mesonychoteuthis hamiltoni* Robson (Mollusca: Cephalopoda): an Antarctic squid. *Vie et Milieu*, **35**, 223–230.

Sokolova, M.N., 1994. Euphausiid 'dead body rain' as a source of food for abyssal benthos. *Deep-Sea Research I*, **41**, 741–746.

Wiebe, P.H., 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. *Fishery Bulletin. National Oceanic and Atmospheric Administration. Washington, DC*, **86**, 833–835.