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Mesozooplankton in the Southern Ocean: spatial and temporal patterns from Discovery Investigations

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ABSTRACT
Mesozooplankton samples taken during the *Discovery Investigations* in the Southern Ocean in the 1930’s were analysed from a series of 5 transects along 80°W. The samples provide a unique level of depth-discrete resolution across large spatial scales, over most of the productive austral season. Stratified net hauls were taken between 0 and 1000 m within the period December 1933 to November 1934. Within the epipelagic (0-100 m), median zooplankton abundance (278 ind. m$^{-3}$) was ~22 times greater than at 1000 m. A 3-4 fold variability of abundance in the epipelagic contrasted with depths >250 m where variability was <1 fold. Depth was the strongest factor separating samples (ANOSIM, R =0.66 $p=0.1\%$), with a clear biological distinction between epipelagic and upper and lower mesopelagic horizons. Results from multi-dimensional scaling indicated that, when plankton abundance was integrated over all depth horizons, 3 different groups could be identified. These ‘communities’ were consistent with the spatial extents of Antarctic, Polar Frontal Zone, and sub-Antarctic water-mass regimes. Such groupings became less distinct when considering only deeper horizons (500-1000 m) and excluding seasonal migrants. Seasonal signals across all data became less distinct with depth. Rarefaction analysis indicated that diversity increased with depth. Although depth alone was the most important influence on sample diversity, ($r^2 = 0.60$), water mass regime and month improved the fit ($r^2 = 0.71$). Overall plankton diversity was highest in the sub-Antarctic zone. Following atmospheric and ocean warming that has taken place close to the study area in the last 80 years we hypothesise that species richness may increase in the Antarctic water masses as sub-Antarctic species increasingly encroach south.

1. Introduction
Within the world’s oceans far more is known about the plankton occupying the epipelagic than the deeper horizons. This is particularly true of the Southern Ocean where the vast majority of investigations have taken place within the surface 200 m. Fewer studies have taken into account the deeper water column and have largely emphasised taxonomy (e.g. Park, 1978, 1983, 1993, Bradford-Grieve, 1994, 1999), or have focused on descriptions of planktonic life cycles and vertical distribution (Andrews, 1966; Voronina, 1972; Atkinson, 1991, Marrari et al., 2011; Wiebe et al., 2011).

Fundamental knowledge of the distribution of plankton abundance and biomass within the Southern Ocean has largely come from the Discovery Investigations carried out during the early to middle part of the 20th century. Plankton samples taken with the N70V net have variously been used for regional comparisons of standing stock in the Southern Ocean (Foxton 1956), understanding the circulation of macroplankton (Mackintosh, 1937), elucidating life cycles and distribution of copepods (Andrews, 1966; Ommaney, 1936; Atkinson, 1991) as well as chaetognaths (David, 1955, 1958). Foxton (1956) used over 2,100 stratified N70V net samples (0-1000 m), from 366 Discovery stations within the Southern Ocean to describe plankton volume on a regional and seasonal basis. Hopkins (1971) similarly sampled to 2000 m in the Pacific sector (~75°W-160°W), obtaining 375 Bé net samples and found biomass distributions to be broadly comparable, both regionally and seasonally with Foxton’s work. Important findings from both of these studies were that within the top 1000 m, seasonal variation in plankton biomass is marginal and also that increases in biomass were observed in the region of the Polar Front (PF). However, Foxton (1956) recognised that the N70V was poor in terms of catching krill which are particularly abundant south of the Polar Front, in the Antarctic Zone (AZ). Important studies by Hopkins and co-workers (e.g. Hopkins, 1985; Hopkins and Torres, 1988; Hopkins et al., 1993a) have investigated the biology and trophic ecology of the water column, including the deeper water
horizons in the Weddell Sea and adjacent marginal ice-zones (MIZ), as well as providing community descriptions and insights into plankton diversity down the water column. Atkinson and Sinclair (2000) used *Discovery* samples to assess the extent of seasonal migration among the plankton and to clarify zonal distributions. Ward et al. (1995, 2006) and Ward and Shreeve (1999) documented seasonal changes in community distribution and biomass down to 1000 m around South Georgia and Marrari et al. (2011) investigated the vertical distribution of zooplankton and habitat partitioning in the deeper water column in the Marguerite Bay region of the Western Antarctic Peninsula (WAP).

Over the last 20 or so years, numerous studies have defined Southern Ocean plankton community structure (e.g. Hosie, 1994; Errhif et al., 1997; Pakhomov et al., 2000, Ward et al. 2003, 2006). This has given us a near consistent view of epipelagic communities which are bounded by the physical gradients and discontinuities often found at frontal zones. What is presently unclear is whether such distinctions between plankton communities exist within the mesopelagic and what patterns of diversity are discernible with respect to water mass and depth. Studies of the mesopelagic (200-1000 m) elsewhere have emphasised that it is here that processes govern the efficiency by which particulate organic carbon is transported to the sea floor (Tréguer et al., 2003; Steinberg et al., 2008; Robinson et al. 2010) although we generally know little regarding the abundance, biomass and vertical structure of the major taxa involved. In the Southern Ocean Hopkins and Torres (1988) found diversity increased below the epipelagic in the Weddell Sea, and Hopkins et al. (1993a, b) have shown that depth was an important factor in determining spatial distance in an ordination of a series of samples taken in the Scotia Sea MIZ in winter. A recent paper on diversity in the Arctic Ocean has also shown depth to be a major structuring element for species distributions and communities (Kosobokova et al., 2011 and references therein).
Extensive sampling of the mesopelagic rarely takes place these days, largely on grounds of cost. Fortunately, *Discovery Investigations* routinely sampled the Southern Ocean to 1000 m with the N70V net and many of these sets, taken ~80 years ago, are still available for study. The aim of this investigation was to examine the basic properties (abundance, species composition and diversity) of a series of plankton samples taken during 5 transects completed by *Discovery Investigations* along 80°W in the Pacific sector just west of Drake Passage, with a further aim of examining the spatial variability (horizontal and vertical) of the plankton community structure. The transects, occupied between December 1933 and November 1934, crossed three zones of the Antarctic Circumpolar Current, extending from the AZ in the south, through the Polar Frontal Zone (PFZ) to the sub-Antarctic Zone (SAZ) in the north (Fig. 1).

In this region of the Southern Ocean, temperatures have risen faster than elsewhere in the Southern Hemisphere, with surface summer temperatures rising more than 1°C during the last part of the 20th century (Meredith and King, 2005). Such changes have been predicted to have detrimental effects on various marine species including Antarctic krill, a key species in the Southern Ocean foodweb with a known dependence on the physical environment (Atkinson et al., 2004), and marine benthos, which is also sensitive to temperature change (Peck et al., 2004). In investigating zooplankton distributions from samples collected 80 years ago, we are establishing what patterns were prior to subsequent ocean changes and potentially forming a baseline against which the future impacts of such physical change might be measured.

2. Method

2.1 Zooplankton sampling and processing
A total of 41 stations were occupied during a series of 5 transects completed during the *Discovery Investigations*. The transects extended from ~68°S to 55°S along 80°W and were investigated during December 1933, March, September, October and November 1934 (Fig. 1). The position, number and horizontal spacing of stations varied between transects (5-10 stations per transect, transect lengths of ~690-1400 km). From these stations, 248 plankton samples were taken with an N70V net used extensively during *Discovery Investigations* to obtain stratified plankton samples. Of these, 9 samples were not located in the Natural History Museum collections and were presumed missing. Others had suffered some spillage during capture and initial processing, as indicated on the sample labels. Although these latter samples were examined, species counts were not included in subsequent data analysis reducing the total number of stations to 39 and samples to 215.

Full details of the N70V net construction are given in Kemp et al. (1929), but briefly it was a 70 cm dia. ring-net with two grades of silk mesh; a forward section of 40 threads per inch (TPI) and a rear section of 74 TPI equivalent to ~195µm and 440 µm respectively (Ward et al. 2012), and a collar of ~6 mm knotted mesh. The net was deployed in an open state and lowered to the bottom depth of the horizon to be fished before being hauled vertically upwards at a rate of 1 m sec\(^{-1}\). Net closure was accomplished by use of a messenger sent down the wire at a predetermined time which triggered a closing mechanism as the net reached the upper depth of the fished horizon. This released the net bridles allowing a rope encircling the net and attached to the closing mechanism to throttle the net. Dependent on water depth, up to six samples were obtained as follows: 50 m to surface, 100–50 m, 250–100 m, 500–250 m, 750–500 m and 1,000–750 m. A full suite of vertical net samples was carried out in ~1.5-2hr.
The samples were taken almost 80 years ago and preserved in formalin. As might be expected, overall condition was variable and not very good in the main. Crustaceans were generally intact, although brittle, and internal tissue was often absent. Specimens of the copepod *Calanoides acutus* had been removed from many samples and preserved separately.

A record of numbers removed was appended to the label in each jar, although the stage structure of the absent fraction is unknown. Appendicularians were also often difficult to identify because of tissue deterioration and thecosome pteropods likewise. Chaetognaths were generally represented only by their jaws with the soft body tissue having dissolved away. Numbers were therefore estimated by counting jaws and dividing by 2. Further information on chaetognath species composition and other elements of the catch was obtained from digitised records of photographs taken of *Discovery* logbook pages pertaining to each haul (data provided by Andrew Mackey). Four species of chaetognaths were identified in these logbooks, *Eukrohnia hamata* and 3 species of the genus *Sagitta*: *S. gazellae, S. maxima* and *S. planctonis*. A comparison of *Discovery* logbook entries with jaw counts indicated that overall, jaw counts underestimated abundance by ~10% (average jaw counts as a proportion of *Discovery* counts = 0.91 (±0.781)). However not all logbook entries were consistent in recording chaetognath numbers and a number of blank entries were apparent although chaetognaths were present in the corresponding samples. For the sake of completeness we have therefore decided to use abundance data generated from jaw counts/2.

Initially samples were looked at in their entirety and rare and/or large specimens removed and counted. Samples were then split successively using a folsom splitter until the resultant aliquots were estimated to contain between 100-200 individuals which were again identified and counted. Finally, further splitting took place to produce aliquots from which counts of the smaller and more numerous size fractions were made. Both aliquots from each final split were counted. An average of 753 (±297) individuals were counted per sample and, across all
samples, a total of 212 taxa/species/stages were identified (see Web appendix). Flow meters were not used by *Discovery Investigations* and volume swept has been estimated from net diameter and the depth of the water column that each net fished through. Thus, ~19 m$^3$ of water was swept in a 50 m vertical tow, ~58 m$^3$ in 150 m tow, and ~96 m$^3$ in a 250 m tow.

2.2 *Oceanography*

Temperature and water for salinity analysis were obtained from each station with Ekman reversing bottles fitted with protected and unprotected reversing thermometers. Thermometers were scaled to 0.1°C and data presented in the station lists to two decimal places. Salinity was analysed by titration against silver nitrate of known strength using potassium chromate as an indicator (Kemp et al., 1929).

We used water mass properties at each of the *Discovery* stations to locate the positions of the sub-Antarctic Front (SAF) and Polar Front (PF) on each transect, enabling stations to be classified into three zones of the Antarctic Circumpolar Current (ACCZ): the SAZ, PFZ and AZ. The frontal locations were determined from potential temperature-salinity curves and confirmed with vertical sections of potential density along the transects (Orsi et al, 1995; Read et al, 1995). Two transects (March and December) sampled south of the southern ACC front but this front was not used to group stations in subsequent analyses.

2.3 *Statistical analysis*

PRIMER (v6) (Clarke and Gorley, 2006) was the principal statistical package used to analyse the species-by-samples dataset. Routines were carried out on the species by stations data matrix using log (x+1) transformed standardised data (ind. m$^{-3}$ or ind.m$^{-2}$ (0-1000 m)), to determine Bray-Curtis similarities before undertaking hierarchical clustering of data into sample groups (CLUSTER), and ordination (Multi dimensional scaling (MDS)). Analysis of similarity (ANOSIM) was used to test for differences between resultant groups. ANOSIM
operates on the resemblance matrix and is approximately analogous to standard univariate
analysis of variance (ANOVA). Similarity percentages (SIMPER) was used to examine
taxonomic contributions towards group structure.

The PAST statistical package (Hammer et al. 2001), was used investigate species
diversity and specifically to undertake sample rarefaction (Mao tau) on the data converted
into a presence or absence matrix with respect to depth horizon. Rarefaction generates the
expected number of species in a small collection of \( n \) samples drawn at random from the
large pool of \( N \) samples (Gotelli and Colwell, 2001). The shape of the curve is steep at first
and then tends to plateau as only the rare species remain to be sampled. Rarefaction curves
generated from the present study were mostly beyond the steep phase but had yet to reach the
plateau phase. Therefore, we extrapolated the curves to determine (i) the expected number of
taxa within each depth interval and (ii) the level of sampling effort required to identify 90%
of this number of taxa. Both a 3-parameter power function and Michaelis-Menten function
were fitted to the rarefaction curves, with the former achieving the best levels of fit
\((R^2 > 0.99)\). The power functions were then extended to three times the original sample size
(from ~36 to 108 samples) for each depth interval, following Colwell et al. (2004). The
rarefaction curves and extrapolations for each depth interval were plotted together for
comparative purposes.

3. Results

3.1 Physical conditions along the transect

Surface and subsurface positions of the fronts were located between the same station
pairs on all transects, with very few stations showing evidence of interleaving that is often
seen close to fronts. Our classification agrees with that of Foxton (1956) who partitioned
plankton standing crop into sub-Antarctic and Antarctic zones, although we additionally define the PFZ (Table 1). At the southernmost stations of each of the transect passes, temperature in the top 100 m of the water column was always less than 0 °C. At the northernmost stations at the same depth, temperature ranged from ~2.7—7.75 °C. A latitudinal increase of 1 °C per 155-200 km within the top 100 m was recorded for each transect, with temperature increasing northwards. The range of the average temperature calculated for the upper 100 m along each transect varied from 4.46 °C on the shortest transect (November) to 8.49 °C on the longer one (March). As expected, this near-surface temperature range was much larger (by a factor of 4.25 on average) than that recorded at 1000 m. Within all five transects, the difference between the minimum and maximum temperature at 1000 m was only 2.15 °C.

3.2 Mesozooplankton abundance by depth

Initially we calculated abundance (ind. m⁻³) within each depth horizon and present these data as medians across all months and ACCZs (Table 2, Fig. 2). Median abundance within the top 100 m was significantly higher than in horizons deeper than 250 m (Kruskal–Wallis H=106.44, p=0.00). Abundance declined down the water column such that below 750 m the median was ~4% of that in the near-surface layers. Within depth horizons, monthly variation in range was greater (absolute and relative) in surface horizons than deeper (factor of 3-4 in top 50 m, 2-3 in 100-50 m and <2 in 250-100 m). Below 250 m the range was <1 and broadly equal across months.

3.3 Month vs ACCZs

There are some gaps in the data matrix when considering abundance with respect to ACCZ by month, which makes it difficult to get a strictly comparable view of monthly mesoplankton distributions by ACCZ (Table 1). Data from the SAZ are absent in November
and the PFZ is represented by only one sample in November and March. We have therefore plotted data showing variation in abundance across months and depth zones (ie ACCZs pooled) and also by variation across ACCZ and depth (ie months pooled). In the former (Fig 3a), the trend was for near-surface abundance to increase from September through till December and then decline slightly by March. In depth horizons below 100 m, no systematic change was observed across months, with the range of values tightly constrained compared to the upper 100 m. Below 250 m, abundance was reduced in each successive depth horizon by almost half in many cases. The ratio of the median abundance in the top 100 m to that in the deepest horizon varied from ~8-31 times across months. Pooling stations by ACCZ, irrespective of time of year (Fig. 3b), indicated that there was a greater range of values within the near-surface AZ compared to elsewhere. Deeper horizons (>500 m) once again appeared quite similar in overall abundance, irrespective of region. The high abundances seen in the near-surface waters of the AZ were due to the presence of limacinid pteropods during December. Median abundance and biomass by depth and ACCZ are presented in Table 2. Sample biomass was estimated from settled volumes provided by Foxton (1956) who included these samples along 80°W in an estimation of zooplankton standing stock in the Southern Ocean. Foxton provided data as displacement volumes (cm$^3$) which we have converted to wet/dry mass assuming that 1 cm$^3$ equals 1 g wet weight and that dry weight represents 10% of this (see Hopkins 1971). Estimated biomass (wet mass mg m$^{-3}$) largely reflects patterns of abundance. Summed over the water column, median wet mass (gm$^{-2}$, 0-1000 m) was uniform, ranging from ~16 g in the AZ and SAZ to ~20 g in the PFZ. Dry mass using the 0.1 conversion advocated by Hopkins (1971) is therefore ~1.6-2.0 gm$^{-2}$ (0-1000 m) across all ACCZs.

3.4 Spatial structure within the sample set
Clustering and multi-dimensional scaling (MDS) of Bray-Curtis similarities (latter not presented) showed that depth was by far the strongest factor in separating samples (Fig. 4). Three main clusters were apparent which could be classified as epipelagic (mainly samples taken in the top 100 m), upper mesopelagic (mainly samples from 100-250 m and 250-500 m horizons) and lower mesopelagic (mainly depths >500 m). Analysis of similarity (ANOSIM) to determine the extent to which the main clusters reflected depth was carried out using sample depth zone as a factor. A value of $R = 0.66$ ($p = 0.001$), indicated that there was indeed a strong case for viewing the water column as broadly divisible into 3 horizons irrespective of ACCZ. We also tested whether month or time of sampling (day or night) had any significant influence on the clustering and found that both had much lower, yet still significant, values of $R$ ($R = 0.23$, $p = 0.001$ for month; $R = 0.03$, $p = 0.046$ for day/night). The larger magnitude of $R$ (which is an absolute measure of differences between groups, as compared with the $p$ level, which is influenced by sample size) for depth shows that differences occasioned by month are slight in comparison with depth.

3.5 Community analysis

Although depth clearly dominated the way in which the sample specific dataset clustered, we also wished to determine the extent to which ACCZ might be a factor in horizontal variability. For the 27 stations which had a full complement of samples down to 1000 m (see Table 1), species stages were aggregated within species resulting in 171 species/taxa and abundance (ind. m$^{-2}$, 0-1000 m). Data were log (x+1) transformed, before clustering, MDS and subsequent routines were again carried out. We also wished to ascertain whether ‘plankton communities’ could be defined in waters >500 m deep. By restricting our analysis to the two deepest horizons fished by the N70V we increased the number of stations available for analysis from 27 to 33. However our first iterations of the 0-1000 m data matrix identified the strong influence on defining communities played by seasonal migrants (see
and smaller, predominantly epipelagic species such as *Oithona similis*.

Therefore we first removed these to produce a species list that better reflected the deepwater fauna (see legend Fig. 5). Following the removal of seasonal migrants and small near-surface copepods, a total of 156 taxonomic categories remained. We examine these analyses in turn.

**0-1000 m**-- A plot of the MDS ordination on the 0-1000 m data set is presented in Fig 5a. At the 73% similarity level station groups comprised an AZ group (9 stns), an AZ/PFZ group (11 stns) and a predominantly SAZ grouping (7 stns).

**500-1000 m**-- By restricting our analysis to the two deepest horizons fished by the N70V, we increased the number of stations available for analysis from 27 to 33. On this occasion we observed two major groupings at ~72% similarity, the first of predominantly AZ and PFZ stations and the second a diverse group of PFZ and SAZ stations (Fig. 5b).

A summary of ANOSIM performed on these data is presented in Table 3. Global R for both ordinations was significant and among the pairwise comparisons of the ACCZs the strongest difference was between AZ/SAZ. The value of R for the AZ/PFZ and PFZ/SAZ pairwise comparisons more than halved (Table 3). This is consistent with the MDS plots (Figs 5a-b) which suggest that stations along the transect form a continuum, with the spatial extremes of AZ and SAZ stations differing most. We have therefore used the output from ANOSIM and defined station groups with respect to ACCZ for subsequent analysis, rather than trying to account for temporal and other differences in the data. The MDS plots generally show stations thus identified as occupying different parts of the ordination.

We then ran the similarity percentages routine (SIMPER) to ascertain which species/taxa were most responsible for within group structure. For the 0-1000 m ordination, the small abundant species contributed most to within group similarity and between group dissimilarity. In table 4 we have presented the 10 species/taxa contributing most to the above
for the 3 groupings identified by MDS (Fig. 5a), making a combined total of 20 species.

Between 50-57% of within group similarity was accounted for by the tabulated taxa and
~40% of between group dissimilarity. Species/taxa so identified showed a range of

distributions and abundances and overall the PFZ stations had the greatest average abundance
of plankton (mean ~8.5 x10^4 ind. m^-2 0-1000 m, see table 5) although not significantly greater
than the other two groups. Among species that often contributed most to dissimilarity
between station groups were seasonal migrants including Calanoides acutus, Calanus
simillimus and Subeucalanus longiceps and species that were widely distributed throughout
the water column such as Ctenocalanus spp. and Oithona similis. The former species are
seasonal migrants that spend spring/summer in near-surface waters and reside in deeper
waters for the rest of the year. However, differences in the timing of life-cycles with respect
to latitude means they are not uniformly distributed with respect to depth over the length of
the transect.

In the 500-1000 m MDS plot (Fig. 5b) stations were once again broadly arrayed
across the ordination. The pairwise comparisons of ACCZs carried out within ANOSIM
showed a greater difference between the AZ and SAZ than of either with the PFZ (Table 3).
In this case the PFZ/SAZ groupings were not significantly different and we have therefore
pooled these before undertaking SIMPER. Again smaller copepod species proved to be the
greatest contributors to within group structure. All except two of the first 10 taxa defining
within group similarity and between group dissimilarity was the same in each of the two
ACCZ groupings (20 taxa in total), with only the rank order changing (Table 6). A number of
the deeper dwelling taxa, including the copepods Metridia curticauda, Mormonilla sp.,
Paraeuchaeta biloba and Scolecithriciid copepodites, as well as Siphonophora and
Thysanòessa spp. were particularly important in defining dissimilarity between groups.

3.6 Seasonality in the mesopelagic
One of the questions we wished to answer was whether seasonal changes in abundance could be detected in the deeper depth horizons. We have presented ‘spring’ (Sept/Oct/Nov) and ‘summer’ (Dec/Mar) abundances of the 20 most abundant taxa (excluding seasonal migrants) in the 500-1000 m depth horizons across all ACCZs (Table 7). Overall there was a suggestion that one or two taxa were more abundant in summer than spring (e.g. *Oncaea* spp., *Metridia lucens* and *Paroithona* sp.) but only *Spinocalanus* spp. was significantly different and the majority of taxa showed very little difference between our seasonal groupings. However, given the length of the transect, there are likely to be ‘seasonal’ differences observed when comparing stations at one end with another. Within the Scotia Sea, Ward et al. (2004, 2006), have found differences in population age of biomass dominants *Calanoides acutus* and *Rhincalanus gigas*, to be as much as 3 months and possibly more, over transects of similar lengths, sampled quasi-synoptically. The possibility that grouping all stations together might be aliasing seasonality was investigated by looking for ‘seasonal differences’ within ACCZs.

We grouped 500-1000 m samples according to season, as before, but undertook comparisons within the AZ, and the PFZ/SAZ ACCZs combined. The majority of ANOVA comparisons showed no difference between seasons. The most significant differences (5/40) were found in the AZ for Chaetognatha, *Paraeuchaeta antarctica* and Ostracoda where spring averages were all greater than summer (*p*<0.05). Among PFZ and SAZ stations, Chaetognaths (Spr<Su) and *Spinocalanus* spp. (Spr<Su) were significantly different. None of the taxa which showed significant seasonal differences in one ACCZ showed them in the other.

### 3.7 Diversity

The results of the rarefaction analysis are illustrated in Figure 6. The curves represent taxa numbers by depth, pooled across all ACCZs based on between 35-37 samples in each
depth horizon. Diversity increased systematically with depth, although the two deepest horizons were virtually indistinguishable. None of the curves reached a plateau indicating that diversity was underestimated. The slope of the curves was broadly identical for the 3 horizons within the top 250 m but steeper below 500 m, indicating a greater level of undersampling of the total number of taxa at deeper depths. We have extrapolated the curves for each horizon to 108 samples (approximately tripling the original sampling size within the limits suggested by Colwell et al., 2004) to estimate the number of taxa expected at that sampling intensity. The number of taxa observed in our analysed sample sets was between 70-80% of the estimated number based on 108 samples. To obtain 90% of the total taxa predicted at 3 times the present sample size would require sample size to be doubled to between 70 and 80 samples.

We have also plotted the median number of species/taxa found within each depth horizon with respect to ACCZ (Fig. 7). The overriding pattern is of an increase with depth across all ACCZs down to 500 m as well as from south (AZ) to north (SAZ). At depths >500 m, species numbers in all but the SAZ dropped somewhat. Further, we performed a stepwise regression on the number of taxa recorded in each sample using depth, ACCZ and month as predictors. This analysis clearly showed that depth alone was the most important factor influencing diversity ($r^2_{adj} = 0.60$), with the fit being improved by ACCZ and month ($r^2=0.71$, Mallows CP = 4.0). Overall plankton diversity was highest in the SAZ.

Across all depths, the mean number of taxa in the 0-1000 m water column with respect to ACCZ was significantly greater in SAZ stations than elsewhere (Table 8). To illustrate the general trends in the vertical and horizontal distributions of the major taxa, we have plotted the median abundances (ind. m$^{-3}$) of families and groups with respect to depth and ACCZ (Fig. 8). Within copepod families, trends were apparent both with depth and across ACCZs. The Calanidae (Calanoides, Calanus, Neocalanus), Clausocalanidae
(Clausocalanus, Ctenocalanus, Microcalanus) and Oithonidae (Oithona, Paroithona) are all copepod families that were essentially more abundant within the surface 100 m. In the case of the Calanidae, this was largely due to the presence of younger stages during the summer months. To a greater or lesser extent, calaniids are interzonal migrants and spend a good proportion of the late summer and winter at depth, coming back into the surface layers in spring to reproduce (Andrews, 1966; Atkinson, 1991; Voronina, 1972). The distributional ‘tail’ reflects overwintering/overwintered stages distributed down to 1000 m. Within the Clausocalanidae, Ctenocalanus spp. was largely responsible for the increased abundance in the upper 100 m and Microcalanus pygmaeus below this. Within the Oithonidae, Oithona similis was largely responsible for the extremely high abundances in the surface 100 m with the less abundant O. frigida and Paroithona lying deeper. The Eucalanids were most abundant in the 100-250 m zones with the two most abundant and widespread interzonal species (Rhincalanus gigas and Subeucalanus longiceps) spread down the water column with a tendency to be more abundant at northern stations. Ostracoda were widely distributed within the top 500 m but also occurred down to 1000 m. A number of families tended to peak within the 50-100 m and 100-250 m depth horizons e.g. Scolecitrichidae, Euchaetidae, Metridinidae, Aetideidae and Augaptilidae, whereas the Heterorhabdidae, Spinocalanidae, Phaennidae and Lucicutidae were generally more abundant below 500 m. A summary of the distribution of principal copepod families shown in the figure with respect to ACCZ is given in Table 9. Here the number of species identified across all ACCZs is given along with the number found within each defined ACCZ. A total of 102 copepod species were identified in the course of analysis although a number of copepod families such as the Oncaeidae, and Spinocalanidae and other non copepod taxa such as the Ostracoda and Siphonophora, were not resolved to species level and will certainly contain more species that are likely to have
distinct regional distributions. The overall pattern of copepod distribution indicated that
~10% more copepod species were found within the SAZ compared to the AZ.

4. Discussion

4.1 Sampling methodology

Given that the samples were collected 80 years ago at a time when navigational and
oceanographic equipment were less technically advanced than today, we first discuss how
this might have impacted upon sample collection and our subsequent interpretation. In a pre-
satellite era, ships’ navigation and positioning away from land was dependent upon celestial
sightings and, between times, dead reckoning. Practical accuracy would therefore have been
to the nearest nautical mile, far short of the level of accuracy achieved by the Global
Positioning System (GPS) today. However, this does not directly influence our interpretation
of data as we are dealing with an oceanographic context determined from the temperature and
salinity data rather than from geographical coordinates. Seawater properties were determined
from water samples taken with Ekman reversing bottles. The sampling depth of these bottles
was estimated from a metering sheave on the hydrographic gantry and checked against depth
determined from protected and unprotected thermometers located on some of the bottles. In
the Discovery station lists (Anonymous, 1942) nominal metered depth can be checked against
actual depth for some of the bottles. The two estimates are generally to within a few meters of
one another even at depths of 3-4 km indicating that we can be confident of the hydrographic
sampling. Temperature is given to 2 decimal places (less than the 4 decimal places generally
used today) although the thermometers used were described as being scaled to 0.1°C (Kemp
et al., 1929). Given that we used the data to determine whether a front lay between relatively
widely spaced stations, this level of accuracy is sufficient for our interpretation.
It is more difficult to assess whether the nominal net depth is as indicated, as no independent estimate of depth was apparently undertaken. However, even though wire angles must have deviated from the vertical at times, the accuracy of the deeper water bottle sampling suggests that depth determination during vertical net sampling may also have been reasonably accurate. Wire deviations are expected to be greater in bad weather. Data on wind speed at each of the 41 stations indicates that, at the vast majority (~88%), the Beaufort scale was ≤ 4 at the commencement of operations further suggesting that this may not have unduly influenced net depths.

Both bottle sampling and netting were accomplished in a relatively short space of time. Generally, two stations were worked each day commencing at around 9am and 8pm. Netting operations of all types took ~ 4 hours to complete, with an N70V net series to 1000 m generally taking ~1.5-2 hours. A series of Ekman water bottles could be hauled to the surface at ~5.5 min per 1000 m of wire out although would have been deployed at a somewhat slower rate. Thus time on station was not excessive and the zooplankton and hydrographical sampling would be spatially related. It is unlikely that, at any one station, hydrographic sampling was undertaken in one water mass and zooplankton sampling in another.

The nets were deployed open to the lower point of the sampled horizon and then hauled vertically upwards before being closed which raises the question of catch contamination, particularly of deeper horizons with surface contaminants. Previous studies have shown that contamination can take place when nets are deployed in this way and plankton are captured as the net jerks upwards when the ship rolls (Grice and Hulsemann 1968, Harding 1972). However, *Discovery Investigations* deployed this net over an accumulator spring which would have tended to have minimised this problem (Atkinson 1988). Additionally, many of the particularly abundant species that occur throughout the water column such as *Oithona similis* and *Ctenocalanus* spp. and which are more likely to be
potential contaminants are known to be seasonal migrants and/or widely distributed within
the water column (Atkinson 1988). Although contamination cannot be quantitatively
examined, the orders of magnitude lower abundances seen in all of the deeper horizons (Figs
2, 3) suggest it is minimal. The isolated occurrences of deeper species in near-surface nets
can in all probability be attributed to insufficient washing down of nets between hauls.

4.2 Abundance and biomass

The pattern of mesozooplankton abundance decreasing with depth was similar across
all months. Abundance was highly variable in the surface 100 m although greatly exceeded
that in the deeper water column. Although somewhat lower overall in the SAZ, both
abundance and biomass were not significantly different between ACCZs when viewed over
the whole sampled water column. Higher zooplankton abundance near the PF has previously
been observed, particularly where phytoplankton biomass was also high (Foxton, 1956,
Pakhomov et al., 2000, Dubischar et al., 2002). In our study area, elevated chlorophyll levels
are today generally restricted to the near continental shelf region (Fig 1), well south of the
position of the PF. It is also likely that, regionally, zooplankton standing stock is lower here
than in many other parts of the ACC because of the low primary production seen in the
region of 80°W (Fig. 1). Abundance and biomass in the depth horizons below 250 m
generally exhibited less variation whether pooled by ACCZ or month.

Biomass estimates along 80°W derived from Foxton’s (1956) data were somewhat
lower (~1.6 to 2.0 g dw m\(^{-2}\) ) than estimates determined by Hopkins (1971) for the Pacific
sector, which were 2.67 and 2.58 g dw m\(^{-2}\) (0-1000 m) for the Antarctic and sub-Antarctic
regions respectively. However Foxton excluded gelatinous zooplankton from his
determinations and the two estimates may be closer than first appears. Different net
performance could also be a factor (see Table 3 Atkinson et al., 2001). Samples for Hopkins’
study were taken with a net mesh size of 202 µm. Recent research has shown systematic
differences between N70V catches and a 200 µm bongo net, with the latter catching ~3 times
more (by abundance) than the former which translates to ~1.6 times greater biomass (Ward et
al., 2012).

4.3 Community analysis

Both MDS ordinations suggested a continuum of stations and species distributions,
rather than groups divided by distinct boundaries. This probably reflects the greater number
of taxa pooled over a greater depth and the ironing out of seasonal differences when the data
were pooled across months. In the deeper ordination (Fig. 5b) community structure was less
clear cut, with PFZ stations appearing close in ordination space to AZ and SAZ stations. This
may in part be due to manipulating the data by removing seasonal migrants and restricting the
analysis to defined depth horizons but also to the lower and more uniform abundances found
at depth as well as the rarity of many species. Numerous studies have previously identified
plankton communities within the ACC (Errhif et al., 1997; Hunt and Hosie 2005; Pakhomov
et al., 2000; Ward et al., 2003). These have generally been based on samples taken from the
epipelagic and are very often defined by changes in species abundance rather than by a
fundamentally different species composition. In these studies, the PF has generally
represented a significant community boundary but, for mesopelagic species, it is less clear cut
(Atkinson and Sinclair, 2000). In the deeper horizons where seasonality is less pronounced
than in the near-surface, abundances are more uniform and many of the copepod species in
particular, whilst widespread, are uncommon. Additionally, previous studies have been
largely synoptic rather than using data that have been pooled from September through to
March.

Mackintosh (1934), Chiba et al. (2001) and Mackey et al. (2012) have all underlined
the importance of temperature in determining the distributions of many species of Southern
Ocean plankton. Atkinson and Sinclair (2000) have also argued that there is little evidence that the PF forms a biogeographic barrier to the distribution of many species owing to their wide-spread distribution at depth. Our analysis also reflects the wider distribution of many species (Tables 4 and 6). The relatively low values of the R statistic for the AZ/PFZ and the PF/SAZ pairwise comparisons versus its high values for the AZ/SAZ comparison (Table 3), suggests that the PFZ represents a transition zone. The PFZ has been characterized by the presence of a mixture of sub-Antarctic, sub-tropical and Antarctic species and as such represents a biogeographic ecotone-type community (Pakhomov et al., 2000). There is also no doubt that many species do have distributions that are relatively unaffected by the presence of the PF. Many of the horizontal gradients at ACCZ boundaries are weak relative to vertical gradients and are too weak to limit species distributions which tend to form a continuum, characterised by core regions and regions of expatriation (Angel 1997).

Nevertheless, many other species exhibit step changes in abundance in passing from one side of a front to the other and watermass preferences are marked (Boltovskoy et al., 1999). In the wider South Atlantic, Boltovskoy et al. (1999) plotted species distributional boundaries against latitude and found that by far the highest number occurred in the transition zone between the subtropical and sub-Antarctic around 30-40°S. This warm-cold water transition was stronger than the second highest found in the vicinity of the PF.

4.4 Seasonality

Despite pronounced seasonality in the near-surface Antarctic pelagial (Clarke 1988; Smetacek et al., 1990) we found no indirect evidence that this was also apparent in the mesopelagic. Abundance and biomass varied little below 250 m (Table 2) and testing by ACCZ only 5 of 40 taxa/species seasonal abundance comparisons were significantly different, suggesting that seasonal differences were not widespread within the 500-1000 m horizons. In many oceans, seasonal flux of organic material to the deep-sea has been detected
at many thousands of metres depth (Billett et al., 1983; Asper et al., 1992). In the North
Atlantic, Koppelmann and Weikert (1999) found evidence that, below 1000 m, many
species/taxa had summer:spring ratios of >1, suggesting a reproductive response to the spring
bloom, particularly in the upper bathypelagic zone (1050-2250 m). This increase was
pronounced among calanoid copepods and in particular the Metridinidae which increased by
a factor of 13.5 between spring and summer. In regions where blooms are largely absent, it
was suggested that such responses would not be detected (Koppelmann and Weikert, 1999).
They cite summer biomass profiles from the Madeira Abyssal Plain (Roe, 1988), where
spring blooms do not occur, as being similar to pre-bloom spring profiles from the
BIOTRANS site in the temperate northeast Atlantic where their study was carried out.

In this part of the Southern Ocean, levels and periodicity of primary production may
also be important. Our contemporary composite of ocean colour (Fig. 1) shows that highest
levels of chlorophyll are generally found south of the transect locations and may be
associated with the retreating ice-edge. To the north of this, chlorophyll is uniformly low
(<0.5 mg l\(^{-1}\)). Production patterns have probably not changed dramatically over the years
because the transect lies upstream of the main sources of iron input into the ACC in this
sector, namely shelf deposits from the Antarctic Peninsula and topographically induced
upwelling (Park et al., 2010). Data on the presence of phytoplankton in the 80°W samples are
given by Foxton (1956) (Table 11c). December and March samples from the AZ contained
phytoplankton in the near-surface layers which implies that ‘summer’ stations in the AZ in
1933/34 were only just experiencing a bloom, suggesting that deep-water fauna would in any
case have had no time to respond to this burst of production. A reproductive response later in
the year (early winter onwards) may explain why spring abundance of some species was
greater than during summer. Interannual variability also may be partly responsible insofar as
the summer grouping (Dec. 1933 and Mar. 1934) precede rather than succeed the spring grouping (Sept, Oct, Nov 1934) and so effectively different cohorts were being assessed.

4.5 Diversity

Within this study a number of taxonomic categories were unresolved into species. Our ‘lumping’ of species manifested itself variously at the level of phylum, e.g. Chaetognatha, Ctenophora; class or order e.g. Ostracoda, Siphonophora, Appendicularia; family or genus e.g. Lucicutiid copepodites, *Oncaea* spp. etc. Of the taxa identified, copepods were the most highly resolved to species level. Reasons for this variously included the state of preservation of some elements of the samples, expedience in wishing to analyse a large number of samples in a timely manner and levels of taxonomic expertise. Nonetheless some clear patterns emerged. Rarefaction analysis highlighted the relationship of increasing diversity with depth when species presence/absence data from all ACCZs were pooled with respect to depth (Fig 6). This was also to an extent mirrored in the clustering of station data with respect to depth (Fig 4) which effectively partitioned the water column across all ACCZs into 3 distinct horizons. The rarefaction curves from the two deepest horizons corresponding to the lower mesopelagic (*sensu* Fig. 4) indicate a greater diversity and have a steeper slope than the shallower depth horizons indicating a different rate of species accumulation. It should be borne in mind that each deep sample represents 5 times the amount of water swept per sample in the upper two horizons in the top 100 m. However, the slope of the species accumulation curve was different and even with an extrapolated sample number (equivalent to a greater volume of water swept) diversity never approaches that of the deeper horizons. Modern net sampling of the deep water column is usually undertaken with larger nets than the N70, using oblique rather than vertical hauls and generally sampling a greater volume of water. This would undoubtedly influence the rate of accumulation of species per haul but the relative pattern between the different horizons is unlikely to change dramatically.
It is difficult to summarise patterns of diversity across such a heterogenous group as plankton. Some groups are taxonomically better investigated than others, using both traditional morphology and modern molecular techniques such as genetic bar coding (Bucklin et al. 2011) but, at a wider scale, the polar and sub-polar biomes are less rich in species across many groups than their tropical and subtropical counterparts (Angel et al., 2007; Boltovskoy et al., 1999; Woodd-Walker et al., 2002). In near-surface samples, Woodd-Walker et al. (2002) have demonstrated the large-scale spatial variation in taxonomic richness of copepod genera across the whole Atlantic Ocean. Higher diversity was apparent in the tropics and sample evenness and diversity also reduced dramatically around 40°S and towards the poles. This has been attributed to the former possessing a relatively stable environment where seasonal changes are minimal, allowing for a largely retentive system in which primary and secondary producers are closely coupled and diversity is characteristically high (Conover, 1979; Longhurst and Pauly, 1987). Polewards, seasonality increases and production and consumption become increasingly uncoupled and diversity is lower. Increasing diversity with depth may therefore reflect the relative stability of the lower part of the mesopelagic in contrast to the seasonal breakdown of the thermocline and the winter overturning of the upper water column (Woodd-Walker et al., 2002). At a smaller spatial scale our analysis suggested that slightly more copepod species were present in the SAZ than in either the AZ or PFZ. This was in large measure through higher species numbers within the families Aetideidae and Augaptilidae being found in the SAZ (Table 9). However, based on the wider literature, Razouls et al. (2005-2012) record 47 and 39 members of the Aetideidae and 27 and 20 members of the Augaptilidae in the AZ and SAZ respectively. Our samples only recovered a relatively small proportion of these totals which reflects sampling effort, regional bias and overall rarity of many of the deeper dwelling species (see E-Table). Large-scale physics in the form of mesoscale eddies (Nowlin and Klinck 1986) may also influence diversity by
introducing species polewards or in some cases equatorwards across the PF. Based on the wider literature extending to the entire Southern Ocean, Razouls et al. (2005-2013) estimate that the number of copepod species occurring in all Antarctic waters totals 295 compared to 275 reported for the sub-Antarctic. They have also suggested that ~80% of copepod species observed in the sub-Antarctic are immigrants and originate from sub-tropical and temperate zones. It is possible that these form ‘pseudo-populations’ (Razouls et al., 2005-2013) and many of these may already be at the limits of their distributional ranges. Other taxonomic groups such as Amphipoda, Ostracoda and Salpidae, appear to have a greater number of species in the SAZ whereas others such as euphausiids, chaetognaths and some radiolarians appear more evenly distributed (Boltovskoy et al., 1999).

4.6 Long-term change

Profound physical changes have occurred in the Southern Ocean in the intervening 80 or so years since Discovery Investigations. At the WAP, close to the 80°W transect, climate change has been rapid. Atmospheric temperatures have risen by ~3°C since 1951 (Vaughan et al. 2003) and extensive glacial retreat has occurred (Cook et al., 2005). The surrounding ocean temperature has also increased by ~1°C in summer (Meredith and King, 2005), and sea-ice duration and cover has declined in this region (Cavalieri and Parkinson, 2008). The potential and actual impacts of such changes are being recognised in various parts of the marine ecosystem, (eg Atkinson et al., 2004; Ducklow et al., 2007; Clarke et al., 2007; Forcada et al 2006; Schofield et al., 2010) and are generally complex.

The transect along 80°W lies north and west of the WAP and is largely north of the seasonal sea-ice zone. Ocean warming throughout the region has not been uniform with depth and, along with decreased salinity, is greater in near-surface waters (Meredith and King, 2005; Böning et al., 2008). Because of warming and freshening, Böning et al. (2008) estimate that density surfaces between the PF and SAF at 800-1000 m have been displaced southwards.
50–80 km in the last 40 years and perhaps 2-3 times this distance at the surface. This may imply a southwards displacement of frontal zones but this is likely to be difficult to detect against the natural background variation in the position of the ACC fronts (Moore et al., 1999; Venables et al., 2012). Plankton distributions frequently show strong temperature dependence in the Southern Ocean (Mackintosh, 1934; Chiba et al., 2001; Mackey et al., 2012). Simplistically, as a consequence of warming, we might expect a southwards penetration of some ‘warmer’ water species and a contraction in the range of cold water species as predicted by Mackey et al. (2012) for macrozooplankton. This seems plausible as Ward et al. (2004, 2006) have shown that, in extensive surveys of the Scotia Sea, mesoplankton, particularly copepods, were much less abundant in ice influenced waters. A polewards movement of the ice-edge may therefore progressively result in increased zooplankton diversity and abundance further south. However, many species have wide distributional ranges, occurring in all ACCZs sampled and over wide depth ranges and without the benefit of time-series data change is not going to be easy to detect (Ward et al., 2008, 2012; Mackey et al., 2012). Nonetheless, Discovery samples were taken over a large part of the Southern Ocean using the same sampling gear and provide a valuable resource with which to undertake comparisons on a regional basis and with contemporary collections.

Acknowledgements

We thank Miranda Lowe and Clare Valentine of the Natural History Museum London for making the Discovery samples available to us. More information regarding these collections can be found at http://www.nhm.ac.uk/research-curation/collections/our-collections/invertebrate-collections/historical-marine-collections/nhm-collections/discovery/index.html
We are grateful to Dr Janet Bradford-Grieve (NIWA) and Prof. Shuhei Nishida (Tokyo University) for identifying some of our copepod material.

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structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer


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chlorophyll-α in the southwest Atlantic sector of the Southern Ocean: Strong topographic


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Fig. 1. Composite satellite image showing mean chlorophyll $a$ during the period September – March 2004–2012, east of Drake Passage. White areas denote missing data due to land/cloud/sea ice cover. Superimposed are Discovery station positions coded by month. Shaded grey rectangles represent the limits within which the sub-Antarctic Front (SAF) and Polar Front (PF) were found during these transects. The chlorophyll $a$ data used in Fig. 1 are MODIS-Aqua 9 km resolution, level 3 data provided by the NASA Goddard Earth Sciences Data and Information Services Center (Acker and Leptoukh, 2007).

Fig. 2. Logged Mesozooplankton abundance (ind m$^{-3}$) with respect to depth. Data shown are median plus interquartile range (box) and 10$^{th}$ and 90$^{th}$ percentiles (whiskers). Dots represent outliers. Data have been pooled within depth horizons across ACC Zones.
Fig. 3. a) Mesozooplankton abundance (ind. m$^{-3}$) versus depth by month. Open symbols represent individual data points, filled circles, median values by depth. Key for depth: 1 = 50-0 m, 2 = 100-50 m, 3 = 250-100 m, 4 = 500-250 m, 5 = 750-500 m, 6 = 1000-750 m.

b) Mesozooplankton abundance (ind. m$^{-3}$) versus ACC zone by depth. Open symbols represent individual data points, filled circles, median values by ACC zone. Key for depth, as for Figure 3. ACC zone abbreviations as Table 1.

Fig. 4. Results of nearest neighbour clustering on the Bray-Curtis similarity matrix containing all sample data. Samples have been coded according to depth horizon. We have sliced the cluster dendrogram at 70% similarity. At $\geq$70% similarity, the dendrogram has been collapsed and stations are represented by symbols at the similarity level at which they first became statistically indistinguishable. Red lines at <70% similarity extend from the point at which the grouping became statistically indistinguishable from one another. Black lines extending to the $x$ axis are statistically dissimilar to other stations.

Fig. 5a) MDS ordination carried out on the 0-1000 m data matrix. Lines encircling stations represent 73% similarity.

5b) MDS ordination carried out on the 500-1000 m data matrix with seasonal migrants omitted (see below). Lines encircling stations represent 72% similarity.

Open circles = AZ stations, filled triangles PFZ stations and open squares SAZ stations.

Taxa omitted from 500-1000 m data matrix were *Calanoides acutus*, *Calanus simillimus*, *Neocalanus tonsus*, *Rhincalanus gigas* plus nauplii, *Subeucalanus longiceps*, *Ctenocalanus* spp. *Clausocalanus laticeps*, *Clausocalanus brevipes*, *Ctenocalanus/Clausocalanus*

Fig. 6. Rarefaction curves based on a presence/absence species by depth matrix. Between 35-37 samples were used from each depth horizon to construct the curves using the “Moa tau” method (bold lines). A 3 parameter power function fitted to each rarefaction curve was then extrapolated to 3 times the sample size (108 samples) following Colwell et al., (2004; fine lines).

Fig. 7. Boxplot of median number of species/taxa in each depth horizon with respect to ACC zone. Data shown are median plus interquartile range (box) and max and min (whiskers) * = outlier. Depth coding as for Fig. 3.

Fig. 8. Median abundance (ind. m$^{-3}$) of major copepod families and other taxa by ACC zone and depth. Data shown are median plus interquartile range (box) and max and min (whiskers), * = outlier. Depth coding as for Fig. 3.
Table 1. *Discovery* stations sampled along 80°W by month with respect to ACC Zones.

Stations emboldened were originally classified as Antarctic stations by Foxton (1956) and the remainder as sub-Antarctic. Antarctic Circumpolar Current Zones (ACCZ) defined according to potential temperature, salinity and potential density sections and potential temperature-salinity curves (see text). Stations with an asterisk are those where one or more samples are missing or the contents had been split.

<table>
<thead>
<tr>
<th>ACCZ</th>
<th>Antarctic Zone (AZ)</th>
<th>Polar Frontal Zone (PFZ)</th>
<th>sub-Antarctic Zone (SAZ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>December (1933)</td>
<td>1220, 1221, 1222, 1223, 1224</td>
<td>1225, 1226*, 1227*</td>
<td>1228*, 1229</td>
</tr>
<tr>
<td>March (1934)</td>
<td>1312, 1313, 1314, 1315*, 1316</td>
<td>1317</td>
<td>1318*, 1319, 1320</td>
</tr>
<tr>
<td>September (1934)</td>
<td>1415*, 1416,</td>
<td>1417, 1418*, 1419*</td>
<td>1420, 1421*</td>
</tr>
<tr>
<td>October (1934)</td>
<td>1447, 1449, 1450</td>
<td>1446*, 1444*</td>
<td>1441*, 1442, 1443,</td>
</tr>
<tr>
<td>November (1934)</td>
<td>1472, 1473, 1474, 1475</td>
<td>1476</td>
<td></td>
</tr>
</tbody>
</table>
Table 2: Median plankton abundance (ind. m\(^{-3}\) (Q1-Q3)) and biomass (wet mass mg m\(^{-3}\) (Q1-Q3)). Biomass derived from settled volume (cm\(^3\)) assuming 1 cm\(^3\) = 1 g wet mass. See original data in Foxton (1956) Table 11c. The formula π x r\(^2\) x h has been used to estimate abundance and volume per m\(^2\) and thence m\(^3\). ACC Zone definitions and abbreviations as Table 1, (n) = no. of samples within each ACC Zone.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>AZ (111)</th>
<th>PFZ (50)</th>
<th>SAZ (54)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>50-0</td>
<td>306 (43-700)</td>
<td>294 (194-464)</td>
<td>187 (127-299)</td>
</tr>
<tr>
<td>100-50</td>
<td>294 (177-565)</td>
<td>211 (107-552)</td>
<td>180 (157-239)</td>
</tr>
<tr>
<td>250-100</td>
<td>92 (55-153)</td>
<td>182 (122-195)</td>
<td>93 (66-147)</td>
</tr>
<tr>
<td>500-250</td>
<td>44 (39-72)</td>
<td>54 (35-67)</td>
<td>56 (40-83)</td>
</tr>
<tr>
<td>750-500</td>
<td>20 (13-36)</td>
<td>26 (20-29)</td>
<td>30 (23-46)</td>
</tr>
<tr>
<td>1000-750</td>
<td>13 (8-21)</td>
<td>10 (8-18)</td>
<td>14 (7-24)</td>
</tr>
<tr>
<td>Biomass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>50-0</td>
<td>21 (5-47)</td>
<td>44 (29-51)</td>
<td>36 (13-60)</td>
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<tr>
<td>100-50</td>
<td>52 (10-88)</td>
<td>47 (23-153)</td>
<td>36 (23-59)</td>
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<td>250-100</td>
<td>21 (10-40)</td>
<td>42 (16-49)</td>
<td>26 (14-41)</td>
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<tr>
<td>500-250</td>
<td>19 (12-22)</td>
<td>14 (11-17)</td>
<td>12 (16-23)</td>
</tr>
<tr>
<td>750-500</td>
<td>12 (8-19)</td>
<td>14 (9-17)</td>
<td>14 (11-19)</td>
</tr>
<tr>
<td>1000-750</td>
<td>7 (5-10)</td>
<td>10 (8-13)</td>
<td>9 (7-10)</td>
</tr>
</tbody>
</table>
Table 3: Analysis of Similarities (ANOSIM), testing how well station grouping reflects ACCZ definitions (see text). ACC Zone definition and abbreviations as Table 1. * = significant difference. No. of permutations = 999.

<table>
<thead>
<tr>
<th>Data matrix</th>
<th>R statistic</th>
<th>Significance Level ($p$)</th>
<th>Watermass Comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-1000 m Differences between ACCZs</td>
<td>0.32</td>
<td>0.008</td>
<td>AZ/PFZ*</td>
</tr>
<tr>
<td></td>
<td>0.87</td>
<td>0.001</td>
<td>AZ/SAZ*</td>
</tr>
<tr>
<td></td>
<td>0.39</td>
<td>0.010</td>
<td>PFZ/SAZ*</td>
</tr>
<tr>
<td>500-1000 m (less seasonal migrants) Differences between ACCZs</td>
<td>0.25</td>
<td>0.016</td>
<td>AZ/PFZ*</td>
</tr>
<tr>
<td></td>
<td>0.74</td>
<td>0.008</td>
<td>AZ/SAZ*</td>
</tr>
<tr>
<td></td>
<td>0.12</td>
<td>0.130</td>
<td>PFZ/SAZ</td>
</tr>
</tbody>
</table>
Table 4: Abundance (mean ind. m$^{-2}$, 0-1000 m (±SD)) of the first ten species/taxa in the analysis shown to be contributing most to within group similarity and between group dissimilarity across all 3 groups of stations (no. of stations). Taxa ranked in terms of overall abundance across all groups. ACC Zone definitions and abbreviations as Table 1.

<table>
<thead>
<tr>
<th>Species/taxa</th>
<th>AZ(16)</th>
<th>PFZ(5)</th>
<th>SAZ(6)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Oithona similis</em></td>
<td>22399 (11274)</td>
<td>32167 (15881)</td>
<td>11616 (6456)</td>
</tr>
<tr>
<td><em>Ctenocalanus</em> spp.</td>
<td>8240 (5557)</td>
<td>17167 (15859)</td>
<td>12565 (7039)</td>
</tr>
<tr>
<td>Pteropoda</td>
<td>15094 (43509)</td>
<td>359 (753)</td>
<td>62 (128)</td>
</tr>
<tr>
<td><em>Oncaea</em> spp.</td>
<td>10827 (6623)</td>
<td>7742 (6091)</td>
<td>6415 (3691)</td>
</tr>
<tr>
<td><em>Oithona frigida</em></td>
<td>6300 (2412)</td>
<td>5720 (2774)</td>
<td>4128 (1779)</td>
</tr>
<tr>
<td><em>Microcalanus pygmaeus</em></td>
<td>3970 (1601)</td>
<td>4587 (820)</td>
<td>7562 (3594)</td>
</tr>
<tr>
<td>Calanoid nauplii</td>
<td>3315 (3511)</td>
<td>3480 (3891)</td>
<td>1650 (1075)</td>
</tr>
<tr>
<td><em>Metridia lucens</em></td>
<td>709 (616)</td>
<td>2598 (2258)</td>
<td>1701 (1165)</td>
</tr>
<tr>
<td>Paroithona sp.</td>
<td>31 (39)</td>
<td>858 (815)</td>
<td>4492 (4889)</td>
</tr>
<tr>
<td><em>Rhinocalanus</em> gigas</td>
<td>1024 (656)</td>
<td>1784 (499)</td>
<td>864 (952)</td>
</tr>
<tr>
<td><em>Calanus similimus</em></td>
<td>740 (2413)</td>
<td>1667 (1165)</td>
<td>1664 (1736)</td>
</tr>
<tr>
<td><em>Calanoides acutus</em></td>
<td>1342 (1051)</td>
<td>610 (1143)</td>
<td>9 (10)</td>
</tr>
<tr>
<td>Ctenocalanus/Clausocalanus* copepodites</td>
<td>447 (761)</td>
<td>486(469)</td>
<td>2257 (1949)</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>489 (201)</td>
<td>998 (335)</td>
<td>1389 (545)</td>
</tr>
<tr>
<td>Chaetognatha spp.</td>
<td>619 (378)</td>
<td>855 (753)</td>
<td>847 (451)</td>
</tr>
<tr>
<td>Appendicularians</td>
<td>881 (1803)</td>
<td>236 (266)</td>
<td>533 (1088)</td>
</tr>
<tr>
<td>Copepod spp. (Unidentified copepodites)</td>
<td>742 (828)</td>
<td>332 (256)</td>
<td>774 (399)</td>
</tr>
<tr>
<td><em>Rhinocalanus</em> gigas nauplii</td>
<td>783 (1383)</td>
<td>347 (455)</td>
<td>31 (76)</td>
</tr>
<tr>
<td><em>Clausocalanus</em> laticeps</td>
<td>34 (73)</td>
<td>266 (263)</td>
<td>859 (1277)</td>
</tr>
<tr>
<td><em>Subeucalanus</em> longiceps</td>
<td>19 (18)</td>
<td>147 (112)</td>
<td>908 (445)</td>
</tr>
</tbody>
</table>
Table 5: Mean abundance ind.m$^{-2}$ (±SD) within the depth horizons indicated with respect to ACC Zone grouping (see Table 3). ACC Zone definition and abbreviations as Table 1. (n) number of stations within respective ACC Zones.

<table>
<thead>
<tr>
<th>Depth</th>
<th>ACC Zone Grouping</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AZ (16)</td>
<td>PFZ (5)</td>
<td>SAZ (6)</td>
</tr>
<tr>
<td>0-1000 m</td>
<td>$8.18 \times 10^4$ (5.17 $\times 10^4$)</td>
<td>$8.50 \times 10^4$ (4.40 $\times 10^4$)</td>
<td>$6.47 \times 10^4$ (3.08 $\times 10^4$)</td>
</tr>
<tr>
<td></td>
<td>AZ (18)</td>
<td>SAZ /PFZ (15)</td>
<td></td>
</tr>
<tr>
<td>500-1000 m</td>
<td>$0.80 \times 10^4$ (0.44 $\times 10^4$)</td>
<td>$0.86 \times 10^4$ (0.44 $\times 10^4$)</td>
<td></td>
</tr>
</tbody>
</table>
Table 6: Abundance (mean ind. m$^{-2}$, 500-1000 m (±SD)) of the first ten species/taxa in the analysis shown to be contributing most to within group similarity and between group dissimilarity across all 3 groups of stations (no. of stations). Taxa ranked in terms of overall abundance across all groups. ACC Zone definitions and abbreviations as Table 1.

<table>
<thead>
<tr>
<th>Species/taxa</th>
<th>AZ (18)</th>
<th>PFZ &amp; SAZ (15)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oncaea spp.</td>
<td>2989 (2268)</td>
<td>2874 (1501)</td>
</tr>
<tr>
<td>Oithona frigida</td>
<td>1983 (963)</td>
<td>1452 (656)</td>
</tr>
<tr>
<td>Microcalanus pygmaeus</td>
<td>1238 (1225)</td>
<td>2150 (1831)</td>
</tr>
<tr>
<td>Metridia lucens</td>
<td>243 (353)</td>
<td>372 (259)</td>
</tr>
<tr>
<td>Metridia curticauda</td>
<td>223 (78)</td>
<td>152 (66)</td>
</tr>
<tr>
<td>Calanoid nauplii</td>
<td>194 (151)</td>
<td>170 (84)</td>
</tr>
<tr>
<td>Ostracoda spp.</td>
<td>178 (80)</td>
<td>165 (62)</td>
</tr>
<tr>
<td>Spinocalanus spp.</td>
<td>225 (215)</td>
<td>72 (43)</td>
</tr>
<tr>
<td>Chaetognatha spp.</td>
<td>115 (66)</td>
<td>171 (118)</td>
</tr>
<tr>
<td>Lucicutia ovalis</td>
<td>200 (96)</td>
<td>54 (62)</td>
</tr>
<tr>
<td>Paroithona sp.</td>
<td>5 (15)</td>
<td>241 (551)</td>
</tr>
<tr>
<td>Scolecithricid copepodites</td>
<td>56 (30)</td>
<td>83 (50)</td>
</tr>
<tr>
<td>Pleuromamma robusta</td>
<td>43 (72)</td>
<td>85 (45)</td>
</tr>
<tr>
<td>Mormonilla sp.</td>
<td>20 (28)</td>
<td>83 (74)</td>
</tr>
<tr>
<td>Siphonophora</td>
<td>12 (13)</td>
<td>51 (53)</td>
</tr>
<tr>
<td>Clione antarctica</td>
<td>15 (21)</td>
<td>30 (37)</td>
</tr>
<tr>
<td>Paraenocheta biloba</td>
<td>8 (14)</td>
<td>22 (13)</td>
</tr>
<tr>
<td>Euphausiid nauplii</td>
<td>14 (25)</td>
<td>14 (27)</td>
</tr>
<tr>
<td>Thysanoessa spp.</td>
<td>6 (21)</td>
<td>11 (9)</td>
</tr>
<tr>
<td>Euactideus australis</td>
<td>0 (0)</td>
<td>12 (15)</td>
</tr>
</tbody>
</table>
Table 7: Mean (±SD) and median (Q1-Q3) abundance (ind. m\(^{-2}\), per 250 m haul in the 500-1000 m depth horizon) of the 20 most abundant species/taxa within the 500-1000 m horizons. Data represent spring (Sept/Oct/Nov) and summer (Dec/March). Only Spinocalanus spp. showed a significantly different seasonal abundance (Anova \(F_{1,69}=5.74, p = 0.019\)).

<table>
<thead>
<tr>
<th>Species/taxa</th>
<th>Spring mean (ind. m(^{-2}), per 250 m haul in the 500-1000 m depth range)</th>
<th>Summer mean (ind. m(^{-2}), per 250 m haul in the 500-1000 m depth range)</th>
<th>Spring median (ind. m(^{-2}), per 250 m haul in the 500-1000 m depth range)</th>
<th>Summer median (ind. m(^{-2}), per 250 m haul in the 500-1000 m depth range)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Oncaea</em> spp.</td>
<td>1199 (879)</td>
<td>1674 (1381)</td>
<td>915 (585-1681)</td>
<td>1122 (686-2359)</td>
</tr>
<tr>
<td><em>Oithona frigida</em></td>
<td>835 (835)</td>
<td>850 (454)</td>
<td>717 (364-1065)</td>
<td>727 (587-1086)</td>
</tr>
<tr>
<td><em>Microcalanus pygmaeus</em></td>
<td>710 (612)</td>
<td>898 (1317)</td>
<td>546 (177-1081)</td>
<td>447 (125-1122)</td>
</tr>
<tr>
<td><em>Metridia lucens</em></td>
<td>122 (207)</td>
<td>165 (252)</td>
<td>30 (8-131)</td>
<td>94 (27-194)</td>
</tr>
<tr>
<td><em>Metridia curticauda</em></td>
<td>103 (61)</td>
<td>90 (72)</td>
<td>87 (64-126)</td>
<td>83 (23-152)</td>
</tr>
<tr>
<td>Calanoid nauplii</td>
<td>89 (87)</td>
<td>86 (77)</td>
<td>83 (42-117)</td>
<td>83 (16-120)</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>91 (46)</td>
<td>79 (53)</td>
<td>87 (61-110)</td>
<td>73 (35-118)</td>
</tr>
<tr>
<td><em>Spinocalanus</em> spp.</td>
<td>47* (61)</td>
<td>100 (115)</td>
<td>23 (10-62)</td>
<td>73 (31-125)</td>
</tr>
<tr>
<td>Chaetognatha</td>
<td>68 (43)</td>
<td>70 (70)</td>
<td>64 (31-89)</td>
<td>42 (25-104)</td>
</tr>
<tr>
<td><em>Lucicutia ovalis</em></td>
<td>67 (96)</td>
<td>62 (70)</td>
<td>26 (0-102)</td>
<td>34 (3-112)</td>
</tr>
<tr>
<td><em>Paroithona</em> sp.</td>
<td>12 (21)</td>
<td>91 (323)</td>
<td>0 (0-21)</td>
<td>0 (0-31)</td>
</tr>
<tr>
<td><em>Heterorhabdus</em> spp.</td>
<td>36 (25)</td>
<td>39 (32)</td>
<td>32 (18-45)</td>
<td>34 (16-51)</td>
</tr>
<tr>
<td>Scolecithricid copepodites</td>
<td>34 (29)</td>
<td>35 (33)</td>
<td>26 (16-52)</td>
<td>21 (10-56)</td>
</tr>
<tr>
<td><em>Pleuromamma robusta</em></td>
<td>35 (60)</td>
<td>26 (41)</td>
<td>16 (0-45)</td>
<td>5 (0-38)</td>
</tr>
<tr>
<td><em>Mormonia</em> sp.</td>
<td>28 (39)</td>
<td>23 (35)</td>
<td>10 (0-42)</td>
<td>10 (0-31)</td>
</tr>
<tr>
<td><em>Gaetanus tenuispinus</em></td>
<td>16 (18)</td>
<td>18 (24)</td>
<td>9 (3-19)</td>
<td>10 (3-27)</td>
</tr>
<tr>
<td>Siphonophora</td>
<td>9 (13)</td>
<td>19 (34)</td>
<td>3 (0-12)</td>
<td>8 (0-19)</td>
</tr>
<tr>
<td><em>Pareuchaeta antarctica</em></td>
<td>14 (13)</td>
<td>9 (14)</td>
<td>10 (5-21)</td>
<td>5 (1-10)</td>
</tr>
<tr>
<td>Scaphocalaniid copepodites</td>
<td>9 (13)</td>
<td>13 (15)</td>
<td>5 (2-10)</td>
<td>8 (3-19)</td>
</tr>
<tr>
<td><em>Scolecithricella dentipes</em></td>
<td>13 (11)</td>
<td>8 (8)</td>
<td>9 (2-23)</td>
<td>8 (3-13)</td>
</tr>
</tbody>
</table>
Table 8: Mean (±SD) number of species/taxa within the 0-1000 m water column with respect to ACC Zone. Of the comparisons carried out among ACC Zones using all taxa and copepods only that between AZ and SAZ was significant; ANOVA $F_{1, 20 \, df} = 14.41, p = 0.001$ for all taxa and $F_{1, 20 \, df} = 16.58, p = 0.001$ for copepods alone. ACC Zone definition and abbreviations as Table 1.

<table>
<thead>
<tr>
<th>Watermass (no. stns)</th>
<th>No. taxonomic categories</th>
<th>No. copepod categories</th>
</tr>
</thead>
<tbody>
<tr>
<td>AZ (17)</td>
<td>60.4 ± 6.1</td>
<td>46.9 ± 3.4</td>
</tr>
<tr>
<td>PFZ (4)</td>
<td>61.5 ± 6.2</td>
<td>47.3 ± 4.7</td>
</tr>
<tr>
<td>SAZ (6)</td>
<td>73.7 ± 9.6</td>
<td>57.0 ± 8.5</td>
</tr>
</tbody>
</table>
Table 9. Number of species of copepods identified within each ACC Zone with respect to Order and Family. Family (n) = no. of species identified within family across all groupings. ACC Zone definition and abbreviations as Table 1. ACCZ (n) = no. samples analysed.

<table>
<thead>
<tr>
<th>Order Family</th>
<th>AZ (117)</th>
<th>PFZ (44)</th>
<th>SAZ (54)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Calanoida</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calanidae (4)</td>
<td>4</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Eucalanidae (5)</td>
<td>2</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Spinocalanidae (2)</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Clausocalanidae (4)</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Tharybidae (1)</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Stephidae (1)</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Aetideidae (16)</td>
<td>8</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td>Euchaetidae (7)</td>
<td>5</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>Phaennidae (5)</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Scolecitrichidae (13)</td>
<td>11</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Arietellidae (1)</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Augaptilidae (11)</td>
<td>4</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>Heterorhabdidae (6)</td>
<td>4</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Lucicutiidae (6)</td>
<td>6</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Metridinidae (6)</td>
<td>5</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Phyllopodidae (1)</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Candaciidae (1)</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Bathypontidae (1)</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Mormonilloida</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mormonillidae (1)</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Cyclopoidea</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oithoniidae (4)</td>
<td>4</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td><strong>Harpacticoida</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ectinosomatidae (1)</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Aeagisthidae (1)</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><strong>Poecilostomatoida</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oncaeidae (2)</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td><strong>Siphonostomatoida</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ratanidae (1)</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>72</td>
<td>63</td>
<td>83</td>
</tr>
</tbody>
</table>
Highlights

1. Plankton samples from 1930’s *Discovery Investigations* in the Southern Ocean analysed

2. Depth was the strongest factor separating samples

3. Mean zooplankton abundance in the epipelagic was ~ 25 times greater than at 1000 m

4. Seasonal signals across all data became less distinct with depth.

5. Rarefaction analysis revealed that depth was a major influence on diversity.