

The distribution of zooplankton in an Antarctic fjord at South Georgia during summer and winter

PETER WARD

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Abstract: Zooplankton was sampled intensively with an RMT 1+8M system in the fjord of Cumberland East Bay, South Georgia during late winter 1983 and summer 1987. In summer, biomass was highest in the surface 20 m, reaching 142 g dw/1000 m³. Copepods dominated the zooplankton comprising 96–99% by numbers, of which 80–90% occurred in the top 100 m of the 265-m water column. The small clausocalanid *Drepanopus forcipatus* was particularly abundant. With increasing depth the proportion of non-copepod biomass, principally Mysidacea and Amphipoda increased significantly. Biomass throughout the water column in winter was generally 4–5 times lower than in summer although again copepods, and in particular *D. forcipatus* and members of the Metridinidae, still numerically dominated the plankton. Biomass levels were some 2–3 times greater than those found in Antarctic oceanic regions but were comparable with estimates from some boreal fjords. The mixture of neritic and oceanic species encountered, and the seasonal presence of some gelatinous zooplankton, particularly ctenophores, appears typical of the community structure of many fjord ecosystems.

Received 14 October 1988, accepted 12 January 1989

Key words: abundance, Antarctic, biomass, Copepoda, productivity, seasonal change.

Introduction

Fjord ecosystems have been the subject of intensive investigations in boreal and arctic regions. Their biological production is generally high and they contain harvestable resources such as fish, crustaceans and bivalves (Brattegard 1980). Fjords are a conspicuous coastal feature of some of the offshore islands of the Southern Ocean, notably South Georgia and the South Shetland Islands. Here, marine research has tended to concentrate on processes occurring in the surrounding oceanic and shelf waters, and fjords have been relatively little studied. It is however becoming apparent that South Georgia fjords mirror their northern counterparts in serving as important areas for fish spawning and recruitment (North 1988). Consequently British Antarctic Survey, as part of their Offshore Biological Programme (OBP), has undertaken surveys in the fjord of Cumberland East Bay to characterize the zooplankton and its interaction with larval fish. This paper provides a preliminary seasonal comparison of zooplankton species diversity, distribution and abundance in the fjord.

Materials and methods

Zooplankton was sampled along a transect in Cumberland East Bay, South Georgia, during September 1983 (late winter) and January 1987 (summer) using an acoustically operated rectangular midwater trawl (RMT 1+8M) (Roe &

Shale 1979). During the first survey in winter, because of uncertainty about bottom topography, nets were fished obliquely upwards through three nominal depth horizons (225–150 m, 150–75 m and 75 m–surface) at four times of day, designated pre- and post-dusk and pre- and post-dawn. Hauls were repeated over a period of six days, although data presented here are based on two days of sampling with an RMT 1 (mesh size 330 µm) (24 samples). During summer a different regime was adopted to increase sampling frequency throughout the day and to increase vertical resolution of the water column. Nets were fished obliquely downwards at six times of day, (the previous times plus local midday and midnight) through the 0–20 m depth horizon and then at 40-m depth intervals down to 220 m. As the RMT 1+8M comprises a triple flight of nets only three of the six vertical horizons could be fished during any one time period. Accordingly a complete series of hauls was spread over two days with the top 100 m being sampled during the designated times on day 1 and the lower 120 m on day 2. This cycle of hauls was repeated three times over a 10-day period. Data presented here are based on a single series of RMT 1 hauls (2 days).

Fishing time in each horizon during winter was 30 min. and in summer 20 min. Distance travelled by the nets was calculated from a flowmeter mounted on the net monitor and volume filtered then calculated from the equations of Pommeranz *et al.* (1983). Filtration was assumed 100% efficient. During the time that the RMT 1+8M was fishing a 1-m² frame net (F net, mesh size 4.5 mm) was deployed from the foredeck to fish the upper 2 m of the water column

principally for fish larvae, but also to investigate macrozooplankton occurrence in the near surface layer.

Salinity and temperature profiles were obtained using a Plessey 9041 STD-SV telemetering unit and data logger. Additional temperature profiles were obtained using XBTs.

The displacement volume of each RMT 1 sample was measured onboard and then entire samples, or 100 ml subsamples if the sample volume was greater, were preserved in 4% borax buffered formaldehyde solution for subsequent laboratory analysis. In the UK, samples were sorted in Steedmans solution under a Wild M20 stereomicroscope; macrocomponents were removed, identified and counted. Nomenclature for Copepoda follows Vervoort (1957), Pteropoda follows Morton (1954), Amphipoda follows Barnard (1969), Euphausiacea follows Kirkwood (1982), Mysidacea follows Tattersall (1955) and Decapoda follows Kirkwood (1984). Sample residues were split using a Folsom plankton splitter until two manageable aliquots (approximately 500–800 animals per aliquot) from each sample were obtained. Zooplankton were then counted and when possible identified to species.

Biomass measurements were made on preserved zooplankton by grouping individuals according to species and maturity stage and drying to constant weight at 60°C. Between 10–100 individual copepods of each identified species stage or grouping were pooled in replicates of three and the resultant mean weight accorded to all individuals of that stage. Macrocomponents such as mysids were grouped according to length and a mean weight obtained for individuals corresponding to each modal class observed. RMT 1 samples were then examined and on the basis of the catch size frequency distribution, biomass was calculated. The smaller and/or rarer fractions of the zooplankton were treated in the manner of Hopkins (1985) by generating weight/length regressions for selected dominant species which were morphologically similar to the rarer or smaller elements. Because of the fragile nature of the gelatinous zooplankton and preservation difficulties it was not possible to estimate their contribution to total biomass. However the abundance and distribution of the dominant forms is summarized. For biomass calculations no distinction was made between summer and winter samples and species were taken at random from both sample sets. Although there are likely to be stage and species specific differences between seasons it was felt that as zooplankton abundance was 4–5 times greater in summer, seasonal differences in total biomass would not be significantly affected.

Results

Physical conditions

Cumberland East Bay (54°17'S, 36°26'W) is situated midway along the north-eastern coast of South Georgia. It shares a

common entrance with Cumberland West Bay and is some 14 km long and 3–7 km wide. The maximum depth is *c.* 275 m with a sill at *c.* 200 m depth occurring at the seaward end. The Nordenskjöld Glacier is situated at its landward end, and is the source of considerable freshwater run-off in summer. The area is subject to strong winds of variable duration.

Temperature profiles taken during both seasons indicated that the water column was generally isothermal. During winter there was an upper layer (2–3 m) of locally warmed low salinity water of 1.5–2.8°C. Temperature decreased to around 0.7°C at 4–5 m depth and remained isothermal to near bottom. During summer there was again a locally warmed upper layer of low salinity this time between 3–4°C. Below this, colder water of 0.5–1.5°C again showed no obvious structure down the water column.

Zooplankton abundance and biomass

During both seasons at all times of day, large (4-fold) variations in zooplankton abundance were evident between

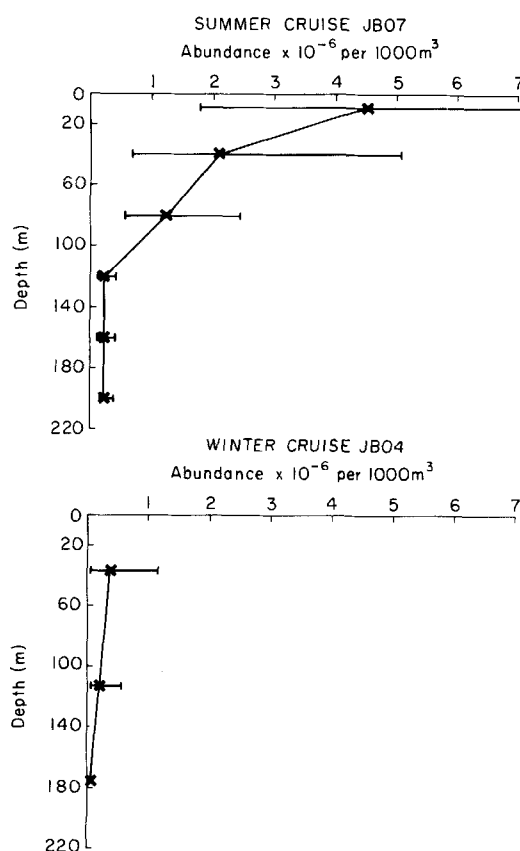


Fig. 1. Depth-related zooplankton abundance in Cumberland East Bay during summer and winter surveys given as means with range. *N* = 6 hauls for each depth horizon in summer and 8 in winter.

hauls, especially in the upper 100 m of the water column. In summer a two-way ANOVA examining the effects of depth and time of day (day/night) indicated that only changes in abundance with depth were significant ($F = 7.80, P < 0.001, 5$ and 30 df). In winter, abundance did not vary significantly in relation to either factor ($P > 0.05$). Data have accordingly been pooled irrespective of time of day and are presented in Fig. 1. In summer the general trend is one of highest abundance occurring in the top 20 m, decreasing to 100 m and then remaining relatively uniform down to 220 m. In winter, variation was still a feature especially in the upper 75 m, although, overall, considerably less than in summer. Below this depth abundance fell to around or below summer levels. Biomass levels (Fig. 2) also showed 4–5 fold levels of variation although in neither season did levels change significantly with either depth or time of day ($P > 0.05$). In summer, biomass maxima ($142 \text{ g dw}/1000 \text{ m}^3$) occurred in the upper 20 m and minima ($15 \text{ g dw}/1000 \text{ m}^3$) in the 180–220 m horizon. Lower winter biomass levels mirrored the drop in abundance and mean levels were some 4–5 times

Table I. Mean copepod and total zooplankton biomass in Cumberland East Bay during summer and winter.

Depth (m)	SUMMER	
	Mean copepod biomass g dw m ⁻²	Mean total zooplankton biomass g dw m ⁻²
0–20	1.93	2.06
20–60	2.60	2.94
60–100	2.01	2.27
100–140	0.75	1.24
140–180	0.82	1.89
180–220	0.50	1.59
Total	8.61	11.99
Depth (m)	WINTER	
	Mean copepod biomass g dw m ⁻²	Mean total zooplankton biomass g dw m ⁻²
0–75	1.12	1.16
75–152	0.78	0.82
152–203	0.31	0.58
Total	2.21	2.56

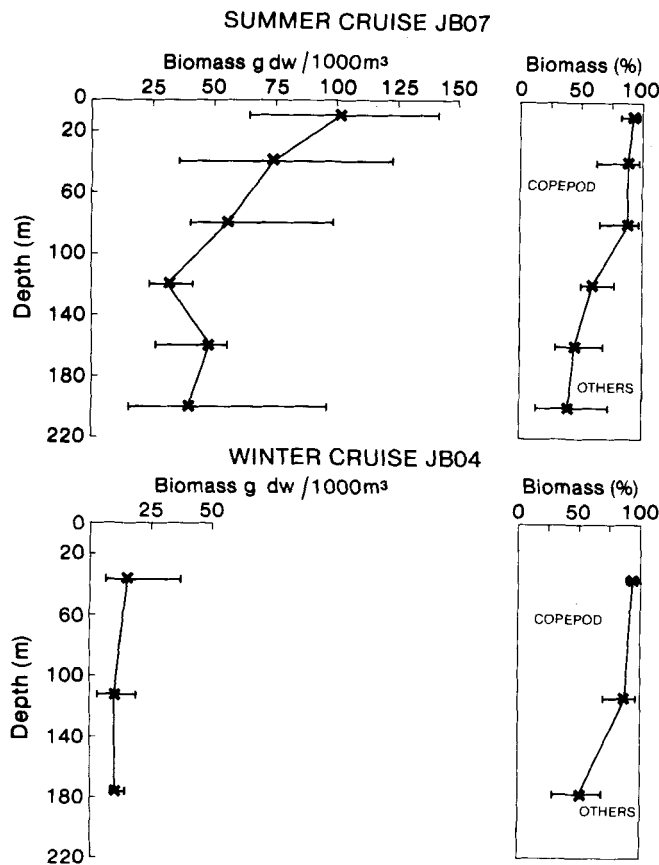


Fig. 2. Depth-related zooplankton biomass and the proportion of copepod and non-copepod contributors in Cumberland East Bay during summer and winter surveys. Data plotted are means with range values. $N = 6$ hauls for each depth horizon in summer and 8 in winter.

lower throughout the water column (Table I). A complete list of taxa and species encountered during the two cruises and their relative abundance is given in Table II.

The Copepoda averaged 97% and 89% of total zooplankton abundance during summer and winter respectively. They generally comprised 85–95% of biomass in the top 100 m. Accordingly only copepod size frequency and biomass data over the whole water column are presented in Fig. 3. Size frequency was polymodal and this was reflected in biomass values. Abundance maxima occurred in the 0.5–1.5 mm cephalothorax size classes, (mainly *Drepanopus forcipatus*, *Ctenocalanus* spp. and early copepodite stages of *Metridia* spp.) with 87% and 81% of total copepod abundance accounting for 59% and 50% of the summer and winter copepod biomass respectively.

The mean summer and winter biomass in each depth horizon broken down into copepod and non-copepod components is illustrated in Fig. 4. In summer the copepods, *D. forcipatus* and *Calanoides acutus* dominated biomass, especially in the upper 100 m, accounting on average for 58% and 30% of total copepod biomass, and 40% and 21% of total zooplankton biomass respectively. Below 20 m *Rhincalanus gigas* was distributed more evenly through the water column with peak biomass occurring between 140 and 180 m. Of the other species *Euchaeta antarctica* and *Ctenocalanus* spp. became more important between 180 and 220 m, although they contributed $< 2.5\%$ to total biomass. Mysidacea dominated the non-copepod biomass. *Mysidetes* spp. were found throughout the water column whereas *Antarctomysis ohlinii* was restricted to depths below 140 m with *Antarctomysis maxima*, the least abundant member of those figured, occupying an intermediate position. Of the

Table II. Comparison of summer–winter abundance of zooplankton taxa and species found in Cumberland East Bay. The vertical distribution of the Copepoda has been assigned where possible according to Atkinson & Peck (1988) and Atkinson & Peck (in press) and sources therein. EPS = epipelagic seasonal migrant, EPNS = epipelagic non-seasonal migrant, M = mesopelagic, N = neritic, * = abundance ratio not calculated as species absent in one of the two seasons.

	Mean abundance		Ratio summer: winter	Vertical distribution	Mean abundance		Ratio summer: winter	Vertical distribution
	Summer	Winter			Summer	Winter		
Copepoda								
<i>Aetideopsis minor</i>	—	25	*					
<i>Calanoides acutus</i>	59926	2193	27:1	EPS				
<i>Calanus simillimus</i>	397	1427	1:3.5	EPS				
<i>Calanus propinquus</i>	246	90	2.7:1	EPS				
<i>Candacia maxima</i>	137	319	1:2.3	?				
<i>Clausocalanus laticeps</i>	4128	63	65:1	EPNS				
<i>Ctenocalanus</i> spp.	94505	7565	12.4:1	EPS				
<i>Drepanopus forcipatus</i>	1136039	151122	7.5:1	N				
<i>Euaetideus australis</i>	—	133	*	EPNS				
<i>Eucalanus longiceps</i>	28	—	*	EPS				
<i>Euchaeta antarctica</i>	808	2187	1:2.7	EPS/M				
<i>Euchaeta biloba</i>	7	92	1:13.1	M				
<i>Euchirella rostramagna</i>	14	5	2.7:1	?				
<i>Gaidius tenuispinus</i>	3	12	1:4	M				
<i>Haloptilus oxycephalus</i>	85	7	12.8:1	EPNS				
<i>Heterorhabdus austrinus</i>	12	25	1:2.1	M				
<i>Metridia</i> spp. CI–CV+CVI♂	12294	28242	1:2.3	M				
<i>Metridia lucens</i> CVI♀	308	1471	1:4.8	M				
<i>Metridia gerlachei</i> CVI♀	367	279	1:3.1	M				
<i>Microcalanus pygmaeus</i>	715	172	4.2:1	EPS ?				
<i>Oithona</i> spp.	12872	5767	2.2:1	EPNS				
<i>Oncaea</i> spp.	565	1341	1:2.4	?				
<i>Pleuromamma robusta</i>	16	3994	1:249	M				
<i>Rhincalanus gigas</i>	4436	4057	1.1:1	EPS				
<i>Scaphocalanus</i> sp.	—	67	*	?				
<i>Scolecithricella minor</i>	462	4022	1:9.5	EPNS				
Ostracoda	538	6502	1:12					
Chaetognatha	832	2037	1:2.4					
Polychaeta								
<i>Tomopteris</i> sp.	9.2	17	1:1.8					
Pteropoda								
<i>Clio</i> sp.	5.9	836	1:142					
<i>Clione antarctica</i>	4.3	—	*					
<i>Limacina helicina</i>	9.5	—	*					
<i>Spongiobranchaea australis</i>	6.1	1.7	3.5:1					
Mysidacea								
<i>Antarctomysis maxima</i>	39	12	3.2:1					
<i>Antarctomysis ohlinii</i>	51	12	4.3:1					
<i>Mysidetes</i> spp.	635	9	71:1					
<i>Pseudomma</i> spp.	11	1.3	8.5:1					
Amphipoda								
<i>Hyperia</i> sp.	8.7	2.5	3.5:1					
<i>Hyperiella dilatata</i>	<1	1.3	1:2.4					
<i>Orchomene plebs</i>	32	10.5	3:1					
<i>Primno macropa</i>	116	145	1:1.3					
<i>Themisto gaudichaudii</i>	8.7	<1	17:1					
<i>Vibilia antarctica</i>	<1	8.9	1:39					
Decapoda								
<i>Chorismus antarcticus</i>	45	—	*					
<i>Notocrangon antarcticus</i>	224	104	2.2:1					
Euphausiacea								
<i>Euphausia frigida</i>	Ad. <1	3.2	1:38					
	Cal.	106	*					
	Fur.	194	60	3.2:1				
<i>Euphausia triacantha</i>	Ad.	<1	*					
	Cal.	<1	41	1:45				
	Fur.	30	—	*				
<i>Thysanoessa</i> spp.	Ad.	10.3	33	1:3.2				
	Cal.	—	<1	*				
	Fur.	273	2	136:1				

Amphipoda, *Orchomene plebs* was dominant, being found from the surface down to 200 m. Decapod larvae (*Notocrangon antarcticus* and *Chorismus antarcticus*) were only present in the top 100 m.

In winter, biomass was considerably less than in summer and although the sampling design does not allow the same fine-scale resolution of the water column, the general pattern of copepods dominating the upper 150 m is repeated. The two major contributors to copepod biomass in winter were *D. forcipatus* and *R. gigas* (43% and 23% of copepod biomass, 32% and 17% of total biomass respectively) with *E. antarctica* becoming progressively more important with depth.

Mysidacea again dominated the non-copepod fraction with *A. ohlinii* being most abundant in the lower depth horizon. *A. maxima* was again distributed throughout the water column although *Mysidetes* spp. were much less abundant than in summer and were restricted to the lower depth horizons.

Gelatinous zooplankton

The gelatinous zooplankton included members of the Ctenophora, Hydromedusae and Scyphomedusae. In summer RMT 1 catches indicated that Ctenophora, principally *Cryptocoda gerlachei* and *Beroe* sp. were almost entirely restricted to the top 20 m although abundance was low (mean abundance 7/1000 m³). Examination of F net catches indicated, however, that they were most abundant in the 0–2 m depth layer (mean abundance 644/1000 m³). In winter, none were collected.

Scyphomedusae, in particular the large cyaneidid *Desmonema glaciale*, were encountered during both seasons. The displacement volume of individuals ranged from 0.5–70.0 l. Frequently only parts of these organisms were found in the nets making it difficult to assess abundance. An indication of their relative abundance was gained by pooling RMT 8 and 1 data and analysing their presence or absence in the total number of nets fished. They were absent in the top

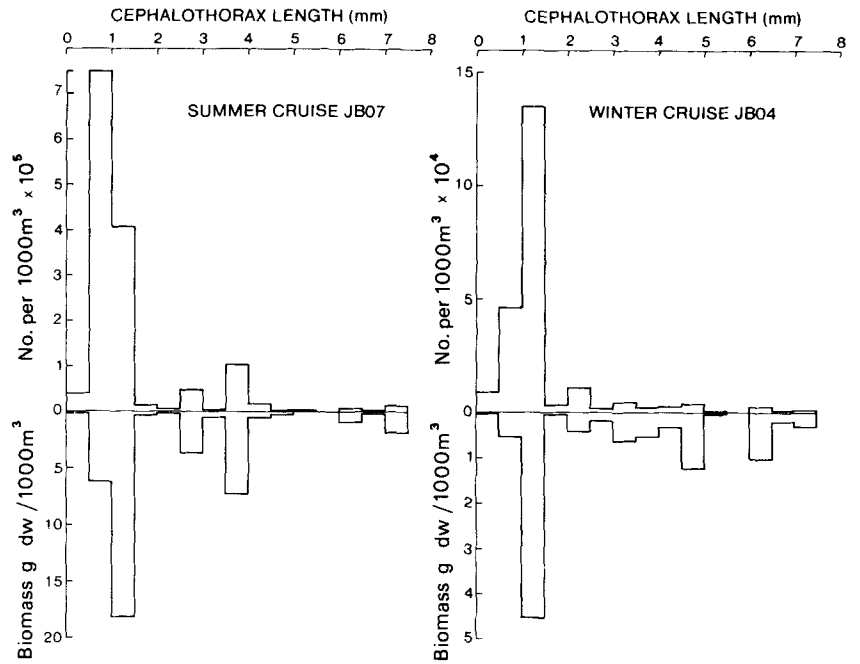


Fig. 3. Copepod size frequency over the entire water column during summer and winter surveys. Data plotted are mean abundance and biomass contributions.

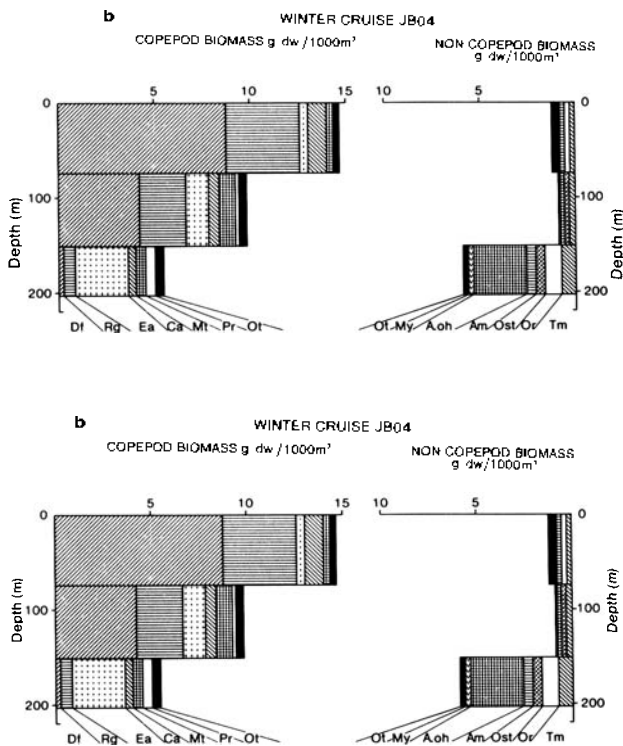


Fig. 4. Mean biomass of copepod and non-copepod zooplankton in relation to depth in Cumberland East Bay during summer and winter surveys. Df = *Drepanopus forcipatus*, Ca = *Calanoides acutus*, Rg = *Rhincalanus gigas*, Ea = *Euchaeta antarctica*, Ct = *Ctenocalanus* spp., Mt = *Metridia* spp., Pr = *Pleuromamma robusta*, Aoh = *Antarctomysis ohlinii*, Am = *Antarctomysis maxima*, My = *Mysidetes* spp., Ost = Ostracoda, Or = *Orchomene plebs*, Tm = *Tomopteris*, Dc = Decapoda, Ot = others.

60 m of the water column during summer and in both seasons abundance increased with depth. There was little overall difference in abundance between seasons (present in 10–13% of all nets fished) nor with time of day.

Vertical distribution

The vertical distribution of the dominant species during the two seasons is presented in Figs 5–7. Few of the species showed any great differences in diurnal distribution and vertical migrations were for the most part not apparent. Many of the species were present throughout the sampled water column during both day and night, although often with a tendency for the bulk of the population to occupy distinct depth horizons above, or below 100 m. Thus, in summer *D. forcipatus* in particular dominated the top 60 m, whilst *E. antarctica* and *Metridia* spp. had distributions centred on the lower part of the water column. However, many of the younger copepodite stages of a given species showed distributions increasingly centred nearer the surface e.g. *Metridia* spp., *C. acutus* and *R. gigas*.

In winter, with only three depth horizons fished, vertical resolution was less than in summer. The overall patterns, however, were broadly similar with *D. forcipatus* being more abundant nearer the surface than the other species and *E. antarctica* and *P. robusta* occupying deeper horizons. Again younger copepodite stages tended to be distributed higher in the water column, e.g. *R. gigas*, *E. antarctica* and

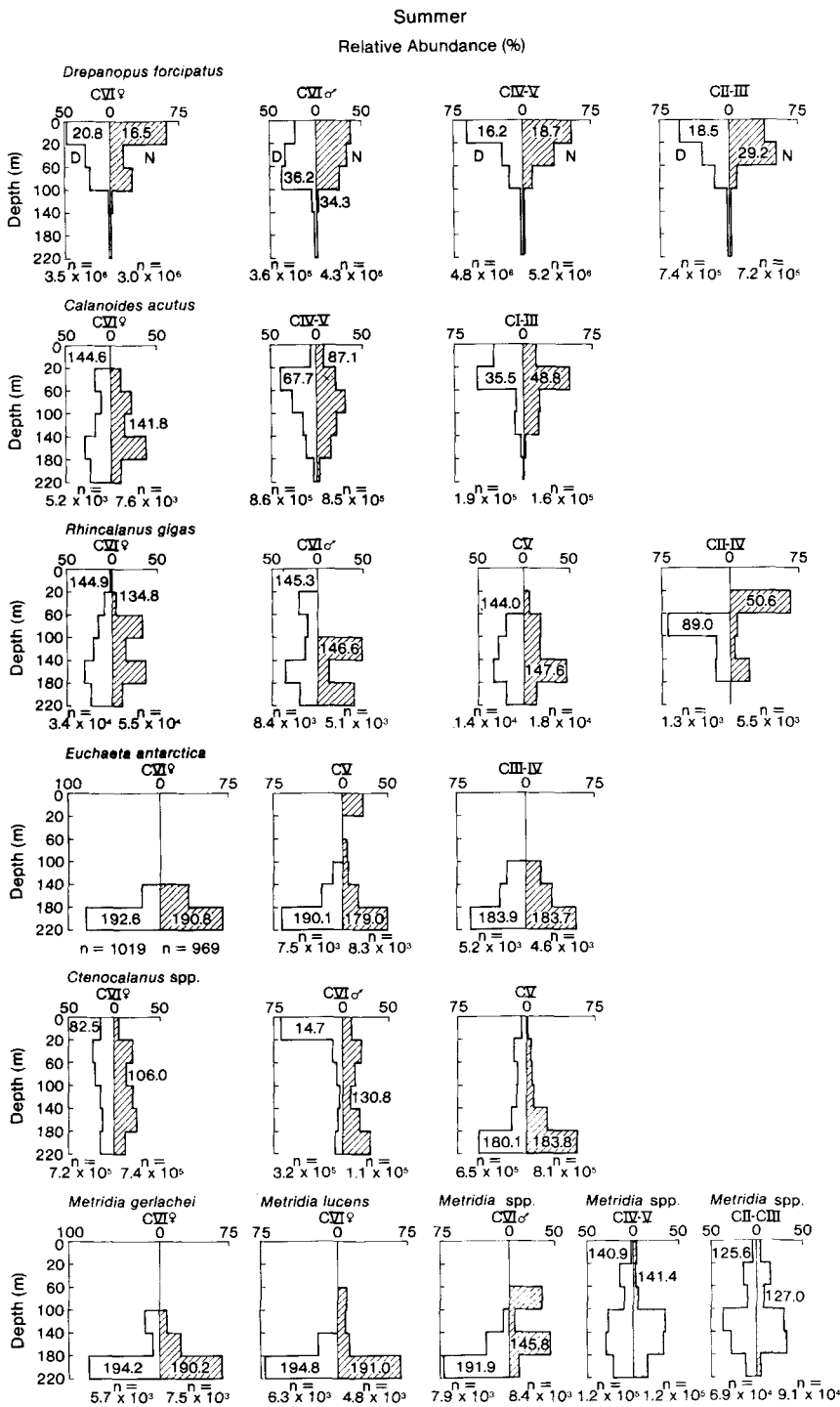


Fig. 5. Diurnal vertical distribution of the dominant copepod species and stages during the summer survey in Cumberland East Bay. Data are pooled values ($n = 3$ hauls) in each depth horizon during day (D) and night (N). The median depth of each species stage is given for day- and night-time hauls.

P. robusta. Diurnal differences were generally more marked than in summer, with the later stages of *E. antarctica* and *P. robusta*, and adult female *M. lucens*, tending to be found closer to the surface at night. Vertical migration was most clearly seen in both cruises amongst the Mysidacea. (Fig. 7).

In summer, *A. maxima* was not found at all in the top 100 m during daylight and *Mysidetes* spp. hardly at all. At night, however, in both cases the median depth of the population had risen to between 70 and 90 m and their presence in significant numbers was apparent right up to the surface. *A.*

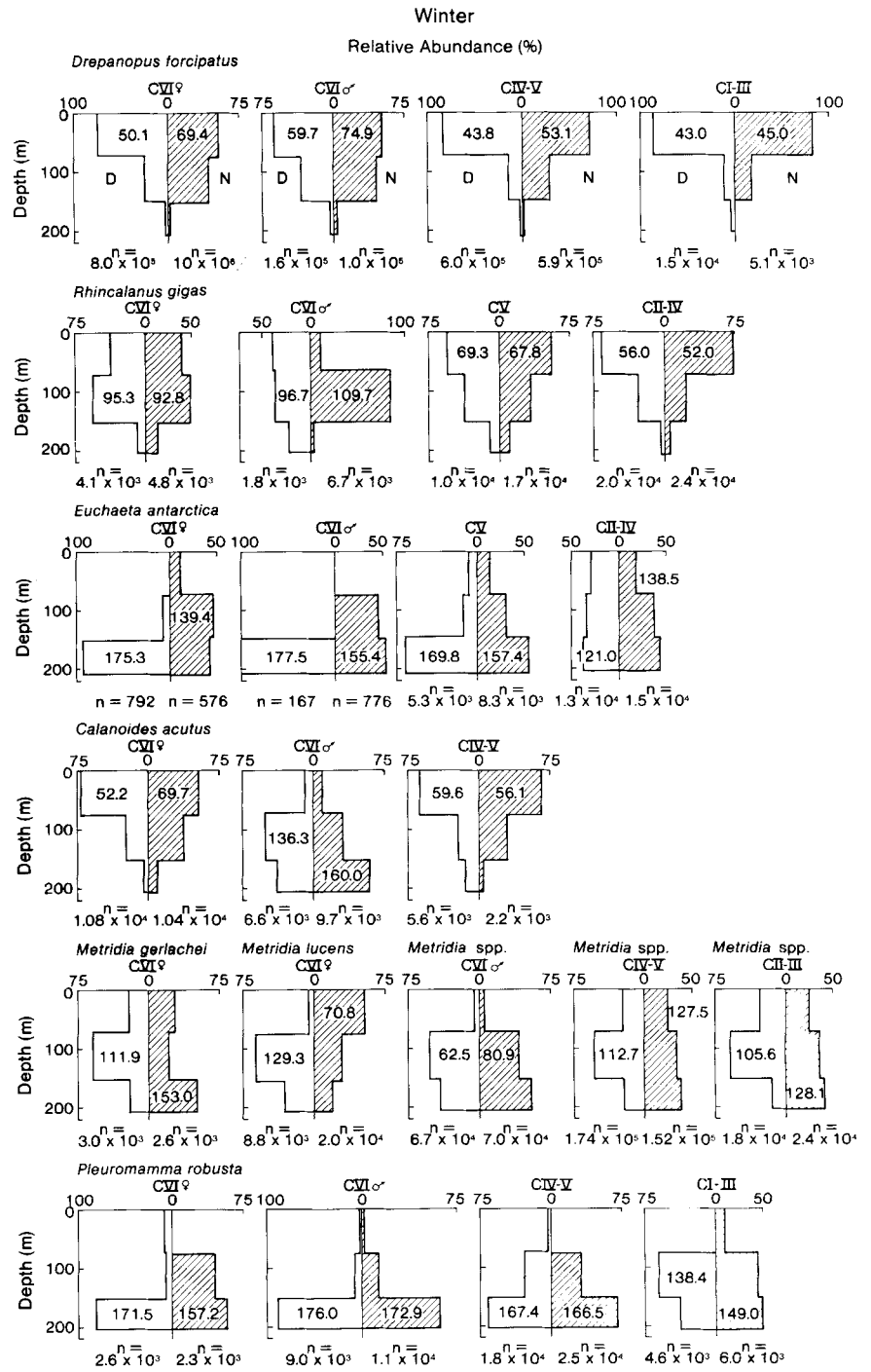


Fig. 6. Diurnal vertical distribution of dominant copepod species and stages during the winter survey in Cumberland East Bay. Data are pooled values ($n = 4$ hauls) in each depth horizon during day (D) and night (N). The median depth of each species stage is given for day- and night-time hauls.

ohlinii, in contrast, occurred deeper during both seasons.

Life histories

The principal seasonal differences in the reproductive status of five of the dominant copepod species can be seen by comparing developmental stage distributions (Fig. 8). Notable amongst these are *C. acutus* and *Metridia* spp. which had a higher proportion of males in the population during winter

and *R. gigas* which, in summer, had a high proportion of adult females and naupliar stages. The median developmental stage of all five species is given in Table III. Species with a generation time of one year (most Antarctic copepods studied to date (Andrews 1966, Marin 1988)) can be expected to be biased towards later copepodite stages and adults the closer they get to reproducing. The probability that younger stages are not being quantitatively sampled by the nets will bias estimates but this may be offset in some cases by nets tending to sample proportionately more of the depth range

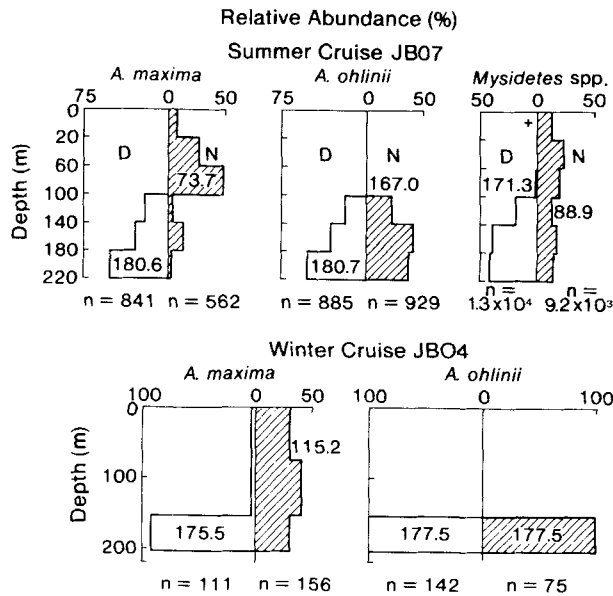


Fig. 7. Diurnal vertical distribution of mysid species during summer and winter surveys in Cumberland East Bay. Pooled data values for summer and winter are the same as in Figs 5 and 6. + = presence at <1%.

inhabited by younger stages (Figs 5–7). For *C. acutus* and *Metridia* spp. the dominance of later stages and the presence of a high proportion of males in the population indicates that spawning was starting in late winter. *R. gigas* on the other hand, had a population dominated by adult females in summer. This, and the presence of naupliar and younger copepodite stages, indicated that reproduction had only just started in January. Data for *E. antarctica* are equivocal and Ward & Robins (1987) have demonstrated that this species has at least two periods of reproduction throughout the year. *D. forcipatus* fell midway between the extremes observed for *C. acutus* and *R. gigas*.

Discussion

During summer zooplankton biomass in Cumberland East Bay was high. Comparable data for other coastal areas in Antarctic waters are rare. Chojnacki & Weglenska (1984) analysed zooplankton abundance and biomass in Ezcurra Inlet (King George Island, South Shetland Islands) during summer 1977/78 and found levels of both were variable but generally low (copepod abundance was 1–480 m⁻³, biomass 0.03–165 mg m⁻³). Comparable or greater levels than found in Cumberland East Bay occur in some Norwegian and Chilean fjords during the summer period of production Matthews & Heimdal (1980). In Antarctic oceanic regions Hopkins (1971) has demonstrated that in the West Wind

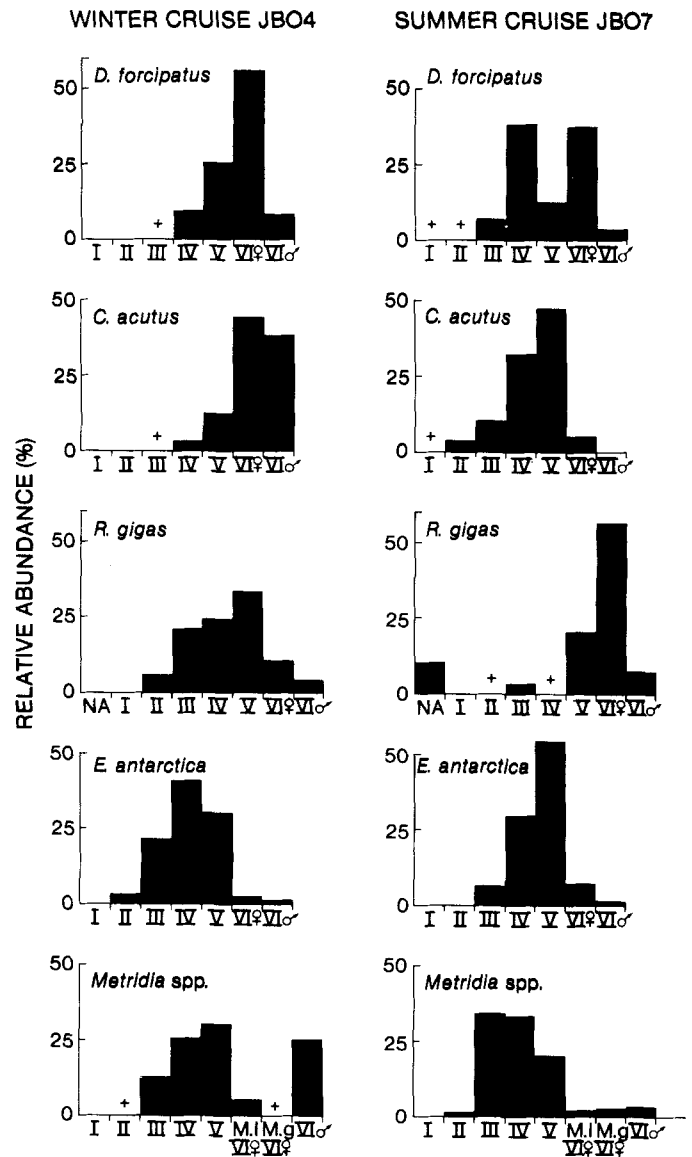


Fig. 8. Developmental stage structure of populations of the five dominant copepod species found during summer and winter surveys in Cumberland East Bay. + = presence at <1%. Mg = *Metridia gerlachei*, Ml = *Metridia lucens*.

Table III. Median developmental stage of the five dominant species of copepod in Cumberland East Bay during summer and winter. CI–CV and adult females and males scored 1–7 respectively.

	Winter median developmental stage	Summer median developmental stage
<i>Drepanopus forcipatus</i>	6.25	5.35
<i>Calanoides acutus</i>	6.33	5.03
<i>Rhincalanus gigas</i>	4.45	6.15
<i>Euchaeta antarctica</i>	4.37	5.15
<i>Metridia</i> spp.	5.17	4.19

Drift biomass levels in the upper 1000 m south of the Polar Front are between 2.1 and 2.7 g dw m⁻²; of which, during the summer months, approximately 50% was found in the surface 250 m and during winter 10–20%. A later study, (Hopkins 1985) during autumn in Croker Passage indicated slightly higher levels (3.1 g dw m⁻²) for zooplankton in the 1–15 mm size range. Comparative estimates for Cumberland East Bay can be obtained by examining the copepod fraction (Table I) where levels are 8.6 g dw m⁻² and 2.2 g dw m⁻² integrated over 0–220 m and 0–200 m during summer and winter respectively. Biomass levels are thus relatively high compared with Antarctic oceanic regions.

The species composition at South Georgia during both seasons reflected a wide range of taxa, many of which display a preference for widely different habitat types within the open ocean. Thus, in addition to the major expected neritic components, (*D. forcipatus*, Mysidacea) we find epipelagic seasonal migrants, (*C. acutus*, *R. gigas*) and non-seasonal migrants (*Clausocalanus* spp., *Oithona* sp.) as well as mesopelagic elements. Species composition was broadly similar during both periods although the relative abundance of species in some cases showed marked seasonal changes (Table II). Despite such changes the same five species dominated the copepod fauna during both periods (Table III) and Mysidacea dominated the non-copepod fraction.

In oceanic areas, the relative seasonal abundance and biomass of a species is likely to change in response to a number of factors. These include the timing of reproduction and the ability of the nets used to retain younger stages. In addition to these, in fjords and nearshore areas, advective processes are likely to be major factors influencing zooplankton communities. Hart (1934) studied the phytoplankton of Cumberland East Bay over the summer of 1930/31 and concluded that the fjord was characterized by continual, often rapid wind-driven movements of the surface layers and by the amount of fine inorganic material suspended in the water. These factors were invoked for the relatively impoverished phytoplankton levels found during his survey. Similar physical condition prevailed in Ezcurra Inlet (Pecherzewski 1980), and although summer copepod abundance and biomass were coincident with peaks of phytoplankton abundance (Chojnacki & Weglenska 1984), water exchange with Bransfield Strait was thought to control abundance of the dominant calanoids. Atkinson & Peck (in press) have reviewed the distribution of zooplankton in relation to the South Georgia shelf and conclude that, on the basis of species composition and abundance, hydrological exchanges between shelf and oceanic water bodies are relatively slow. This does not exclude the possibility of fine-scale changes such as wind-driven and tidal movements influencing the fjord community but may indicate that, under normal circumstances, significant changes in species abundance and biomass will not be subject to short-term fluctuations.

Seasonal differences in abundance were usually most

extreme for the rarer species (usually present in one season but absent in the other) although many of the species dominating biomass showed high (1–27 fold) levels of variation. Some of this can be attributed to reproduction and species with high relative summer abundance, e.g. *C. acutus*, *D. forcipatus*, had, or were in the process of spawning. Indeed, the observed sequence and timing of reproduction of at least two of the dominant species (*C. acutus*, *R. gigas*) agrees well with previously published accounts (Andrews 1966, Voronina *et al.* 1978). In neither season, however, was the entire water column sampled, and in the case of some seasonally migrating species, a proportion of the population may have been overwintering below the level fished by the nets. Certain other species were more abundant in winter and these cases may be linked to macroscale changes in the circulation pattern observed around South Georgia during 1983. Atkinson & Peck (1988), in a survey of zooplankton around South Georgia, have indicated that during winter 1983 the Polar Frontal Zone had moved south and lay across the general area resulting in increased influence of subantarctic surface waters. This resulted in Antarctic epipelagic species (e.g. *E. superba*) being replaced by subantarctic or cosmopolitan ones. Species with increased abundance in Cumberland East Bay during winter included *Calanus simillimus*, *P. robusta* and *Metridia lucens*, all more typical of subantarctic waters. No comparable data exist for the summer survey but the presence of *Euphausia superba* around the island during 1987 (British Antarctic Survey, unpublished) may be indicative of a more usual epipelagic Antarctic fauna.

During both the seasons studied a number of mesopelagic species were present in at South Georgia. Of the 25 genera and species of copepod identified, at least seven are mesopelagic. Their presence in the fjord is puzzling. Atkinson & Peck (in press) have shown that during summer and winter surveys mesopelagic species were greatly depleted in South Georgia shelf waters and Hardy & Gunther (1935) also indicated that deep-water forms were rare. Their presence may perhaps be best explained by either local upwelling of deep-water at some time prior to our surveys, or, that being vertical migrators, they may have been carried onto the shelf at night and thence into Cumberland East Bay. Chojnacki & Weglenska (1984) report a similar phenomenon occurring in Ezcurra Inlet with bathypelagic species being encountered at night.

The gelatinous component of the zooplankton mainly comprised carnivorous Ctenophora and Scyphomedusae which despite their restricted distributions were prominent, especially in summer. Large stocks of medusae and ctenophores are a commonplace seasonal occurrence in fjords and population growth can be high under suitable conditions (Huntley & Hobson 1978, Turner *et al.* 1983). The high summer levels of abundance of early copepodite stages in the surface layers of Cumberland East Bay may provide the necessary food for these organisms to flourish.

Acknowledgements

Thanks are due to the officers and crew of RRS *John Biscoe* and members of the Offshore Biological Programme for assistance in the field and to J.M. Peck who helped with sample analysis. The referees are thanked for their thorough reading of the manuscript.

References

- ANDREWS, K.J.H. 1966. The distribution and life-history of *Calanoides acutus* (Giesbrecht). *Discovery Reports*, **34**, 117–162.
- ATKINSON, A. & PECK, J.M. 1988. A summer–winter comparison of zooplankton in the oceanic area around South Georgia. *Polar Biology*, **8**, 463–473.
- ATKINSON, A. & PECK, J.M. In press. The distribution of zooplankton in relation to the South Georgia shelf in summer and winter. In KERRY, K. & HEMPEL, G., eds. *Ecological change and the conservation of Antarctic ecosystems. Proceedings of the 5th SCAR Symposium on Antarctic Biology*. Berlin: Springer Verlag.
- BARNARD, J.L. 1969. The families and genera of marine Gammaridean Amphipods. *United States National Museum Bulletin*, **271**, 1–535.
- BRATTEGARD, T. 1980. Why biologists are interested in fjords. In FREELAND, H.J., FARMER, D.W. & LEVINGS, C.D., eds. *Fjord oceanography*. Nato Conference Series 4, Marine Science 4. New York: Plenum Press, 53–66.
- CHOJNACKI, J. & WEGLENSKA, T. 1984. Periodicity of composition and vertical distribution of summer zooplankton (1977/1978) in Ezcurra Inlet, Admiralty Bay (King George Island, South Shetland). *Journal of Plankton Research*, **6**, 997–1017.
- HARDY, A.C. & GUNTHER, E.R. 1935. The plankton of the South Georgia whaling grounds and adjacent waters 1926–1927. *Discovery Reports*, **11**, 1–456.
- HART, T.J. 1934. On the phytoplankton of the south-west Atlantic and the Bellingshausen Sea, 1919–31. *Discovery Reports*, **8**, 1–268.
- HOPKINS, T.L. 1971. Zooplankton standing crop in the Pacific sector of the Antarctic. *Antarctic Research Series*, **17**, 347–362.
- HOPKINS, T.L. 1985. The zooplankton community of Croker Passage, Antarctic Peninsula. *Polar Biology*, **4**, 161–170.
- HUNTLEY, M.E. & HOBSON, L.A. 1978. Medusa predation and plankton dynamics in a temperate fjord, British Columbia. *Journal of the Fisheries Research Board of Canada*, **35**, 257–261.
- KIRKWOOD, J.M. 1982. A guide to the Euphausiacea of the Southern Ocean. *ANARE Research Notes*, **1**, 1–45.
- KIRKWOOD, J.M. 1984. A guide to the Decapoda of the Southern Ocean. *ANARE Research Notes*, **11**, 1–47.
- MARIN, V. 1988. Independent life cycles: an alternative to the asynchronism hypothesis for Antarctic calanoid copepods. *Hydrobiologia*, **167/168**, 161–168.
- MATTHEWS, J.B.L. & HEIMDAL, B.R. 1980. Pelagic productivity and food chains in fjord systems. In FREELAND, H.J., FARMER, D.W. & LEVINGS, C.D., eds. *Fjord oceanography*. Nato Conference Series 4, Marine Science 4. New York: Plenum Press, 377–398.
- MORTON, J.E. 1954. The Pelagic Mollusca of the Benguela Current. Part 1. First survey, RRS *William Scoreseby*, March 1950. With an account of the reproductive system and sexual succession of *Limacina bullimoides*. *Discovery Reports*, **27**, 163–200.
- NORTH, A.W. 1988. Distribution of fish larvae at South Georgia: horizontal, vertical and temporal distribution and early life history relevant to monitoring year class strength and recruitment. (WG-FSA-87-16) *Scientific Committee of the Convention for the Conservation of Antarctic Marine Living Resources Selected Scientific Papers 1987*, 105–141.
- PECHERZEWSKI, K. 1980. Distribution and quantity of suspended matter in Admiralty Bay (King George Island — South Shetland Archipelago). *Polish Polar Research*, **1**, 7–82.
- POMMERANZ, T., HERRMANN, C. & KUHN, C. 1983. Mouth angles of the Rectangular Midwater Trawl (RMT 1+8) during paying out and hauling. *Meeresforschung*, **29**, 267–274.
- ROE, H.S.J. & SHALE, D.M. 1979. A new multiple rectangular midwater trawl (RMT 1+8) and some modifications to the Institute of Oceanographic Science's RMT 1+8. *Marine Biology*, **50**, 283–288.
- TATTERSALL, O.S. 1955. Mysidacea. *Discovery Reports*, **28**, 1–190.
- TURNER, J.T., BRUNO, S.F., LARSON, R.J., STAKER, R. D. & SHARMA, G.M. 1983. Seasonality of plankton assemblages in a temperate estuary. *Marine Ecology*, **4**, 81–99.
- VERVOORT, W. 1957. Copepods from Antarctic and sub-Antarctic plankton samples. *Report of the British-Australian-New Zealand Antarctic Research Expedition, Series B*, **3**, 1–160.
- VORONINA, N.M., VLADIMIRSKAYA, Y.V. & ZMIYERSKAYA, M.I. 1978. Seasonal variations in the age composition and vertical distribution of common zooplankton species in the Southern Ocean. *Oceanology*, **18**, 335–338.
- WARD, P. & ROBINS, D.B. 1987. The reproductive biology of *Euchaeta antarctica* Giesbrecht (Copepoda: Calanoida) at South Georgia. *Journal of Experimental Marine Biology and Ecology*, **108**, 127–145.