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Summer–winter differences in copepod distribution around South Georgia

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Abstract

Zooplankton was sampled on a synoptic grid of stations centered on South Georgia during the austral summer of 1981/82 and winter 1983. Within the top 1000 m layer at oceanic stations, copepods averaged 48% of the total biomass in summer and winter, but outnumbered all other taxa combined by a factor of 10. In winter the mean zooplankton biomass within the top 1000 m was 68% of its summer level. Copepod biomass was 77% of its summer level. During both surveys, the large and abundant *Calanoides acutus* and *Rhincalanus gigas* dominated the copepod biomass and, with several other species, showed a marked downwards seasonal migration out of the top 250 m layer in winter. Antarctic epipelagic species predominated around the island during summer but tended to be replaced by sub-Antarctic and cosmopolitan species during the winter. Factors likely to influence our estimates of overall copepods abundance and changes in species composition include seasonality of reproduction, net mesh selection and differences in water mass distribution. The observed trends are attributed mainly to variation in the position of the Polar Front which lay north of the island during the summer survey yet lay across the survey area in winter. This resulted in a greater influence of sub-Antarctic water around South Georgia in winter and the displacement of Antarctic species.

Introduction

The Island of South Georgia (54° S, 37° E) is situated within the limits of the Antarctic zone in the Atlantic Sector of the Southern Ocean. Biological productivity in the waters around the island is high, due to the interaction of the island's shelf with the Antarctic Circumpolar Current as well as its proximity to ocean fronts. The former importance of South Georgia as a whaling ground prompted the Discovery Investigations and the zooplankton study by Hardy & Gunther (1935) remains the most detailed and integrated investigation yet undertaken in this particular area. Since the Discovery Investigations, most seasonal studies have tended to compare the distribution of zooplankton biomass (Foxton, 1956; Hopkins, 1971), or the life cycles of individual species (for example Voronina *et al.*, 1978).

The British Antarctic Survey conducted two intensive synoptic surveys around the island during the austral summer of 1981/82 and winter 1983, forming part of a long term ecosystem monitoring programme. This paper reports on copepod biomass and vertical distribution in the oceanic area around South Georgia (water depth greater than 2000 m), and relates them to those of the other major components of the zooplankton.

The summer–winter differences in abundance of individual species, and their associated changes in vertical distribution are then related to seasonal cycles and the macroscale circulation pattern.

Materials and methods

The summer and winter surveys were conducted between 24th November and 19th December 1981 and from 27th July to 20 August 1983 respectively. The surveys covered a 240x180 nautical mile rectangular grid of stations centered on South Georgia (Fig. 1) with stations spaced 30 nautical miles apart.

Zooplankton were sampled at each station with acoustically operated RMT 1 nets of mesh size 330 μm. The nets were fished obliquely downwards at a towing speed of approximately 2 knots. Depth horizons sampled at each station are indicated in Fig. 1. The 10–250 m and 250–500 m hauls took approximately 30 minutes each and the 500–1 000 m hauls an hour. Net hauls were made as soon as the ship arrived on station, irrespective of time of day. The increased day length during summer resulted in a higher proportion of net hauls (75%) being made during daylight, c.f. 34% in winter. Distance travelled by the nets was calculated from a flowmeter mounted on the net monitor and the volume filtered then calculated from the equations of Pommeranz *et al.* (1983). Filtration was assumed 100% efficient.

Total zooplankton volume was measured on board by the displacement method before preservation in 4% buffered formalin. Laboratory analysis proceeded in the conventional manner (see Atkinson and Peck, in press) and involved subsampling using a Folsom plankton splitter. Non copepod species were removed from each sample leaving copepod residues. The volumes of the residues were estimated by the displacement method and copepod biomass in the samples calculated by simple proportion. The biomass of krill (*Euphausia superba*) in the samples was also measured, enabling the volume of remaining zooplankton to be calculated.

The copepod fractions were then split and adult copepods and copepodite stages were counted, sexed and identified as far possible to species level. An average of 745 copepods was counted in each sample. All abundances (adults plus all identifiable immature stages) have been standardised to 1 000 m^{-3} of water filtered.

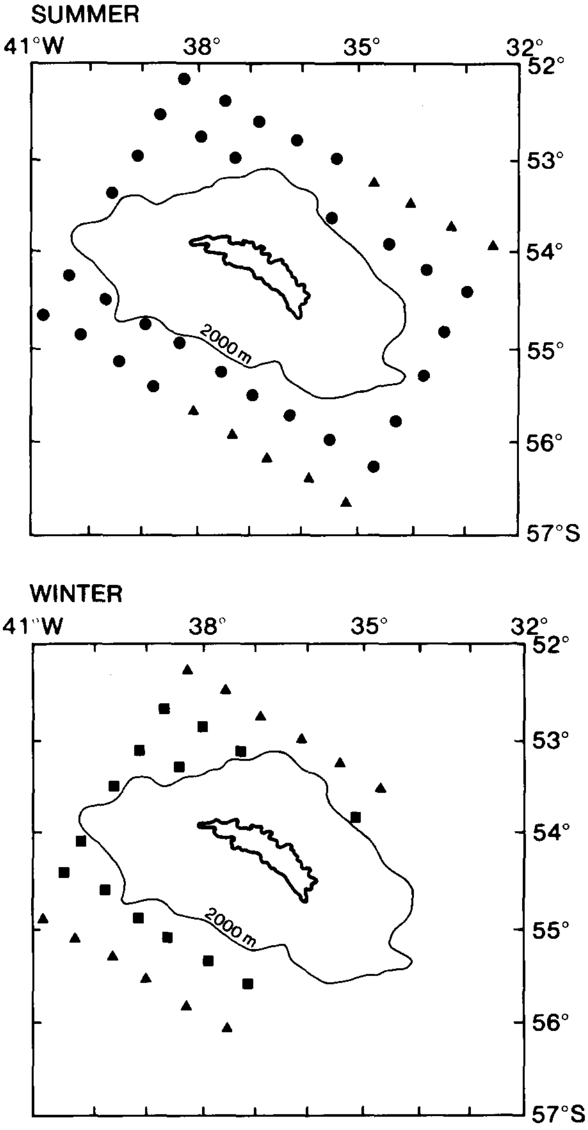

Fig. 1. Position of oceanic sampling stations during the summer survey and winter survey.
● = a single 10–250 m RMT haul.
■ = 10–250 m haul plus 250–500 m haul.
▲ = 10–250 m haul, 250–500 m haul plus 500–1 000 m haul.

The environment

A simplified picture of the water circulation in the Southern Ocean is summarised by Gordon & Goldberg (1970). The Antarctic Surface Water, the sub-Antarctic Surface Water and the Warm Deep Layer (Circumpolar Deep Layer) comprise the Antarctic Circumpolar Current, which flows in a predominantly easterly direction. Complex and variable frontal structures separate the surface water masses (Nowlin & Klinck, 1986). Following the terminology of Whitworth (1980), the sub-Antarctic and Antarctic Surface Waters are separated by a broad zone of mixed water known as the Polar Frontal Zone, the southern boundary of which is known as the Polar Front.

The variability in position and structure of frontal systems is especially marked in the Atlantic Sector. Satellite imagery has indicated that the Polar Front can vary widely in position from week to week, presumably due to changing meteorological conditions (Legeckis, 1977; Heywood, pers comm). The maximum displacement of the front (approximately 200 km, Whitworth, 1980) is thought to be limited by bottom topography (Gordon, 1967).

Hydrographic conditions around South Georgia during the summer and winter survey

Detailed descriptions of the water masses and circulation patterns around South Georgia during the summer and winter surveys are given by Priddle *et al.* (1986) and Heywood *et al.* (1985) respectively. The Polar Front lay to the north of the survey grid in the summer although temperature and salinity characteristics of several of the

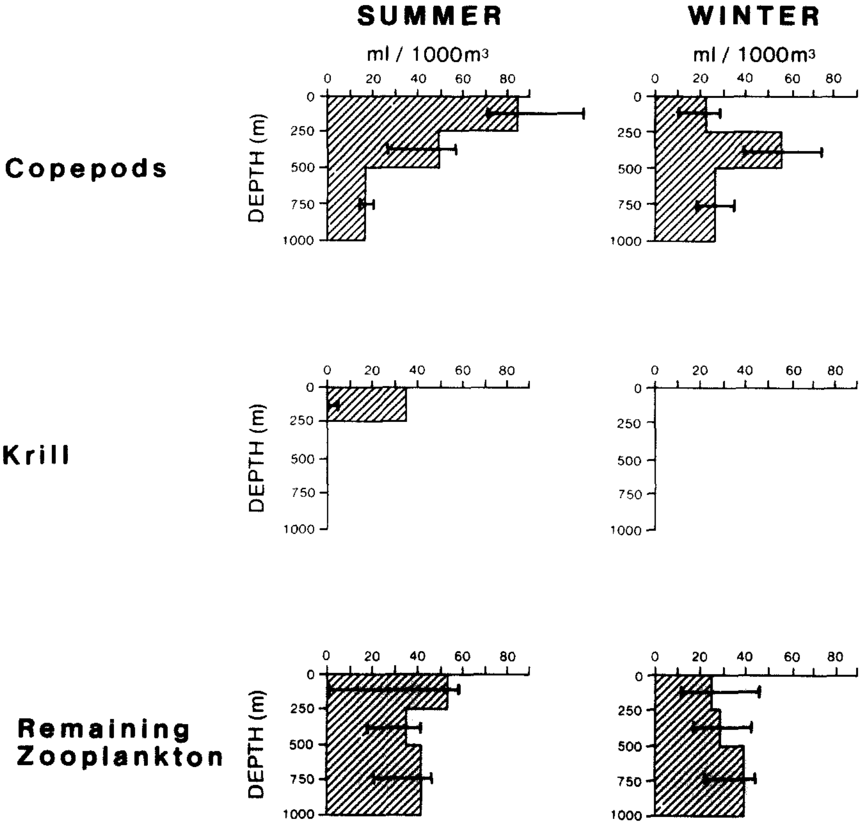

Fig. 2. Mean biomass (displacement volume) of the three components of the zooplankton within the three depth horizons fished in summer and winter. The interquartile ranges are indicated.

northernmost stations showed mixing of small quantities of sub-Antarctic Surface Water with the Antarctic Surface Water. Weddell Sea water was absent from the survey area at this time.

During the winter survey, the island lay within the Polar Front, which was broad and diffuse in the eastern Scotia Sea. Consequently there was a greater degree of mixing of sub-Antarctic Surface Water with the Antarctic Surface Water around the island, and a rise in surface temperature towards the NW of the survey grid.

Results

Summer–winter changes in copepod biomass

Mean catch volumes of copepods, krill and remaining zooplankton (standardised to 1000 m^{-3} of water filtered) were calculated from all oceanic stations in all depth horizons sampled, and the summer and winter profiles obtained are shown in Fig. 2. During the winter survey, total zooplankton biomass within the top 1000 m fell to 68% of its summer level. Copepods decreased to 77%, krill to less than 0.1% and remaining zooplankton biomass fell to 76% of summer levels.

Metridia spp was the most abundant genus within the top 1000 m, although copepod biomass was dominated by the large herbivores, *Calanoides acutus* and *Rhincalanus gigas*. The winter redistribution of copepod biomass (Fig. 2) within the water column is largely due to the downward seasonal migration of these two species. During both surveys, copepod biomass was approximately 50% of the total biomass within the top 1000 m. However, copepods outnumbered all other taxa put together by a factor of ten.

Summer and winter biomass estimates (mean displacement volume) from the top 1000 m of the water column are presented in Table 1 and compared with those obtained by Foxton (1956) and Hopkins (1971). Foxton's data presented here are drawn from latitudes 50–55° S, mainly from the Atlantic sector of the Southern Ocean and refer to the displacement volume of the catch after removal of krill and large gelatinous plankton; being essentially a measure of the biomass of copepods, chaetognaths and small euphausiids. Hopkins' (1971) estimates come from the sub-Antarctic, convergence and Antarctic zones of the Pacific sector and refer to dry weight estimates of the whole catch which we have here converted to an equivalent displacement volume, using Hopkins' own conversion factors. Our estimates are, in all cases somewhat higher than the other two. Summer to winter biomass ratios within the top 1000 m however, agree closely and in all cases are approximately 80% of summer levels.

Summer–winter changes in abundance

The summer–winter abundance ratios of the important species occurring in the top 1000 m are presented in Table 2. A number of copepod species were more abundant in summer whilst others achieved peak abundance in winter. Where

Table 1. Comparison of mean biomass within the top 1000 m in summer and winter around South Georgia with results from previous oceanic surveys. All results refer to mean displacement volumes (mls 1000 m^{-3} filtered). RMT 1 results are for copepod fractions only. Biomass of copepod plus remaining zooplankton fractions are given in brackets.

	Net used and mesh size	Summer biomass (ml 1000 m^{-3})	Winter biomass (ml 1000 m^{-3})	Winter/summer biomass
Foxton (1956)	N70V (350 μm)	35	29	0.82
Hopkins (1971)	Bé (202 μm)	30	25	0.83
Present Study	RMT 1 (330 μm)	43 (86)	33 (66)	0.77 (0.77)

Table 2. Comparison of summer–winter abundances and zoogeographic distribution of copepods and other dominant zooplankters. Species are ranked in descending order of summer–winter abundance ratios.

Species (Copepod species indented)	Summer–winter ratio of mean abundance within top 1000 m	Zoogeographical distribution
Euphausia superba	897	Antarctic
Themisto gaudichaudii (amphipod)	109	Antarctic and sub-Anctarctic
Vanadis antarctica (polychaete)	21.3	Antarctic
Diphyes antarctica (hydrozoan)	19.0	Antarctic
Metridia gerlachei	15.1	Antarctic
Clausocalanus laticeps	12.7	sub-Antarctic
Clione antarctica (pteropod)	4.82	Antarctic
Tomopteris spp. (polychaete)	4.39	?
Vibilia antarctica (amphipod)	3.86	Antarctic ?
Sibogita borchgrevinki (hydrozoan)	3.78	Antarctic
Calanus propinquus	3.28	Antarctic
Pelagobia longicirrata (polychaete)	2.71	Antarctic (mainly)
Calanoides acutus	2.67	Antarctic
Haloptilus oxycephalus	2.02	Antarctic and sub-Antarctic
Oncaea antarctica	1.76	Antarctic ?
Chaetognatha spp.	1.46	?
Ctenocalanus spp.	1.45	?
Scolecithricella minor	1.41	Antarctic (mainly)
Heterorhabdus spp.	1.39	Antarctic
Spongiobranchia australis (pteropod)	1.36	Antarctic and sub-Antarctic
Metridia curticauda	1.30	Antarctic and sub-Antarctic
Gymnosomata spp. (pteropod)	1.16	?
Primno macropa (amphipod)	1.07	Antarctic and sub-Antarctic
Oithona spp.	1.06	?
Salpa spp.	0.993	?
Racovitzanus antarcticus	0.967	Antarctic
Ostracoda spp.	0.941	?
Gaidius tenuispinus	0.915	Antarctic and sub-Antarctic
Euchaeta antarctica	0.876	Antarctic
Cyllopus spp. (amphipod)	0.795	?
Rhincalanus gigas	0.752	Antarctic and sub-Antarctic
Thysanoessa spp.	0.698	?
Euphausia triacantha	0.615	Polar Frontal Zone
Eucalanus longiceps	0.566	sub-Antarctic
Cyphocaris richardii (amphipod)	0.467	Antarctic and sub-Antarctic
Euaetideus australis	0.434	Antarctic and sub-Antarctic
Euphausia frigida	0.424	Antarctic
Calanus simillimus	0.280	sub-Antarctic
Travisiopsis spp. (polychaete)	0.220	?
Pleuromamma robusta	0.0895	sub-Antarctic
Metridia lucens	0.0721	sub-Antarctic (mainly)

possible, species have been assigned as principally occurring in either Antarctic or sub-Antarctic waters according to previously published accounts of their distribution (mainly from Vervoort, 1957, 1965; Park 1978, 1980; Marin 1987). Although not entirely consistent, the trend is for those species which were more abundant in winter, to be inhabitants of sub-Antarctic waters, whilst in summer, Antarctic species predominated.

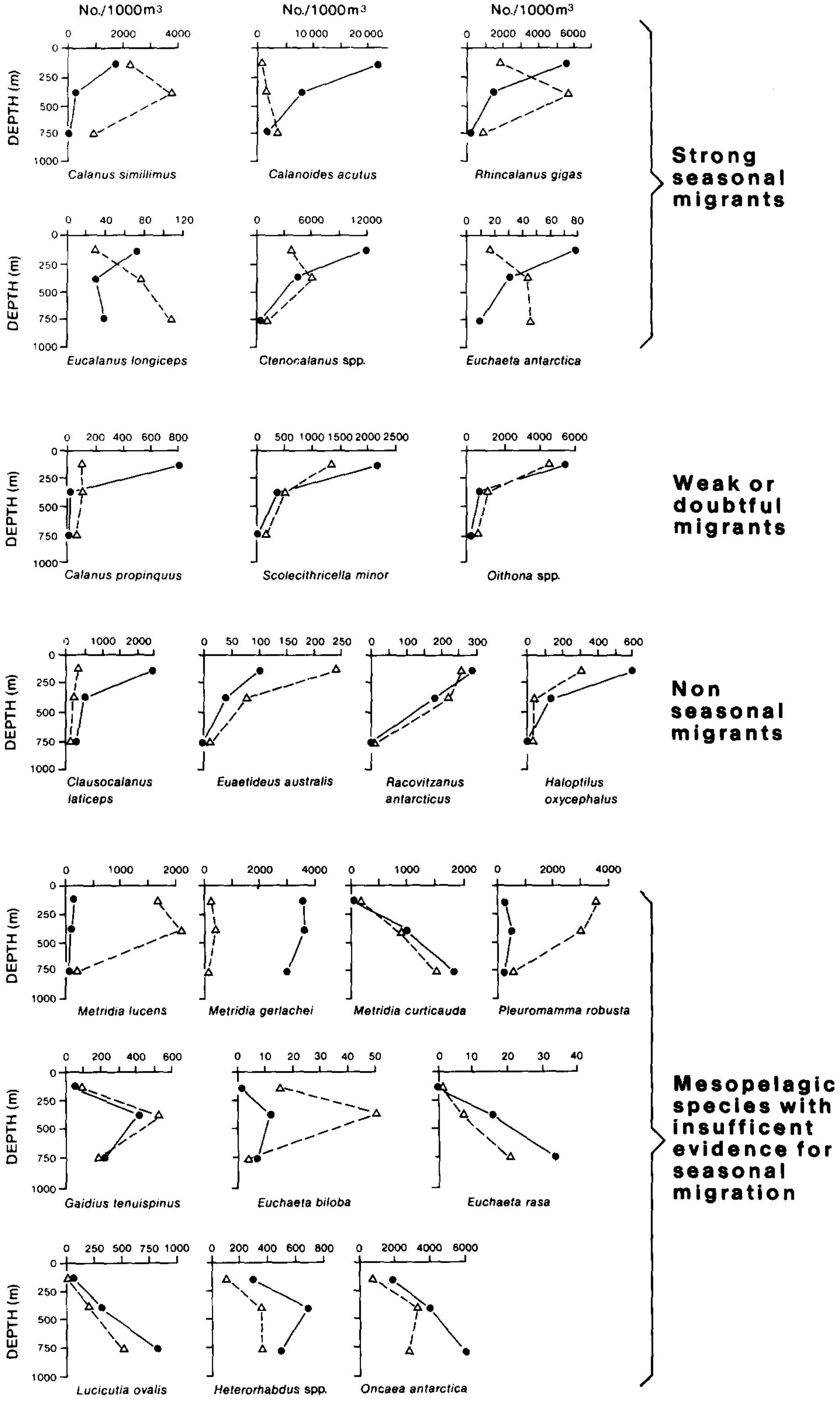

Fig. 3. Vertical distribution of major copepods in summer and winter. Mean abundance in summer (●–●) and in winter (△–△) are plotted against mean depth for each of the 3 horizons fished.

Vertical distribution of copepod species in summer and winter

Vertical profiles of abundance of the major copepod species in summer and winter are compared in Fig. 3. Several species, including *Metridia lucens*, *Euchaeta antarctica* and *Scolecithricella minor* have been shown to make extensive diurnal vertical migrations (Hardy & Gunther, 1935) so an observed vertical distribution of these species at any station is more a reflection on time of day than time of year. However, hauls were made effectively at random times of day or night so when abundance within each depth zone is averaged from all stations, it should represent mean vertical distribution for the time of the year.

The majority of abundant epipelagic herbivores, for example *Calanoides acutus*, *Rhincalanus gigas*, *Calanus simillimus* and *Ctenocalanus* spp. show clear evidence for downward seasonal migration, appearing in maximum abundance in winter, usually in the 250–500 m zone. However, no evidence for seasonal migration was found for *Clausocalanus laticeps* or the rarer species *Euaetideus australis*, *Racovitzanus antarcticus* and *Haloptilus oxycephalus* (Fig. 3).

A higher percentage of epi-mesopelagic and mesopelagic copepods are omnivorous (for example Metridiidae) or carnivorous (for example Euchaetidae) and although sampling was only to 1000 m in winter, these species showed no evidence for seasonal vertical migration. Although there is a large summer–winter difference in overall abundance of *Pleuromamma robusta*, it appears to occupy a higher average position in the water column in winter.

Discussion

The summer and winter biomass estimates presented here from the South Georgia region higher than those reported by Foxton (1956) and Hopkins (1971). Vladimirskaya (1975) also found zooplankton biomass from No. 38 mesh Juday nets in the autumn – winter period in the Scotia Sea to be three times higher than Foxton's (1956) results. However, zooplankton sampling methods and in particular net mesh size have been shown to have a significant influence on biomass estimates and species composition of the catch (Hopkins, 1966), and it is likely that methodological differences between workers have a significant influence. In all cases, however, winter levels of biomass in the top 1000 m were consistantly about 80% of their summer levels. The actual seasonal difference within the entire water column is likely to be even smaller than this. Andrews (1966) for example found that a proportion of the population of *Calanoides acutus* overwintered deeper than 1000 m, as did Mackintosh (1937) for *Rhincalanus gigas*, and the same may be true for other strong seasonal migrants. These results therefore reinforce the idea that there is no marked summer–winter variation in zooplankton biomass within the Southern Ocean.

The most striking differences between the summer and winter plankton were the pronounced changes in vertical distribution of several copepod species (Fig. 3) as well as large changes in the overall abundance of others (Table 2). Although nothing can be inferred as to preferred water type in cases where identification has simply been made to genus or broader grouping it can be seen from Table 2 that species which were more abundant in summer tend to be Antarctic species whereas in winter they tend to be inhabitants of warmer water.

There are several possible reasons for a species occurring in higher mean abundance in either summer or winter around South Georgia, but before these trends are linked to environmental conditions some problems in the interpretation of these data need to be addressed. Firstly, in comparison with many other abundant zooplankters, copepods have relatively short life cycles which can result in large monthly fluctuations in overall abundance (Voronina *et al.*, 1979, 1980). Also, early copepodids of many of the smaller copepods such as *Scolecithricella minor*, *Clausocalanus laticeps*, *Oithona* spp. and *Oncaea antarctica* are too small to be retained by the meshes of the RMT 1 net. It is likely that if summer sampling takes place just after a small species has spawned, many of the adults will have died, and the large numbers of early copepodids will be too small for retention by the net. This would result in a summer underestimate of abundance of the species.

Secondly, as has been mentioned above, a proportion of the populations of *Calanoides acutus* and *Rhincalanus gigas* overwinter deeper than 1 000 m. The summer–winter abundance ratios of these species are therefore artifically high, and the same may be true for other strong seasonal migrants. Thirdly, the sampling grids covered slightly different areas during the two surveys, extending further southeast in summer (Fig. 1). However, preliminary analysis of horizontal distribution indicated that most species showed no clear regional differences in abundance during the summer, so this factor alone cannot account for these changes.

Any, or all of the factors above may be responsible for seasonal differences in abundance, although none can account for the overall trend of replacement of Antarctic species by warmer water species during the winter survey. This trend seems best explained by the macroscale circulation pattern. However, when presented with only two 'snap shots' of the zooplankton around South Georgia, it is difficult to deduce the extent of variation caused by hydrographic differences between surveys, to that brought about by normal seasonal cycles of the zooplankton. One such regular cycle was noted by Mackintosh (1934) in his analysis of macrozooplankton (including larger copepods) taken over a wide area of the Atlantic Sector of the Antarctic including South Georgia. He noted that 'cold water' species predominated in early summer, but tended to be replaced by 'warm water' species as the summer progressed, and that these 'warm species' remained in the area throughout the winter. This observation is superficially very similar to our own. However, the samples analysed by Mackintosh (1934) only came from the top 100 m of the water column, and as Voronina (1970) and others have stressed, it is important to sample the majority of the depth range inhabited by a species at any time of year. The seasonal changes in abundance noted by Mackintosh (1934) can therefore be partially explained by seasonal vertical migration.

Indeed, after later analysis of samples taken as deep as 1 000 m, Mackintosh (1937) postulated that by making such a migration between Antarctic Surface Water and the Warm Deep Layer, an Antarctic species might maintain its distribution within the Antarctic zone. The northerly component in the flow of the Antarctic Surface Water would carry it towards the Polar Front in summer and the southerly component in the movement of the Warm Deep Layer would return it southwards in winter. This would presumably cause the limit of the population to extend northwards throughout the summer and retreat southwards in winter. However, this regular seasonal movement of the northern limits of seasonally migrating species relative to the Polar Front has never been reported. Mackintosh (1937) for example plotted monthly profiles of abundance of dominant zooplankters from transects crossing the Polar Front in the Western Drake Passage. The northern limit of *Calanoides acutus* was found not to change significantly, lying just north of the Convergence throughout the year. The results of Andrews (1966) from transects along the O° meridian endorse this.

The observed changes in abundance of copepods and other zooplankton therefore seems better explained by movement of the Polar Front relative to the island than by normal reproductive and migratory cycles. The magnitude and speed of movement of the Polar Front (up to 100 km in 10 days; Priddle *et al.*, in press) is much greater than the velocity of northerly and southerly components in the movement of the water masses. As a result of the movement of the Polar Front, there was a greater influence of sub-Antarctic Surface Water around the island in winter than in summer. Antarctic species were therefore probably displaced to the south of the island during the winter, and replaced by a predominantly sub-Antarctic fauna.

The largest changes in abundance tended to occur in those species normally resident within the top 500 m (Table 2, Fig. 3). There were no large summer–winter differences detected in the structure of the underlying Warm Deep Layer

(Heywood, pers comm) so this layer would possibly represent a more stable environment for overwintering plankton. This displacement of the Polar front during the 1983 winter was linked to an anomalous period of southward airflow (Priddle *et al.*, in press), and it is clear that the physical factors causing such movements are both numerous and complex. These factors interlink with the vertical migration cycles of copepods and are superimposed on their natural changes in abundance. A better understanding of such processes is required prior to the further study of either large scale oceanic distributions or oceanic-shelf interactions around South Georgia.

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