Mesozooplankton Community Structure in the Scotia Sea during the CCAMLR Survey: January-February 2000.

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Abstract

An analysis of mesozooplankton community structure in the Scotia Sea was carried out, based on 123 RMT1 double oblique hauls (0 -200 m) taken during the 'CCAMLR 2000' synoptic survey. Standardised sample data (log abundance 1000 m^{-3}) was grouped into taxonomic categories and subjected to cluster analysis and multi dimensional scaling. Two ordinations were performed, the first based on a reduced taxonomic data set (31 categories out of a full 120) obtained by pooling ontogenetic stages within species and by only including those taxa that contributed at least 4% to total abundance at any one station. This disclosed two major station groups (1 and 2) which separated north and south, forming 'warm' and 'cold' water communities respectively, whereas four minor groups were mainly associated with stations around the Antarctic Peninsula and within the Weddell Scotia Confluence. Mean zooplankton abundance (238,000 ind. 1000 m^{-3}) within the northerly group 1 was up to 12 times higher than in other groups. The second ordination using all taxonomic categories disclosed an additional intermediate group (1a), which was geographically consistent with the southern part of the northern group 1 from the previous ordination. However because of taxonomic similarities between all the major station groups it was concluded that they represented a single community, which differed only in its phenological development and the mass occurrence of patchily distributed organisms such as krill larvae. Testing of the relationships of station groups with the position of water masses and frontal boundaries indicated that the Weddell Front was broadly coincident with the boundary of the northern and southern communities over much of its length. However the presence of stations belonging to group 2, to the north of the Weddell Front, west of the Antarctic Peninsula and around the South Sandwich Islands, was consistent with the distribution of ice influenced surface water. Low zooplankton abundance and species developmental composition suggested that this ‘community’ was largely in an over-wintered state. Copepods and Euphausiids dominated the mesozooplankton throughout the study area with small copepods (*Oithona* spp., *Ctenocalanus* spp. and *Metridia* spp.) particularly abundant.

Key Words: Zooplankton, community structure, Southern Ocean, frontal zones, copepods, euphausiids.

Introduction

The Atlantic sector is arguably one of the best studied regions of the Southern Ocean (SO). It was the focus for the extensive Discovery Investigations undertaken during the 1920-30’s and again in the early 1950’s and for many other national and international programmes including BIOMASS (Biological Investigations of Antarctic Marine Systems and Stocks) which generated the First and Second International Biological Experiments (FIBEX and SIBEX). The major focus of these programmes was to extend our knowledge of the living resources of the SO and in particular the Antarctic krill (*Euphausia superba*), however parallel research greatly increased our ecological understanding of other polar zooplankton and some of the factors governing their distribution. Various approaches to the large-scale characterisation of plankton distributions in the SO and their relationship to the physical environment have been advanced in recent years. Mackintosh’s (1936) initial view of the region south of the Antarctic Polar Front (APF), based on 600 samples collected between 1927-31in the top 100 m of the water column, emphasised the distribution of cold and warm water plankton and spatio-temporal variability in its richness. Communities were distinguished which were broadly associated with different water masses; a northern zone populated by typically warm water species, a region of permanently scarce plankton in the region of the Antarctic Peninsula and a zone enclosing the line separating Bellingshausen and Weddell Sea faunas. Hempel (1985) reviewed the geographical distribution of plankton in the SO and described the occurrence of latitudinal zones which were mainly determined by seasonal variations in ice-cover. There are obvious parallels between this view of ecological zonation and the patterns described by Mackintosh in that the latter connected the distribution of coldwater species and pack-ice movement. The regional oceanography developed by Longhurst (1998) based on algal ecology emphasised the importance of frontal zones within the SO as separating ecological provinces. The annular ring between the APF and the Antarctic Divergence (AD) is synonymous with the southern branch of the Antarctic Circumpolar Current (ACC) and was viewed as a single province with its ecology driven by the presence of krill, salps and copepods. Most recently Pakhomov and McQuaid (1996) and Pakhomov et al. (2000) have described the distribution of zooplankton communities along transects running from the region of the Sub-tropical Convergence (STC) across the SO to the Antarctic Continent in which the major fronts variously serve to delimit and define community structure. However, some frontal features such as the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary (SACCB) have only recently been described (Orsi et al., 1995) and their importance in terms of zooplankton dynamics and distribution has not been assessed. The ACC in the Atlantic sector is a very dynamic region and downstream of Drake Passage meandering of frontal zones and eddy shedding can geographically alter the distribution of plankton (e.g. Atkinson et al., 1990). Additionally large scale movements of water masses due to atmospheric forcing have been reported which can also fundamentally alter plankton distributions (eg Priddle et al., 1998) and more recently there has been speculation about the affect ENSO events might have on large scale distribution patterns (Quetin et al., 1996).

Unlike the Indian Ocean sector where a number of large-scale oceanographic surveys have recently taken place (see Hosie 1994, Chiba et al., 2001, Hosie et al., 2000) there have been few opportunities until now to assemble a comparably large-scale view of the Atlantic sector. The ‘CCAMLR 2000’ survey covered an extensive area, (approximately 15 degrees of latitude and 50 degrees of longitude) and in the normal way a synoptic view of the plankton over such a large area would have been difficult to achieve without temporal aliasing of the data. However the 4 ship survey allowed us to complete observations in only 29 days. Analysis of the resulting 123 RMT1 samples collected over an area stretching from the South Sandwich Islands through the Scotia Sea and down the western side of the Antarctic Peninsula, an area of just over 2×10^6 km^2 has provided a synoptic basin scale view of plankton distribution and allowed us to investigate community structure and assess the importance of frontal regions as community boundaries.

Methods

Double oblique RMT1 samples (0-200-0 m) were taken as part of a suite of standard netting protocols carried out at each station (see Watkins et al. this volume). Nets were towed for an average of 32 min (quartile ranges 27- 39 min) and the resulting samples, or in some cases subsamples, were preserved in 10% v:v formalin in seawater and shipped to the UK for analysis. Here they were sorted for macroplankton and large species such as krill, salps and other gelatinous forms were removed. Samples were then split using a folsom plankton splitter into a series of aliquots. Two fractions of between a 1/2 to 1/64 of the preserved amount were usually counted to ascertain the numbers of larger mesozooplankton (copepods chaetognaths euphausiid larvae etc) and two fractions usually between 1/256 – 1/512 for the smaller end of the spectrum (Oithiniids, *Ctenocalanus* spp. copepod nauplii etc). Data were standardised to abundance 1000 m^{-3} based on flow rates determined from flowmeters placed in the RMT 8 nets. It is known that the RMT1 can fish independently of the RMT8 and presents a mouth area to the water which is dependent on ships speed (Pommeranz et al., 1983). We determined that the average speed of the net through the water for all deployments was 2.25 kts (quartile range 2.04- 2.53 kts) at which speeds the mouth area ranges from around 0.5-0.65 m^2 (mean ~ 0.6 m^2). Data were standardised accordingly.

A total of 120 taxonomic categories were enumerated including species, species stages, genera, or in some cases higher taxa. Copepods were the dominant organism (67 taxonomic categories) along with euphausiids (22 taxonomic categories). Data were analysed using the statistical package Plymouth Routines in Multivariate Ecological Research, PRIMER 5 (PRIMER-E Ltd 2000) see Clarke and Warwick (1994). Copepod species stages and larval euphausiids were initially pooled within species to give overall totals, thus reducing the data set to 77 taxonomic categories. Standardised data were log transformed and a similarity matrix created containing those zooplankton that contributed ≥4% of the total abundance at any one station which further reduced the list to 31 taxa. Data were then subjected to nearest neighbour clustering (Bray Curtis) and non-metric multi-dimensional scaling (MDS) and station groups arbitrarily identified. These groupings were then subjected to the ANOSIM and SIMPER routines to determine the significance of differences between groups and to identify the species contributing to similarity within, and differences between, groups. The routines BIOENV, and BVSTEP were used to test the extent to which measured environmental variables (mean temperature in the top 50 m, salinity, density, latitude and surface chlorophyll) accounted for pattern in the species data and to test for redundancy in the taxonomic data set by seeing if a limited subset of species could produce the same pattern.

A second series of analyses (as above) was then performed on the full (unpooled) data set to investigate whether the inclusion of ontogenetic species stages altered the basic patterns which resulted from the initial analysis.

Results

Community structure

Results of clustering analysis and MDS on the reduced data set are shown in Fig 1.

Two main groups (1 & 2) were identified as a result of clustering the data, containing 60 and 42 stations respectively and a further four groups (3-6) with 3, 7, 9 and 2 stations respectively.

When overlaid on the survey area the two largest station groups (1 and 2) showed strong geographic integrity, with group 1 occupying the northern most part of the survey area forming a boundary with group 2 to the south, broadly along the line of the Weddell Front (Fig 2). However stations belonging to group 2 were also found on the western side of the Antarctic Peninsula and around the South Sandwich islands suggesting that this was a cold water community and was influenced by the extent of ice influenced surface waters (see Brandon et al. this volume, Fig ?). The four minor groups (3-6) were geographically consistent with neritic waters around the South Shetland Islands and also water influenced by the Weddell Scotia Confluence (WSC). Mean zooplankton abundance within group 1 was up to 12 times higher than in the additional groups (Table1 and Figure 3).

Differences between stations grouped in this way were tested using the statistical routine

ANOSIM. Overall the station groups derived from clustering were shown to be a robust way of grouping the data. The null hypothesis that there were no differences between groups was not supported by the global R statistic (R=0.726) and values of R in all pairwise comparisons between the major groups and minor groups were all >0.615 (p =0.001).

Analysis of similarity (SIMPER) was carried out to establish which species were responsible for similarities within and dissimilarities between groups. Data from the first ordination are summarised in Table 2 where mean abundance (ind.1000 m^{-3}) of the 17 taxa, which comprise in various permutations, the 10 highest percentage contributions to within group similarity, across all groups, is presented. In the first ordination, taxonomic composition was very similar between groups 1 and 2, with the same 10 taxa broadly accounting for between 66-76% of within group similarity for each group. For the remaining groups, 80-90% of within group similarity was accounted for by the listed species. Dissimilarity between groups 1 and 2 was primarily accounted for by species that were more abundant in group 1, reflecting the increased zooplankton abundance in this group and the more northerly distributions of many of its component taxa eg *Limacina helicina*, *Calanus simillimus*, *Rhincalanus gigas* and *Clausocalanus laticeps* as well as *Oncaea* spp.

Groups 3 and 5 were both characterised by relatively low abundance and although group 5 contained many of the species serving to characterise groups 1 and 2, it was dominated by swarm forming zooplankton *Thysanoessa macrura.*, *Euphausia superba* and *Salpa thompsoni* blastozooids. Group 4 encompassed a number of stations occurring between the tip of the Antarctic Peninsula and the South Orkneys Islands and was distinguished from all others by the presence of high abundances of *E. superba* larvae.

An ordination of stations based on the full selection of species stages identified ie without pooling stages within species, or selecting those that contributed a certain percentage of the abundance was also performed. This time five groups were identified in the log transformed data, with 3 containing in excess of 30 stations and two with 6 and 4 stations respectively (Fig 4). The northern group 1 was smaller than previously and its boundary was now approximately coincident with the SACCF. Group 2 was also smaller and mainly restricted to the area around the South Sandwich Islands. An intermediate group (1a) was present to the south of the SACCF which now incorporated a number of stations from the southern part of group 1 in the first ordination and others that were previously found along the southern perimeter of the survey area (Fig 4.). Stations within this group were characterised by many of the small copepod species such as *Ctenocalanus* sp. and *Oithona* spp. as well as the younger and intermediate stages of some of the biomass dominant copepods such as *Calanus propinquus* CII and *Calanoides acutus* CIII. It was distinguished from group 1 by the presence of *E. superba* calyptopis stage 1 and reduced numbers of the more northerly distributed species such as *Clausocalanus laticeps*, species stages of *Calanus simillimus* and additionally *Limacina helicina*. With minor changes, the remaining groups were largely as identified in the first ordination.

The PRIMER routine BVSTEP was used to identify the smallest subset of taxa in the reduced species by station matrix which could explain most of the pattern in the data. This identified a subset of eighteen of the original 31 species/stages in the matrix ($\rho = 0.953$). Twelve of these taxa (along *Calanus simillimus*, *R. gigas* nauplii, *Oncaea* spp., *Pelagobia longicirrata*, Ostracoda and *Euphausia frigida*) were previously identified as contributing most of the within group similarity (Table 2) and hence their distributions are presented in Fig. 5 as they describe much of the variation between station groups. Distribution patterns of these taxa fell into 3 basic types; those that were abundant in the north of the survey area eg *L. helicina* and *R. gigas*, those abundant to the south eg *E. superba* larvae and *Salpa* blastozooids, and a number of other taxa, which despite varying enormously in abundance, were nonetheless widespread.

Relationships with water mass distributions and environmental factors

To test how robust grouping the stations on the basis of which water mass they occurred in, we characterized each station on where it lay in relation to the main frontal positions (Brandon et al. this volume). Global R for both ordinations was considerably lower than for the original station groupings (R = 0.175) and significant differences only existed between the grouping of stations corresponding to the northern part of the ACC (mainly group 1) and those south of the SACCB (R = 0.323) and south of the Weddell Front (WF), which comprised mainly stations from group 2 (R = 0.303). On this basis we conclude that the original grouping of stations (Fig 2) was most robust and that the SACCF in particular had little overall effect on community structure.

Further analysis using the BIOENV procedure to assess the correspondence and significance of environmental data to the station groupings was carried out. Of the environmental variables tested with the pooled species by station matrix, the best fit was for water density alone ($\rho = 0.139$), rather than in combination with any other variables. However the low values of the rank correlation coefficients indicated little relationship between density or any other environmental variable and the biotic data (see Clarke and Ainsworth, 1993).

Discussion

Species occurrence and distribution:

Major differences in zooplankton abundance were apparent between station groups and also in the proportions of the dominant taxa, copepods and euphausiids (see Tables 1 and 2). Within the two largest groups defined in the first ordination, (groups 1 & 2), they accounted for ~ 90% of total abundance and between 53% ~ 75% for remaining groups.

Copepods: The dominance of small copepod species was confirmed throughout the study area with *Oithona* spp. and *Ctenocalanus* spp. contributing greatly to the increased abundance in group 1 (Table 1). Similar findings have been made by Sushin et al. (1985), Errhif et al. (1997), Atkinson and Sinclair (2000), Pakhomov et al. (2000) and Chiba et al. (2001). The highest overall abundances of many of the important species *Oithona* spp., *Oncaea* spp and *Metridia* spp. were located in the northern part of the region and to the east of South Georgia and the lowest in the vicinity of the Antarctic Peninsula (Fig 3). Without exception all of the copepods (and many of the non copepod taxa) that comprised >4% of the total sample abundance (see methods) were more abundant in the northern group 1 (Table). We suppose that here the combination of lower latitude, warmer water and enhanced production (see Holm-Hansen et al., this volume) has promoted the recruitment of species which in Weddell sea waters have yet, or are only just beginning to reproduce. Temporal delays of the order of 3 months or so have previously been found between commencement of recruitment of copepod species in the Scotia and Weddell Seas (Atkinson et al., 1997, Ward et al., 1997). In this survey the presence of copepodite stage V *C. acutus* from the summer generation in the northern part of the survey area and of early copepodite stages or adult females from the overwintered generation to the south also indicates a lag in the timing of recruitment of the order of 2-3months. Such differences are often seen in this sector of the SO, particularly where the meridional extent of the ACC is wide. Marin (1987) also found pronounced age differences for *C. acutus* and *C. propinquus* during the Melville study with a younger population present in waters south of the WF.

Euphausiids: had their highest proportionate share of abundance in groups 3-5 (19-32%) with 7-9% in groups 1 and 2. Highest mean abundances of euphausiids were found in group 4, largely as a result of *E. superba* larvae which occurred at all 7 stations and contributed 12% to within group similarity. *E. superba* larvae were also present in both of the main station groups but were concentrated along both sides of the WF and occurred in somewhat lower abundance up to the approximate position of the SACCF (Fig 5 see also Siegel et al. this volume). Previous work on euphusiid larvae from the Melville expedition (Brinton, 1985) has also highlighted the importance of this frontal region for reproduction in *E. superba* and Spirodonov (1995) has characterized the region as one in which krill reproduction starts early and has a variable but normally long duration. *Euphausia frigida* occurred throughout the region but were more abundant to the north of the position of the SACCF as were older calyptopes and furcilia stages. Calyptopis stage 1 was widespread but had a more southerly distribution. This is somewhat similar to *E. superba* larvae and suggests that larvae are moved north and east in surface waters. Makarov (1977) in a survey of the central Scotia Sea in December/January also highlighted the widespread distribution of larval forms but concluded that the most intense reproduction took place in the WF zone.

Thysanoessa spp. calyptopes were generally widespread, although once again furcilia and post larvae generally occurred in greater numbers further north. Previous work around South Georgia has established that the majority of these are likely to belong to *T. vicina* , whereas a separate category of large *Thysanoessa* spp (>16 mm TL are probably *T. macrura* see

Mauchline, 1980) were concentrated at the eastern end of the survey area distributed in the region of the outflow of Weddell water.

Other species: Chaetognaths were not separated into species or genera because in many cases they were too badly damaged to identify consistently. Nonetheless they were generally abundant throughout the survey area, the exception being the region of the South Sandwich Islands in the cold outflow of Weddell Sea water. Mackintosh (1936) characterised them as being a warm water group that may sometimes occur in colder water.

Salp blastozooids (*Salpa thompsoni*) were one of the very few taxa that were more abundant in the coldwater community group 2. They were largely absent north of the latitude of South Georgia and were concentrated in a zone straddling the WF and up to the approximate position of the SACCF. Salps are heterogeneously distributed within the SO although Mackintosh (1936) indicated that along with *E. superba* they had a tendency to occur in colder waters, although Siegel et al. (1992) and Park and Wormuth (1993) indicate a preference for warmer water masses (see also Kawaguchi et al., this volume).

The pteropod *Limacina helicina* was abundant in the north of the region with a southern boundary to its distribution that approximately followed the line of the SACCF. Previous work has established this feature as the southern distribution to the mass occurrence of this genus (Grachev, 1991 cited in Pakhomov et al., 2000).

Community structure

Overall the mean abundance of zooplankton within group 1 was much greater than for group 2 and higher than determined in many other studies within the ACC (see Sushin et al., 1985, Pakhomov et al., 2000). Regional studies by Foxton (1956) and Hopkins (1971) have demonstrated a latitudinal decrease in mesozooplankton biomass and low zooplankton biomass seems to be typical of the East Wind Drift and Weddell Sea areas. Hopkins and

Torres (1988) commented on the low zooplankton biomass in a study in the western Weddell Sea compared to the stations in the ACC although in a study by Boysen-Ennen et al. (1991) no difference in mesoplankton biomass was found between the Weddell Sea oceanic community and other data reported for the SO. The remaining station groups were largely associated with the WSC and Antarctic Peninsula regions. They were characterised by low numbers of stations, lower within group similarity, and with the exception of group 4, much lower abundance. Previous work has reflected the fact that this is a hydrodynamically complex area where many of the frontal zones lie close together and that consequently there is the potential for zooplankton from different sources to be present in the region (Jazdzewski et al., 1982, Piatkowski, 1989, Siegel and Piatkowski, 1990). Most however are in agreement with Mackintosh (1936) in that compared to other areas, the plankton in Bransfield Strait is impoverished (Jazdzewski et al., 1982, Mujica and Torres, 1982, Mujica and Ascencio, 1985). Reasons for this have been variously ascribed to the influence of upwelling water masses (Mackintosh, 1936) or variations in ice cover (Foster, 1981). Schnack-Schiel and Mujica (1994) have reviewed the zooplankton found in this region and conclude that an oceanic community influenced by the West Wind Drift and a neritic one influenced by the Weddell Sea in Bransfield Strait and by Bellingshausen water off the Palmer Archhipelago are present. Jazdzewski et al. (1982) also conclude that oceanic and Continental Zone (CZ) communities are present in the region separated by the Continental Water Boundary. They also found that the mean volume and abundance of plankton was much less in Bransfield Strait and inshore of the 500m isobath compared to offshore, where it was 3-4 times greater. This is somewhat similar to the findings of Siegel and Piatkowski, (1990) although as the latter make clear, separation of communities based simply on abundance or biomass, which can change over time, is inappropriate. Evidence for the existence of a neritic community in the Weddell Sea and around the Antarctic Peninsula has been provided by Boysen-Ennen and

Piatkowski (1988) and Siegel and Piatkowski (1990) respectively. They describe not only changes in abundance of species which also occur in the oceanic community but the presence of different dominant species such as *Euphausia crystallorophias* and *Pleurogramma antarcticum*.

Our own data although not as finely resolved as many of the surveys in this region shows the presence offshore of AAZ and Weddell Sea influenced station groups, although within the Bransfield Strait groups 3 and 5 predominate with stations from group 3 extending along the WSC to the South Orkneys

Frontal regions as faunal boundaries

Deacon (1982) drew attention to the fact that the rise in surface temperature from the Antarctic continent northwards is not uniform. A number of sharp transition zones exist in addition to the break between the continental shelf and deep water, and these frontal regions often appear as discontinuities in the distribution of phytoplankton and zooplankton (Pakhomov and McQuaid, 1996 Errhif et al., 1997, Pakhomov et al., 2000). Within the CCAMLR survey area our analysis initially suggested that two main zooplankton groups were present, broadly separated along the line of the WF. This broad boundary zone is the product of the mixing of waters of three different origins (ACC, Bellingshausen and Bransfield Strait) interacting with water from the Weddell Sea. It is a mobile feature and is characterised by meanders and eddy like structures, particularly east of the South Orkneys, where it becomes very diffuse (Foster and Middleton, 1984). For some taxa it is reported as the southernmost limit of distribution e.g. the copepods *C. simillimus*, (Kanaeva, 1968, Vladimirskaya, 1978, Marin, 1987), and *Clausocalanus laticeps* (Jazdzewski et al., 1982, Marin 1987) and it is an important spawning area for at least two species of euphausiid *E. superba* (Marr, 1962, Brinton, 1985, Spirodonov, 1995, Siegel et al., this volume) and *Euphausia frigida* (Makarov, 1977, Brinton, 1985). Marin (1987) viewed the WF as an important boundary in terms of the abundance and age structure of zooplankton populations, although concluded that it did not separate two distinct communities as the order of abundance of species did not differ significantly. A similar conclusion was also reached by Siegel et al. (1992).

Within the Scotia Sea a number of full depth frontal features have been observed (Orsi et al., 1995) all of which lie close together in the region immediately downstream of Drake Passage, before diverging further eastwards (Brandon et al., this volume). A number of studies have emphasised the fact that the APF marks an important transition between subAntarctic and Antarctic faunas and the WF (continuing as the AD in other sectors of the SO) between the oceanic and continental shelf communities (Deacon, 1982, Boysen-Ennen and Piatkowski, 1988, Longhurst, 1998, Hosie et al., 2000). However while fronts may reflect distinct changes in some species distributions, for many others, they do not represent a boundary (Mackintosh, 1960, Atkinson and Sinclair, 2000). In an analysis of copepod distributions taken from the surface – 1000 m, in waters ranging from the subAntarctic to the Weddell Scotia Confluence (WSC), Atkinson and Sinclair (2000) discounted Deacon's suggestion of the APF as a biogeographic boundary. They found some species to be more abundant within the front itself, rather than it representing either the northern or southern limits to distributional ranges. They concluded that there was no indication of species clustering into warm or coldwater types and that a continuum existed between the two extremes. In the Indian Ocean sector of the SO Errhif et al. (1997) investigated copepod composition and community structure on a transect running past Kerguelen and Heard Islands towards the Continent. They found highest densities in the region between the APF and the AD with peak abundance in the region of the AD. Increased abundance within fronts is commonly seen as they are often productive (see Lutjeharms et al., 1985, Fransz and Gonzalez, 1997 and Pakhomov et al., 2000) or may act to physically concentrate plankton (Voronina, 1970, Franks, 1992). A transect of closely spaced stations run from Cape Town to Sanae in the Atlantic sector resolved 4 major station groupings separated by 3 major frontal systems, the Sub Antarctic Front (SAF), APF and STC (Pakhomov et al., 2000). Within the group south of the APF a further 3 subgroups were apparent, the first associated with the Marginal Ice Zone and a further two in the Polar Open Ocean Zone, roughly separated by the Northern Extension of the Cold water layer (NEC) which coincides with the northernmost extent of the 0^oC isotherm and approximates to the northernmost limit of winter sea-ice. The latter feature appears synonymous with the SACCF, and according to Pakhomov et al. (2000) approximates the northern limit of Antarctic krill distribution and the southern limit of *Salpa thompsoni*, although in the Atlantic sector there is considerable overlap in the distribution of both species (see Mackintosh, 1936, Kawaguchi et al., this volume). Nonetheless their analysis, like those of Marin (1987) suggested the existence of a single oceanic community south of the APF. Our own data lends only limited support to the idea of frontal regions defining the limits of oceanic zooplankton communities in this sector of the SO. Our samples were all obtained polewards of the APF and although both ordinations suggested the WF as being a feature separating the two main groups, similarities in species composition between groups 1 and 2 lead us to conclude that they essentially belong to the same biological community, differing only in their degree of development, probably because of differences in the timing of seasonal productivity. Although the division between the two groups broadly followed the line of the WF, particularly west of 40W, there was a pronounced northwards extension of group 2 across the front to the east. This follows the path of the outflow of Weddell Sea water (Maslennikov and Solyankin, 1980) and consequently stations north of the WF around the South Sandwich Islands also belong to group 2. The second ordination also shows this as being a strong structuring feature. The presence of stations belonging to this group over the shelf and shelf break area of the Antarctic Peninsula also suggests that this is more likely to be 'coldwater community' rather than being derived exclusively from the Weddell Sea, although Weddell Sea water is known to intrude into Bransfield Strait (Stein and Heywood, 1994). The secondary frontal features such as the SACCF and the SACCB did not appear to be important in terms of defining community structure. Ordination 2 using the full species stages data set introduced an additional group in the Scotia Sea which lay broadly between the positions of the SACCB and the SACCF. However the composition of this group had distinct similarities with adjacent groups and as such was only separable in terms of differing proportions of some species stages.

The distribution of the cold, ice affected Antarctic Surface Water (Brandon et al. this volume) fairly closely follows the boundary between groups 1 and 2 (Fig 2) and may be largely responsible for differences between the two. Thus the existence of a single community modified by the presence of seasonal ice cover is indicated.

Conclusions

Our basin scale synoptic view of zooplankton community structure within the Atlantic sector is compatible with a number of previous studies, which have been more localised in extent (eg Jazdzewski et al., 1982, Marin, 1987, Siegel et al., 1992). Mackintosh (1936) published the only study on a comparable scale, based on data compiled during 4 summers. Despite this difference in approach, there are strong parallels between our grouping of stations and his faunistic divisions, both emphasising the strong structuring effect pack-ice distribution and temperature have on zooplankton communities. Mackintosh also emphasised that the boundaries between his divisions were not geographically fixed and that variability was a fundamental property of 'community' composition. This is apparent from the seasonal changes he noted in the proportions of 'warm' and 'coldwater' species and the differences in the timing of ontogenetic development with latitude. The latter is also reflected in our data and that of Siegel et al. (1992) and as 'communities' develop seasonally then temporal differences between them will vary. Movement or weakening of frontal zones may also fundamentally alter ‘community’ distributions (Priddle et al., 1988). Sushin et al. (1985) noted the differences in the balance of species within the Scotia Sea between seasons when the balance of water masses differed and Shreeve et al. (2002) have documented similar changes around South Georgia.

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Figure legends

Figure 1

A) Results of Bray Curtis Clustering of the reduced species by station data matrix. Station labels have been omitted for clarity.

B) MDS ordination of the reduced species by station matrix.

Figure 2.

Geographical distribution of station groups in the CCAMLR 2000 survey area derived from the reduced species by station ordination. Position of fronts are given from north-south these are the SACCF, SACCB and WF.

Figure 3.

RMT 1 total abundance (nos. ind. 1000 m^{-3}) by station.

Bubbles represent 5 abundance categories; 1-10000, 10000-50000, 50000-250000, 250000-750000, 750000- 1250000.

Figure 4.

Geographical distribution of station groups in the CCAMLR 2000 survey area derived from the full species by stages ordination. Position of fronts as in fig 2.

Figure 5.

Species by station abundance. The twelve species that were common to the SIMPER and BIOENV analyses (see text for further details).