The summertime plankton community at South Georgia (Southern Ocean): comparing the historical (1926/27) and modern (post 1995) records.

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Abstract

The earliest comprehensive plankton sampling programme in the Southern Ocean was undertaken during the early part of last century by Discovery Investigations to gain a greater scientific understanding of whale stocks and their summer feeding grounds. An initial survey was carried out around South Georgia during December 1926 and January 1927 to describe the distribution of plankton during the summer, and to serve as a baseline against which to compare future surveys. We have reanalysed phytoplankton and zooplankton data from this survey and elucidated patterns of community distribution and compared them with our recent understanding of the ecosystem based on contemporary data. Analysis of Discovery data identified five groups of stations with characteristic phytoplankton communities which were almost entirely consistent with the original analysis conducted by Hardy and Gunther (1935). Major groupings were located at the western end of the island and over the northern shelf where *Corethron* spp. were dominant, and to the south and east where a more diverse flora included high abundances of *Nitzschia seriata*. Major zooplankton-station groupings were located over the inner shelf which was characterised by a high abundance of *Drepanopus forcipatus* and in oceanic water >500 m deep that were dominated by Foraminifera, *Oithona* spp., *Ctenocalanus vanus*, and *Calanoides acutus*. Stations along the middle and outer shelf regions to the north and west, were characterised by low overall abundance. There was some evidence that groupings of stations to the north of the island originated in different water masses on either side of the Southern Antarctic Circumpolar Current Front, the major frontal system in the deep ocean close to South Georgia. However, transect lines during 1926/27 did not extend far enough offshore to sample this frontal region adequately. Interannual variability of zooplankton abundance was assessed from stations which were sampled repeatedly during 7 recent British Antarctic Survey cruises (1995-2005) to the region and following taxonomic harmonization and numerical standardization (ind. m^{-3}), a subset of 45 taxonomic categories of zooplankton (species and higher taxa) from 1926/27, were compared with similar data obtained during the BAS cruises using a linear model. Initially comparisons were restricted to BAS stations that lay within 40 km of Discovery stations although a comparison was also made using all available data. Despite low abundance values in 1926/27, in neither comparison did Discovery data differ significantly from BAS data. Calculation of the percentage similarity index across cruises did not reveal any systematic differences in species composition between 1926/27 and the present. In the light of ocean warming trends, the existence of more subtle changes in species composition is not ruled out, but an absence of finely resolved time-series data make this impossible to determine.

Key words: marine plankton communities, interannual variability, physical oceanography, long-term change, Antarctica, Southern Ocean, South Georgia.

1. Introduction

Decadal-scale links between plankton and climate have been extremely difficult to observe in many of the world's oceans, due primarily to the short duration of the plankton collections and the lack of concomitant oceanographic data from earlier eras. However, the lengthening of such time series in recent years has enabled some insights into the climatic forcing of ocean ecosystems on these timescales (Hays et al., 2005). Although such time-series are still few in number and generally have a temporal extent of considerably < 60 years, strong evidence for world-wide changes in plankton abundance and community structure has emerged. Studies to date have emphasised the sensitivity of plankton communities to climatic signals (Roemmich and McGowan, 1995; Planque and Taylor, 1998; Beaugrand et al., 2002) as well as their non-linear response to meteorological variables such as cloud cover and wind (e.g. Fromentin and Planque, 1996; Planque and Fromentin, 1996; Taylor et al., 2002). Climatic fluctuations as reflected in atmospheric models such as the North Atlantic Oscillation (NAO) may be seen as a proxy for regulating forces in aquatic and terrestrial ecosystems. Evidence suggests that the NAO influences ecological dynamics in both marine and terrestrial ecosystems and its effects may be seen in variation at the individual, population and community levels (Ottersen et al., 2001).

Climate variability in the Southern Ocean is characterised by a number of coupled modes of variability in addition to secular change. Of the former, El Niño-Southern Oscillation (ENSO) events have been particularly highlighted as significant forcing agents of ecosystem change (Stenseth et al., 2002; Smith et al., 2003). Various links between ENSO, ocean temperature and marine biology have been reported, with squid stock recruitment, breeding performance and population sizes of seabirds and seals, and population dynamics of Antarctic krill (*Euphausia superba)* being amongst the ecosystems indicators influenced (Waluda et al., 1999; Reid and Croxall, 2001; Smith et al., 2003; Ainley et al., 2005; Guinet et al., 1998; Murphy et al., 2007). ENSO is known to have a particularly strong influence on the Southern Ocean in the southern and southeast Pacific sector, and through to the South Atlantic, where clear relationships with sea-ice cover are evident (Kwok and Comiso, 2002; Stammerjohn et al., 2003; Meredith et al., in press). In addition to ENSO, the Southern Annular Mode (SAM) has more recently been identified as a key determinant of temperature in the Southern Ocean (Meredith et al., in press).

South Georgia is an island located at the northeast limits of the Scotia Sea in the southwest Atlantic sector of the Southern Ocean (Figure 1a). As such, it sits within the zonation of the Antarctic Circumpolar Current (ACC), with the Southern ACC Front (SACCF) being located particularly close to the island (e.g. Thorpe et al., 2002; Meredith et al., 2003). Interannual variability of ocean temperatures close to South Georgia has been linked with ENSO events (Trathan and Murphy, 2003; Meredith et al., 2005; Meredith et al., in press), and more recently with the SAM (Meredith et al., in press). Long-period (decadal-scale) changes in the ocean temperatures around South Georgia are also evident, with a pronounced warming observed from the 1920s up to present (Whitehouse et al., submitted).

Despite the growing understanding of oceanographic changes in this area, the general absence of long-term plankton data sets make it difficult to assess the impact that atmospheric/oceanic coupling may have had on pelagic marine communities at decadal and longer timescales. To compound this difficulty, Antarctic marine ecosystems have already been subjected to dramatic anthropogenic change within the last century, with disruption of ecosystem function having occurred through the exploitation of whales and seal populations and latterly through the exploitation of fish and krill stocks (Atkinson et al., 2001).

The earliest comprehensive sampling programme at South Georgia was undertaken by Discovery Investigations in the 1920s as part of a series of commissions aimed at gaining a greater scientific understanding of the whale stocks and their summer feeding grounds (Kemp, 1929). The initial survey, undertaken in December 1926/January 1927, was described by Hardy and Gunther (1935) with one of their stated objectives being, ‘To describe the actual distribution of these species at the time of the survey for comparison with surveys in later years’ (p.361). Although further surveys were undertaken in the late 1920s and early 1930s no explicit community comparison between years was made. In the South Georgia region, whaling stations ceased operation in the 1960s, but commercial fisheries targeting fish and krill commenced working alongside dense colonies of dependent predators. Soviet work on plankton and hydrography continued in the region through this period (e.g. Bogdanov et al., 1969; Maslennikov, 1972; Vladimirskaya, 1978), with renewed interest in exploiting the living resources of the Southern Ocean (principally fin-fish and krill; Everson, 1977) during the 1970’s, leading to new research initiatives aimed at achieving a more general understanding of the Southern Ocean marine ecosystem (El-Sayed, 1994). Pelagic scientific research, once again aimed at understanding the plankton and its interactions with predators with a focus around South Georgia, recommenced in the late 1970s. During the period 1995-2005 a series of cruises undertaken by British Antarctic Survey (BAS) around South Georgia provided plankton data with which we can assess interannual variability and that we can compare to the initial survey results obtained some 70-80 years previously.

Our objectives in making a comparison were first to investigate patterns of community distribution in the early samples and to compare these with our recent understanding of the ecosystem, and second to test whether there was any evidence that the plankton had changed in either a qualitative or quantitative way in the intervening period.

2. Methods

The 1926/27 survey comprised a series of 7 transects (Fig. 1b), along which stations were located at approximately 10 nautical mile intervals. These commenced 5 miles from the coast and ended when soundings of 1000 m or more were encountered. Stations along transects were sampled by two ships, namely the Discovery and William Scoresby. Stations along transects A-E were worked on the north side of the island between 17th-23rd December 1926 and stations along transects F and G, on the southern side of the island, between 7th-21st January 1927 (Fig. 1b). In the January survey, line B (first surveyed in December) was extended to include stations B4 (2) and B9, the latter some way north of the other stations but which we have included in our analysis, making a total of 46 stations. Data obtained during 7 BAS cruises around South Georgia (Fig. 1c and Fig. 2), undertaken during December and January within the period 1995-2005 were compared with Discovery data. Although regional coverage differed between cruises, and no one cruise gave a synoptic view of the entire shelf and surrounding ocean, samples were collectively obtained within the same general area. Sample numbers within cruises varied from 11- 57 with a total of 189 stations across all 7 cruises.

2.1 Physical Oceanography

At the Discovery stations, hydrographic measurements were made at standard depths using water bottles (Nansen-Petterson and Ekman reversing bottles) (Kemp et al., 1929). Temperature was read via a thermometer inserted into the top of the insulated water chamber in the former and by reversing thermometers in the latter. Salinity was determined by titration against a solution of silver nitrate of known strength. Temperatures and salinities are accurate to +/- 0.01 deg C and 0.01 respectively. Contemporary physical oceanographic data were collected with Conductivity-Temperature-Depth (CTD) instruments, namely a Neil Brown Mk IIIB CTD (prior to 1999) and a SeaBird 911plus (1999 onwards). CTD salinities were calibrated using discrete samples drawn from a 12 bottle rosette and analysed on a Guildline Autosal 8400 (prior to 1999) and 8400B (1999 onwards). CTD potential temperatures and salinities are accurate to +/- 0.002 degC and 0.002 respectively.

2.2 Sample collection and treatment

During the course of the Discovery survey three types of net were employed, a 50 cm dia net (N50V) used to capture phytoplankton, constructed with 200 meshes per linear inch (mpi), equivalent to ~60 µm, a 70 cm dia net (N70V) used to sample mesozooplankton and made with 2 grades of silk netting 40 mpi (~350 µm) in the foremost part and 74 mpi (~200 µm) behind, and a coarser net of 1m dia (N100H) with mesh openings of up to 4 mm in the main part of the net, which sampled macroplankton whilst being towed horizontally at 2 kts. Information regarding net construction and deployment are provided by Kemp et al. (1929). All 3 nets were deployed at full routine stations, but here we are concerned only with the N50V which was lowered to 100 m and then hauled vertically to the surface at 1 m sec^{-1}, and the N70V which was equipped with a throttling rope and messenger system and so could be used to fish discrete depth horizons. Dependent on water depth, up to 6 samples were obtained as follows, 50 m to surface, 100-50 m, 250-100 m, 500-250 m, 750-500 m and 1000-750 m. Samples from both nets were preserved in formalin. In the laboratory, the N50V samples were diluted to a definite volume, 50, 100 or 150 ml according to bulk and then sub-sampled with a 0.5 ml stempel pipette. In extreme cases further dilutions were necessary. The contents of the pipette were then placed into a slide counting chamber and examined under a microscope using a 2/3in objective (equivalent to a primary magnification of 10x) or if small forms dominated a 1/6in objective was used (equivalent to a primary magnification of about 42x) (Dr Brian Bracegirdle pers comm.). Coupled with a 10x eyepiece this would have provided 100x and 420x magnification respectively, which is comparable to that used in similar analyses undertaken today. N70V analysis consisted of removing larger organisms (>2 mm) from samples followed by an examination for rarer taxa before sub-sampling with a stempel pipette. Full details are provided in Hardy and Gunther (1935). Overall data from a total of 43 stations were used in the N50V and 46 for the N70V analyses.

During 7 BAS cruises mesozooplankton were sampled with a paired bongo net of 0.62 m dia equipped with a 200 μm net which was deployed vertically from 200 m (or near bottom if water depth <200 m) to the surface. Numbers of samples across cruises varied from 11-57 (total n =189 across 7 cruises) and were restricted to those taken within the region sampled by the 1926/27 Discovery surveys. Samples were preserved in formalin and analysed according to protocols detailed in Ward et al. (2005).

2.3 Taxonomic issues

Before data analysis commenced a number of taxonomic inconsistencies needed to be resolved between the Discovery and BAS samples. Foremost was the identification by Andrew Scott, who analysed the copepod fraction of the Discovery samples, of the most abundant species of *Oithona* (Copepoda:Cyclopoida) taken around South Georgia in 1926/27 as *Oithona frigida,* and the observation that *Oithona similis,* which is abundant throughout much of the World's Oceans, including the Southern Ocean (Atkinson, 1998; Galliene and Robins, 2001; Ward and Hirst, 2007), was only encountered at one station north of the Polar Front. Hardy and Gunther (1935) also thought this curious (p189), as did Vervoort (1951), particularly as *O. similis* had previously been widely recorded between New Zealand and the Antarctic continent by Farran (1929). To clarify this we examined 0-50 m samples from four Discovery stations (1201, 1202, 1204, 1211) taken around South Georgia in November/December 1933 to see which species was abundant and found only *O. similis*. We therefore think it highly probable that *O. similis* Claus (1866) was identified erroneously as *O. frigida* Giesbrecht (1902). *Oithona similis* is by far the commonest species identified in contemporary collections around South Georgia and elsewhere in the Southern Ocean (Metz, 1996), and it seems inconceivable that such a major shift in distribution occurred in the 7 years following 1926/27. However, hereafter we refer to both species as *Oithona* spp. although *O. similis* greatly outnumbered *O. frigida* in BAS collections. Other taxonomic issues generally involve the renaming of taxa in the 80 years that have elapsed since Scott's analysis. *Drepanopus pectinatus* at South Georgia is now recognised as *Drepanopus forcipatus,* the former only occurring at islands in the Indian Ocean sector of the Southern Ocean (Hulsemann, 1985). *Eucalanus acus* Farran (1929) is now *Subeucalanus longiceps* Matthews (1925) (Razouls, 1995). *Microcalanus pygmaeus* and *Microcalanus* sp. were considered by Scott to be two separate species. However, Vervoort (1957) considers that only a single species exists, and we have accordingly pooled Discovery counts as *M. pygmaeus*. Within BAS collections we have only recognised a single species. *Clausocalanus arcuicornis,* listed as present at South Georgia in 1926/27 is presently widespread in tropical and subtropical waters (Bradford-Grieve et al., 1999) and was therefore probably mistakenly identified. We have elected to keep the category *Clausocalanus* sp. as there is one other species (*Clausocalanus brevipes*) which has been occasionally encountered around South Georgia in recent collections. Within euphausiid species, adult and cyrtopia stages (stage subsequent to furcilia and pre-adult see Dilwyn John, 1936) were combined into a single postlarval category (adult/subadult). In the case of *Thysanöessa vicina* and *T. macrura,* which are extremely difficult to tell apart (Ward et al., 1990), and in which furcilia are frequently damaged during sampling, both species and furcilia were pooled into a single *Thysanoessa* spp. category. *Salpa fusiformis* var. *aspera* Chamisso (1819) is now recognised as *S. thompsoni* Foxton (1961).

2.4 Data treatment

Discovery net catch data are provided in Appendices I (Phytoplankton) and II (Zooplankton Table1) of Discovery Report 11 (Hardy and Gunther, 1935). Only the most ‘important’ taxa were included in the phytoplankton table and total sample estimates were provided along with an indication of the fraction examined so that the reader can make their own assessment of the numbers counted (Hardy and Gunther, 1935). A total of 32 phytoplankton taxa are provided in the table out of a total of 90 taxa recorded during the survey. Likewise for the N70V zooplankton samples, total catch data are provided for the 54 most abundant taxa and the distribution of less important species is given in the text.

For the current analysis data from both tables were input into taxa by station matrices and in the case of the zooplankton, those less abundant species indicated in the text were also included, giving a total of 73 taxa. To facilitate a comparison of the Discovery and BAS zooplankton data we grouped the former into categories routinely used in the analysis of BAS data. We achieved this by aggregating some species into higher taxonomic groupings, resulting in a total of 55 compatible categories (see Appendix II). However, a number of Discovery taxa were not counted in the BAS samples, notably Foraminiferans and Radiolarians, which collectively contributed around 7% of total abundance. They were left in the zooplankton matrix for the initial community analysis of the Discovery data but were omitted from later comparisons (see below).

Discovery phytoplankton counts were directly input into the matrix as each net routinely fished to 100 m. Abundances of Discovery zooplankton catch data (per m^{-3}) were integrated from surface to 250 m (or near bottom if shallower) prior to analysis. BAS data sampled within the top 200 m (or near bottom if shallower) was standardised in the same way. Any depth mismatch between the two data sets is unlikely to result in systematic error as during the summer months most of the plankton around South Georgia is located within the top 200 m (Ward et al 1995).

In order to characterise and assess the depth distribution of the plankton in 1926/27, four large interzonal calanoid copepods, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus simillimus* and *Calanus propinquus* were chosen and a comparison was made by averaging across 13 Discovery hauls taken in water > 750 m deep. The proportion of species populations resident in the top 250 m was then compared with similar data obtained from a Longhurst Hardy Plankton Recorder (LHPR) during a cruise to the area undertaken in January 1990 (Ward et al., 1995).

2.5 Data analysis

Phytoplankton cell counts and mesozooplankton data were initially analysed independently with the statistical package PRIMER 5 (Primer-E Ltd). In both analyses data were restricted to those taxa that contributed ≥ 2% abundance at any of the stations. For phytoplankton this procedure reduced the number of taxa from 32 to 18 and for zooplankton from 55 taxa to 24. Cell counts and standardised (ind. m^{-3}) zooplankton data were then $\log_{10}$ transformed and subjected to *q* type cluster analysis based on the Bray-Curtis similarity and group average linkage classification (Field et al., 1982). The SIMPER (similarity percentages) routine was also performed on both data sets. SIMPER examines how much each species/taxa contributes to the average sample similarity within, and dissimilarity between groups (Clarke and Warwick, 2001).

To assess interannual variability we examined zooplankton abundance at a series of 6 stations, located at the northwestern end of South Georgia, which were sampled during at least six of the of the seven BAS cruises (see Fig.1c). Data from only 5 of these stations were available for cruise years 1995/96 and 1996/97. We estimated the variance components for cruises, stations and the residual to assess which component influenced our comparison most.

The statistical analysis uses a linear model in which the log abundance is expressed as a sum of random effects for cruise, station and residual, i.e. if y_{ij} denotes the log abundance for the *i*th station in the *j*th cruise

$$y_{ij} = m + s_i + c_j + \varepsilon_{ij}$$

where m denotes an overall mean $\log_{10}$ abundance, s_i is a random effect for the *i*th station, c_j is a random effect for the *j*th cruise, and ε_{ij} is a residual random effect. Random effects are assumed to vary independently with zero mean and variances V_s, V_c and V_e, respectively. The model was fitted using the statistical programme GENSTAT with variance components estimated by REML (Residual Maximum Likelihood).

In comparing BAS and Discovery data we attempted to minimise spatial variation by selecting BAS stations close to the original 1926/27 Discovery positions as follows. Distances between the Discovery stations and those sampled during the BAS cruises were calculated, and 40 km chosen as the maximum distance within which comparisons could be made. This choice reflected a balance of reasonable proximity without overly reducing the number of Discovery stations. Where two or more 1926/27 stations had the same matched station in any one BAS cruise the nearest was used. This procedure resulted in 36 of the Discovery stations with a matching station in one or more of the BAS cruises (see Fig. 2).

Comparison of abundances between the 1926/27 and BAS cruises was then based on the above statistical model modified to allow the mean level in log abundance to depend on the cruise, i.e. $m = m_1$ ($j = 1$; 1926/27 cruise) and $m = m_2$ ($j = 2,\ldots,8$; BAS cruises JR11,17, 28, 38, 57, 70 and 116). The difference between cruises in the two periods $d = m_2 - m_1$ corresponds to a ratio of abundances $R = 10^d$.

In addition we calculated the percentage similarity index (PSI: Whittaker, 1952; Rebstock, 2001) of taxa across cruises rather than make simplistic comparisons between individual species on the basis of their absolute abundance. To achieve this we harmonised Discovery and BAS taxonomic categories as follows. In addition to foraminiferans and radiolarians (present in contemporary samples but not routinely counted, see above) other taxa were also either ignored, because they were not routinely counted in one or other of the analyses (e.g. copepod nauplii stages were not enumerated in Discovery samples), or aggregated into higher taxonomic groupings (e.g. euphausiid cyrtopia, a stage not routinely distinguished/recognised in contemporary samples). A common matrix of 45 remaining taxa resulted (see Appendix II) and the percentage contribution of each to the overall abundance across all stations within a cruise was determined. This was deemed a robust measure as data were averaged over the entire cruise area and would therefore integrate any interstation/regional variability. Initial analysis showed that the inclusion of *Drepanopus forcipatus* had a marked effect on the subsequent calculation of PSI. We know that this species was present over the shelf in 1926/27 as well as in contemporary samples but its patchy distribution across all cruises

(0.3-45% of total abundance) was problematic, so to avoid any unnecessary bias it was omitted from the data matrix used to calculate PSI.

The PSI index is given as

$PSI = 100 - 0.5\Sigma|Ai - Bi| = \Sigma\min(Ai,Bi)$,

where $A_{i'}$, B_i = the percentage of species i in samples A and B respectively.

3. Results

3.1 Physical Oceanography

Figure 3 shows the potential temperature/salinity characteristics of the 1926/27 Discovery Expedition data (marked as black crosses) in comparison with the recent series of BAS cruise data (coloured lines). The water mass characteristics are typical of those generally observed in this sector of the Southern Ocean (c.f. Meredith et al., 2005). The deepest (densest) layers seen adjacent to South Georgia have potential temperatures colder than 0 ºC and salinities in the range 34.65-34.67. This is Weddell Sea Deep Water, the densest component of the Antarctic Bottom Water that penetrates into the South Atlantic by traversing the Scotia Sea. Above this lies the comparatively warm and saline Circumpolar Deep Water (CDW), the upper and lower components of which have potential temperatures as high as 2 ºC and salinities of the order of 34.70 respectively. Close to South Georgia, Southeast Pacific Deep Water has also been observed (e.g. Meredith et al., 2001), though this is most obvious in measurements of tracers (e.g. dissolved silicate), and is not so easily distinguishable from CDW on the basis of potential temperature and salinity data.

Above CDW lies the surface and near-surface layers that are commonly referred to as Antarctic Surface Waters (AASW). During summer, when all the measurements used here were collected, AASW can be as warm as 4 ºC at the very surface, but is more often closer to 2 ºC. Below the very surface, summertime AASW includes a marked subsurface potential temperature-minimum layer at around 50-150 m depth; this is remnant of the previous winter's deep mixed layer, and is commonly referred to as Winter Water (WW). WW potential temperatures close to South Georgia lie in the range -1 to 1 ºC, with salinities of approximately 33.9-34.0 (Figure 3).

With regard to changing water mass properties close to South Georgia, it is immediately obvious from Figure 3 that the 1926/27 Discovery Investigations data are cold in the upper layers, specifically the surface waters and WW layer. The 1926/27 data compare most closely with data collected during Jan-Feb 1998 (Cruise JR28; green lines). Other recent data from BAS cruises are warmer, by 1°C or more in the WW layer. We comment on the cause of these changes in section 4.1.

3.2 Phytoplankton

The results of the nearest neighbour clustering of Discovery phytoplankton data are illustrated in Fig 4a. and the corresponding geographical distribution of station groups (Gps) illustrated in Fig. 4b. The results are similar to Hardy and Gunther's (1935) grouping of stations which was most likely on a subjective basis (Fig. 4c). Gp1 is represented in our analysis by two stations, one of which was classified as an outlier in Hardy and Gunther's original analysis. They were both characterised by high abundances of *Rhizosolenia styliformis* and *Corethron criophilum* (Table 1). Gp 2 was located at the western end of the shelf and species of *Corethron*; *C. socialis*, *C. valdiviae* and *C. criophilum* were dominant. Gp 3 was largely present over the northern shelf and was dominated by *C. valdiviae* and Gp 4 to the east, on and around the edge of the eastern shelf, where a more diverse flora was apparent (Table 1). Gp 5 was characterised by low abundances of many taxa and included several near coastal stations. An outlying station in both analyses (B9, Gp6 in Fig 3b) was characterised by the presence of *Chaetoceros schimperianus.* Phytoplankton biomass measurements during the 1926/27 surveys were restricted to cell counts and settled cell volumes. Close congruence between these two variables existed with both highest in a broad swathe over the southern shelf with a small pocket of enhanced levels between transects B and C on the north side of the island.

3.3 Zooplankton

The results of the nearest clustering of the zooplankton data and a map showing the geographical location of station groups are shown in Figs. 5a and 5b

Gp 1 (13 stations) was mainly located over the inner shelf and along lines E, F and G (Fig. 1b). It was characterised by high abundances of *Drepanopus forcipatus* which accounted for 58% of within group similarity followed by *Oithona* spp. (35%). *Drepanopus* is typically a neritic species and its average abundance in Gp 1 is over 10 times greater than in all other groups with the exception of station 126 (Gp 5) which was also located over the inner shelf. As a result of its presence, combined average abundance (m^{-3}) was highest within this group (Table 2).

Gp 2 (12 stations) comprised the outermost stations mainly located in oceanic water >500 m deep along lines C-G. Four taxa, *Oithona* spp., Foraminifera, *Ctenocalanus vanus*, and

Calanoides acutus contributed 89% of within group similarity and these, plus many of the other taxa within this group, had higher average abundances than in other groups (Table 2).

Gp 3 (16 stations) occupied stations to the north and west of the survey area (predominantly transects A-C) along the middle and outer shelf. Stations were characterised by modest abundances of *Oithona* spp., and *Ctenocalanus vanus* and average total abundance (m^{-3}) across all groups was the lowest of the 3 main groups.

Gp 4 (4 stations) were widely spaced and were characterised by extremely low average abundances of *Oithona* spp. and also *Ctenocalanus vanus*.

The relative abundance of zooplankton (ind. m^{-3}) within the survey area is shown in Fig. 4c. Highest abundances were seen at near-coastal stations towards the southeast of the island (mainly station group 1) where *D. forcipatus* was abundant. Elsewhere, lower abundances were seen, particularly at stations affiliated to Gps 3 and 4 (See Table 2).

3.4 Interannual variability and a comparison between Discovery and BAS data

Of the total variation in log abundance at the 6 stations sampled across 7 BAS cruises, 32% was attributable to cruise, 9% to station and 59 % to residual variation (Table 3) i.e. of the two components (cruise and station), cruise, although not as large as residual variation, was proportionately larger than station position. Variation between cruises was statistically significant ($F_{6,28} = 4.16$, $p = 0.004$).

In assessing whether the Discovery and BAS data differed we have firstly restricted our comparison to BAS stations occurring within 40 km of Discovery stations.

In this case the estimated difference was $d = 0.60$ (se = 0.33, $p = 0.071$) with corresponding ratio $R = 4.0$ (Table 3). Note, however, that the p-value is likely to be too small because the test is approximate as it ignores the uncertainty in the estimated variance components. A more conservative approach based on the 6 degrees of freedom of the variance component for cruises gives $p = 0.12$.

A comparison using all the BAS and Discovery data (ignoring station effects) gives $d = 0.48$ (se = 0.37, $p = 0.19$) (Table 3).

A comparison of $\log_{10}$ mean abundance with respect to year of all stations sampled (Fig.1c), those within 40 km of the Discovery stations (Fig. 2) and the nominal six stations sampled each year to the NW of South Georgia during BAS cruises (Fig. 1c.) is made in Figure 6. There is generally a close agreement between values within years, particularly with respect to the full data set and those matched within 40 km of Discovery stations. The values for the nominal 6 stations sampled to the NW of South Georgia also reflect interannual trends.

3.5 Percentage Similarity Index analysis

The results of the PSI analysis investigating whether differences in taxonomic composition were apparent between cruises are illustrated in Fig. 7. Here PSI values are plotted as a sequential series starting from 1926/27 and finishing in 2005. With one exception, mean PSI value for all cruises ranged between 70-80%. PSI is strongly influenced by the most abundant species (Rebstock, 2001) and the decline in the average PSI during 1998/99 was largely due to the presence of higher proportions of pteropods (*Limacina* spp.) (average 28%) and a correspondingly lower proportion of *Oithona* spp.

(26%). This cannot be construed as a systematic change as the mean value reverted to its more normal range following this anomalous year.

Rank order of mean percentage occurrence across cruises is given in Table 4. Given that the PSI is strongly influenced by the dominant species it is possible that there are more subtle changes occurring. For example the colder summer temperatures experienced in 1926/27 (~1.5°C < contemporary cruise data; Whitehouse et al. submitted) may have influenced the development of zooplankton populations. In the absence of stage frequency data in 1926/27 we compared the rank order of abundance of 4 species of large calanoid copepods across all cruises and found it differed in 1926/27. *Calanus propinquus*, second in rank order in 1926/27, was ranked a distant fourth in all contemporary cruises.

A comparison of the proportion of the large interzonal calanoid copepods resident within the top 250 m compared to the rest of the sampled water column, revealed a much lower percentage of the *R. gigas* population present in the top 250 m in the 1926/27 season compared to 1990, although it appeared not to have impacted upon the other 3 species. With the exception of *Rhincalanus gigas*, which had a lower average percentage in the top 250 m in Discovery samples, the remaining 3 species had similar proportions of the population present in both years (Table 5).

4. Discussion

4.1 Physical oceanography

We investigated oceanographic conditions around South Georgia in order to assess the cause and extent of physical change in the last 80 years. The upper ocean was ~1°C colder in 1926/27 than in most of the more recent BAS cruises, with 1998 being the sole exception. We do not believe that the warming observed is due to changes in the location of the local frontal systems (in particular the SACCF) around South Georgia, since there is no evidence from deep water properties (especially those of CDW) for such a shift, and these are the most reliable local indicators of local fronts (see Meredith et al., 2003, following Orsi et al., 1995). In practice, our modern concept of the local circulation system based on data from the 1990s/early 2000s, with the SACCF looping anticyclonically around South Georgia from the south before retroflecting to the east (Fig. 1a), is supported well by the 1926/27 Discovery data. Thus, whilst nomenclature may have changed since the days of Deacon (1933; 1937), the flow patterns in this part of the Southern Ocean have not. This contradicts Hardy and Gunther's (1935) view that the colder parts of their survey were influenced by waters from the Weddell Sea.

Another potential cause of the observed temperature differences could be interannual variability related to coupled modes of climate variability. In this context, Meredith et al. (2005) discussed in detail the causes of the colder temperatures encountered during Jan-Feb 1998 compared with other recent cruises around South Georgia, and concluded that they were caused by the strong El Niño event of 1997/8. Both oceanic and atmospheric teleconnections were found to be important, and processes controlling these teleconnections were elucidated further by Meredith et al. (in press), with emphasis on explaining the timescales of variability. Evidence for a similar event during 1926/27 is equivocal. Using various proxies, Quinn et al. (1987) have found evidence for an El Niño during 1925/26, and the timescales of the oceanic teleconnection are such that this could feasibly have influenced the region around South Georgia in

1926/27. However, examinations of various atmospheric measures of ENSO (including the Southern Oscillation Index, and individually the Darwin Mean Sea Level Pressure) shows little evidence for such an event (Phil Jones, Climatic Research Unit, University of East Anglia, pers. comm.)

A further potential cause of the observed temperature change could be a long-period (decadal) warming trend in this part of the Southern Ocean. This would be consistent with the observation that ocean temperatures around South Georgia in 1926/27, although cold by present standards, were not unusually cold compared with the rest of the sequence of Discovery Investigations to this region (1925-1937 inclusive; see Deacon, 1977). Such a trend is also consistent with the work of Gille (2002; 2008) who indicates a substantial surface-intensified warming around the circumpolar Southern Ocean since the 1950s, and Whitehouse et al. (in press) who compared all available data from around South Georgia (including the Discovery data) and derived a warming in excess of 1°C in the upper 200m in this region.

Overall, it seems that the apparent warming we observe is most likely due to a long-period (decadal) warming trend in this sector of the Southern Ocean, with the possibility of some interannual variability also contributing. Shifts in frontal positions do not appear to be a contributory factor. The causes of the warming trend are explored in more detail by Whitehouse et al. (in press).

4.2 Phytoplankton

There was close agreement between Hardy and Gunther's station classification with regard to phytoplankton composition and that of the nearest neighbour clustering suggesting distinct differences between station groups. Hardy and Gunther (1935) linked their station groupings to what they saw as the dominant water masses in the region ie Weddell Sea and Bellingshausen water and areas of mixing between the two. Of the major groups, Gp2 and Gp3 were thought to occupy areas of mixing over the southwestern and northern shelf areas respectively, whereas Gp4 was thought to be of Weddell Sea origin. Stations affiliated within Gp5 were located in coastal waters. As indicated above there is no evidence of the occurrence of Weddell Sea water *per se* within the region, although a number of less common species of diatoms (see Hardy and Gunther, 1935, Fig. 36) are almost exclusively contained within the generally colder waters of Gp 4, suggesting a distinct oceanic origin, similar to the distribution of zooplankton Gp 2. In a later survey around South Georgia, undertaken in spring 1981, Theriot and Fryxell (1985) and Priddle et al. (1986) both considered that large-scale phytoplankton species distribution reflected the interaction of the ACC with the island and the Scotia Ridge, upon which were superimposed small-scale factors such as nutrient availability and grazing, imposing local variation. A similar interpretation was proposed by Froneman et al. (1997) for observations made during January/February 1994. The existence of distinct shelf and oceanic communities at South Georgia has been observed by Ward et al. (2007) and differing distributions of dominant species *Fragilariopsis kerguelensis* and *Eucampia antarctica* attributed to Fe limitation (Whitehouse et al., 2008).

4.3 Zooplankton

Hardy and Gunther (1935) broadly contrasted the differences between coastal plankton dominated by *Drepanopus* and oceanic waters with deepwater forms such as *Metridia* and *Scolecithricella*. Their hypothesis that the phytoplankton groups might have characteristic faunas associated with them was confounded to an extent by what was seen as the 'remarkable sameness' of the zooplankton with respect to the phytoplankton groups. The major groupings of stations identified by nearest neighbour clustering of zooplankton data are, however, consistent with many of the more recent surveys carried out around South Georgia. Shelf groupings of stations, often characterized by *D. forcipatus* have been observed previously (e.g. Atkinson and Peck, 1988; Ward et al., 2002; 2005; 2007) although its patchy distribution and interannual variation in abundance means that it does not always dominate in the way that it did Gp1 in the 1926/27 survey. The shelf at South Georgia is extensive and it has been suggested that slow flow and limited exchange with oceanic waters can lead to a build up of production (Atkinson and Peck, 1988; Meredith et al., 2005) which can be retained over the shelf for periods in excess of 3 months (Ward et al., 2007). To the north of the island, groupings of stations consistent with different water masses either side of the SACCF have also been observed (Ward et al 2002; 2005), although in 1926/27 transect lines did not extend far enough offshore to cross the frontal region. There was nonetheless a degree of congruence between phytoplankton and zooplankton station groups as determined by nearest neighbour clusterings. Although zooplankton Gp1, largely reflecting the dominance of *D. forcipatus,* comprised stations that were variously affiliated to phytoplankton Gps 2, 3 and 4, there was a stronger correspondence between zooplankton Gp 3 (n=16) and phytoplankton Gp 3 (n=14) which had 10 stations in common, as did zooplankton Gp2 (n=12) and phytoplankton Gp 4 (n=13). This may reflect a common origin, in the case of the former groups, in 'mixed' water to the north and west, and in the latter, of oceanic water to the south and east. However, it should be emphasized that primary and secondary producers will inevitably develop over different spatial and temporal scales, which when coupled with advection in oceanic water, will tend to obscure relationships. As in all such mesoscale investigations, whilst differences between groups are often distinct they tend to represent variations in abundance of a common set of taxa rather than more fundamental shifts in community composition (Mackas and Sefton, 1982; Marin, 1987; Pakhomov et al., 2000).

4.4 Interannual variability

The analysis of inter-annual variability based on the six stations from the BAS cruises showed that although variance attributable to cruise exceeded that due to station, ignoring station effects could lead to a confounding of spatial and temporal variation. Having restricted our comparison with Discovery data to BAS stations lying within 40 km of the original Discovery station positions to allow for spatial variation, large interannual variations in zooplankton abundance were still apparent which meant that despite having the lowest abundance across all years, data from 1926/27 nonetheless fell within the range displayed by contemporary data.

Low abundance in 1926/27 may be partly attributable to differences in equipment. Although the N70V has a rear section of approximately 200 μm mesh, the front section is somewhat larger at ~350 µm which could lead to an under-sampling of the smaller forms relative to the bongo net (200 µm mesh) used for the contemporary hauls. Equally the timing of sampling in relation to season and the developmental cycles of the plankton will be reflected in abundance (see Ward et al., 2006a). There is no information on developmental stage structure available for season 1926/27, although being a cold year, population development may have been slow.

The PSI analysis indicated that there were no obvious differences between contemporary data and that from1926/27. With the exception of cruise JR38 (1998/99) when the mean PSI value fell to just over 60%, due to high abundances of the pteropod *Limacina* spp. in that year, it was consistently between 70-80%. In comparisons of this sort, survey timing and spatial coverage can influence results. As far as timing is concerned we have restricted our comparison to cruises that took place in either December or January, although interannual variations in zooplankton abundance were very apparent (see also Shreeve et al., 2002). This is unsurprising given that the occurrence of zooplankton at South Georgia results from the variable balance of advection and *in situ* production (Ward et al., 2007). However the stability in taxonomic composition observed at South Georgia further suggests that populations are advected from source regions that are themselves stable in this respect.

Spatial coverage was also variable between cruises, with a greater proportion of oceanic stations sampled during BAS cruises. It is possible that localized sampling may influence regional estimates of certain taxa e.g. population development and hence abundance of large calanoids was found to vary regionally during the course of at least one previous summer investigation (Atkinson, 1989). Nonetheless given these caveats it appears that the mesozooplankton population has been relatively stable at least in terms of the dominant taxa since the 1920's. However, given that the PSI is strongly influenced by the dominant taxa it possible that more subtle changes may be occurring. By aggregating species into higher taxa a certain amount of information is 'lost' in the comparison but as can be seen from Table 4, relatively few taxa dominate the mesozooplankton, the majority comprising considerably <1% of total abundance. Many of the zooplankton found within the ACC have wide spatial distributions although tend to reach maximum abundance within one or other of the various water types (Atkinson, 1991; Atkinson and Sinclair, 2000). Of the four main biomass-dominant species of calanoid copepod, *Calanus propinquus*, which is more abundant within the colder parts of the ACC and was the least abundant of the four in contemporary South Georgia samples, was second most abundant in 1926/27. The significance of this finding is unknown. Its higher relative abundance in 1926/27 may have been due to their presence in colder water to the south of the ACC and/or alternatively cooler water may have retarded the population development of the warmer water species *Calanus simillimus* and *Rhincalanus gigas*. In summer these species are all largely active in the near-surface layers but the timing of the ascent of overwintered stages varies between species, and also it appears, between years. Ward et al. (2006b) found that the slow retreat of the pack-ice edge in the Scotia Sea during summer 2003 was characterised by populations of over-wintered copepods compared to years when the ice retreated broadly in line with the 25 y mean and a spring generation was present. The absence of information on population stage structure makes such observations difficult to set in context, but in the only comparably cold year within the contemporary data series (Cruise

JR28, 1998), *C. propinquus* was least abundant. However, cold conditions in this year appear to have resulted from an ENSO event propagating through Drake Passage rather than cold waters spreading from further south where *C. propinquus* is regionally more abundant.

4.5 Long-term change

Whilst physical changes in the Southern Ocean are becoming increasingly apparent and regional warming trends documented, particularly at the Western Antarctic Peninsula (Smith et al., 2003; Meredith and King, 2005;Meredith et al., in press), the consequences for the marine ecosystem are largely unknown due to the lack of long-term studies (Clarke et al., 2007). Convincing evidence of changes in population size and distribution of vertebrate predators has been demonstrated (Reid and Croxall, 2001; Croxall et al., 2002; Ainley et al., 2005), in which commercial fishing pressure may also be implicated but impacts on the plankton are less clear. In contrast, extensive climatically induced changes in North Atlantic plankton communities over the last 40 years, have been recently described by Beaugrand et al. (2002). Using Continuous Plankton Recorder (CPR) time-series data it was shown that ecosystems of the northeast North Atlantic have changed towards a warmer dynamic equilibrium whereas those in the northwest Atlantic ecosystems have shifted towards a colder dynamic equilibrium, particularly in the Sub-arctic gyre. In the Southern Ocean, krill abundance in the Scotia Sea has declined over the last 30 years and an increase in salps has occurred (Atkinson et al., 2004), against a background of rising sea temperature. The possibility of change within the plankton elsewhere in the Southern Ocean has been suggested by Kawamura

(1986; 1987). He compared historical and contemporary N70V catches from the Indian Ocean sector and concluded that although there had been little change in plankton biomass since Discovery days, the abundance of large calanoids had decreased dramatically. However, this perceived decrease was principally based on comparisons with Discovery samples from South Georgia and the Scotia Sea where subsequent research has demonstrated the presence of high standing stocks of plankton, particularly copepods, relative to other parts of the Southern Ocean (Atkinson, 1998). In a later study Vuorinen et al. (1997) compared the spatial and temporal variation of copepods in the Weddell Sea based on samples taken in 1929-1939 and 1989-1993. Their comparison of samples taken with N70 (V) and WP2 (200 μm mesh) nets, while finding no change in overall abundance between periods, did detect recent increases in the abundance of *Calanus propinquus* juveniles and adults. However, other changes were only marginally significant and they concluded that overall there were no uniform and consistent changes that could be linked to environmental change; in particular with their hypothesis that a putative krill surplus, consequent to the harvesting and demise of whales (Laws, 1977), should have trophically disadvantaged copepods.

The consequences of over-exploitation of top predators in the Southern Ocean for ecosystem structure and function are presently unclear (Croxall et al., 2002; Ballance et al., 2007), as we have a limited understanding of what conditions were before sealing and whaling began. Warming of the South Georgia ecosystem has taken place in common with other parts of Southern Ocean (Whitehouse et al., in press, c.f. Gille, 2002; Gille, 2008) and there have been changes in the abundance and distribution of many of the top predators (Reid and Croxall, 2001), as well as more recent commercial exploitation of fin-fish and krill (Agnew, 2004). Whilst krill abundance has declined over the last three decades (Atkinson et al., 2004), this study is unable to conclude whether similar declines in mesozooplankton abundance have taken place, although taxonomically the composition appears stable.

There is a lack of appropriate time-series in the broader Southern Ocean against which change in the mesozooplankton can be gauged. However, there has been an advent of new sampling initiatives (foremost among them the CPR; Hosie et al., 2003), aimed at establishing base-line measurements against which secular change can be viewed. These are strongly welcomed, and we urge their continued implementation.

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Figure legends

Fig.1. The study area

Fig. 1a. South Georgia located in the Scotia Sea. APF = Antarctic Polar Front, SACCF = Southern Antarctic Circumpolar Current Front, SB = Southern Boundary. The 2000 m and 500 m isobaths are shown by the pale and dark tones respectively.

Fig.1b. Positions of 46 stations sampled during the December 1926/ January 1927 survey undertaken by RRS Discovery and RSS William Scoresby. Original station nomenclature is given in Figure 13 (p 22) of Hardy and Gunther (1935).

Fig.1c. Stations sampled during seven British Antarctic Survey cruises undertaken between 1995-2005. The six stations circled to the northwest of South Georgia were sampled during each of the cruises

Fig. 2. Stations sampled by cruise. The filled circles on each panel indicate BAS stations that lay within 40 km of the Discovery station positions and also the 36 matched Discovery stations (see methods). Open circles are stations without a match. 1995/96-cruise JR11 (11 stations), 1996/97-cruise JR17 (14 stations), 1997/98-cruise JR28 (16 stations), 1998/99 –cruise JR38 (17 stations), 2000/01-cruise JR57 (39 stations), 2001/02-cruise JR70 (45 stations), 2004/05-cruise JR116 (57 stations).

Fig. 3. Potential temperature/salinity characteristics of waters sampled during the 1926/7 Discovery Expedition around South Georgia (black crosses), plotted alongside more recent data (1996-2001) collected from this same region by the British Antarctic Survey (coloured lines). Discovery data are from discrete bottle measurements, whereas recent data are from 2-dbar averaged hydrographic data. Contours of density anomaly are marked in the background. AASW = Antarctic Surface Water, CDW = Circumpolar Deep Water, WW = Winter Water.

Fig. 4. Results of hierarchical clustering of Phytoplankton counts

Fig. 4a. Phytoplankton cluster diagram. Station notation as in Fig.1a

Fig. 4b. Phytoplankton data grouping according to Hardy and Gunther (1935)

Fig. 4c. grouping according to nearest neighbour clustering (this study)

Fig. 5. Results of hierarchical clustering of Zooplankton counts

Fig. 5a. Zooplankton Cluster diagram. Station notation as in Fig 1a

Fig. 5b. Zooplankton station groups according to nearest neighbour clustering.

Fig. 5c. Zooplankton abundance (ind. m^{-3}) during

Fig. 6. Log zooplankton abundance (ind. m^{-3} ±SD) by cruise. Open-fill for all stations sampled during a cruise, mid-tone for stations with a 40 km match to Discovery stations, dark tone for 6 stations sampled to the NW of South Georgia during BAS cruises.

Fig. 7. Percentage Similarity Index (PSI) based on a common matrix of 45 taxa (see methods 2.5) Open circles represent PSI comparisons for that year and every other year in the series. Solid line is the mean across all comparisons.

Phytoplankton taxa	Group 1 (n=2)	Group 2 (n=7)	Group 3 (n=14)	Group 4 (n=13)	Group 5 (n=6)
Diatoms					
Corethron valdiviae	21	353	1348	149	3
Corethron criophilum	46	29	47	692	2
Corethron socialis	0	169,572	0.2	29,644	0
Corethron oppositus?	3	0.3	0.6	37	0.7
Thalassiothrix antarctica	0	5	0.5	33	1
Nitzschia seriata	0	5	0	14,065	0
Fragilaria antarctica	5	11	0	692	1
Eucampia antarctica	0	3	0	30	0.2
Rhizosolenia styliformis	1622	0.4	0.4	8	0.2
Coscinodiscus bouvet	0.05	1	0.5	7	0.3
Coscinodiscus curvulatus	0	0	1	2	0
Coscinodiscus oculoides	0.15	0.7	0.5	0.25	0.2
Thalssiosira antarctica	0.3	0.9	0.3	13	0.1
Dinoflagellate					
Peridinium spp.	0.15	0.8	0.04	15	0.8

Table 1 N50V phytoplankton hauls (0-100 m). Average abundance (ind. * 10^3) with respect to phytoplankton station groups of taxa contributing ≥ 2% to within group similarity or between group dissimilarity in the SIMPER analysis.

	Group 1 (n=13)	Group 2 (n=12)	Group 3 (n=16)	Group 4 (n=4)	Group 5 (n=1)
Foraminifera	3.3	51.4	2.8	8.6	0
Radiolarians	0.2	2.1	2.2	0.8	5.3
Copepoda					
Calanus simillimus	1.3	0.9	0.5	0.4	0.1
Calanus propinquus	2.2	4.7	1.2	4.2	1.3
Calanoides acutus	7.4	16.3	3.3	1.3	1.1
Rhincalanus gigas	0.5	0.7	1.8	0.6	1.3
Metridia spp.	0.2	1.7	0.8	6.3	3.1
Clausocalanus laticeps	0.1	1.3	0.3	0.8	0
Clausocalanus arcuicornis	0	0	0	0.17	0
Drepanopus forcipatus	294.0	24.3	14.5	0.1	237.0
Scolecithricella minor	0.1	1.0	1.0	0.5	0
Ctenocalanus vanus	7.6	28.7	11.3	8.8	13.5
Microcalanus pygmaeus	0.05	0.7	0.9	0.1	7.7
Microcalanus sp.	0	0.1	0	0.2	0
Oithona spp.	80.0	159.0	73.0	6.8	0
Oncaea spp	1.2	6.1	0.8	0.7	81.0
Chaetognatha	0.2	1.1	1.0	0.3	0.8
Polychaeta	1.3	3.4	0.8	0.8	0
Pelagobia longicirrata	0.6	2.1	0.3	0	0.03
Ostracoda	0	0.5	0.2	0.2	0
Euphausiacea					
Thysanoessa spp.	0.45	1.1	0.2	0.3	0
Thecate Pteropoda					
Limacina spp.	0.4	.4	0.2	0.02	0
Tunicate					
Salpa fusiformis	0	0.2	0.1	0.6	0
Appendicularians	0.9	2.2	0.03	0	0

Table2 N70V zooplankton hauls (0- ≤250m). Average abundance (ind m^{-3}) with respect to zooplankton station groups of taxa contributing ≥ 2% to within group similarity or between group dissimilarity in the SIMPER analysis.

				Variance component (% of total)			
Data / Model	Difference 1926 – BAS (se)	*W*	*p*	Cruise	Station	Residual	Total
a) BAS cruises. Six stations located NW of South Georgia (see text)	-	-	0.004	0.075 (32)	0.021 (9)	0.139 (58)	0.235
b) Matched stations Random effects for cruise & station	0.60 (0.33)	3.27	0.071	0.093 (41)	0.045 (20)	0.087 (37)	0.225
b) All data. No matching of stations Random effects for cruise	0.48 (0.37)	1.74	0.19	0.114 (51)	-	0.109 (49)	0.223

Table 3 Summary of models and data used to test for differences within BAS cruises and between BAS cruises and Discovery data from 1926/27. W - Wald test

	Mean percentage	Standard deviation	Minima	Maxima
Oithona sp.	51.400	13.579	26.393	68.429
Ctenocalanus vanus.	11.400	3.265	6.766	16.955
Metridia spp	9.400	5.220	0.969	16.720
Limacina (thecate pteropod)	8.600	9.086	0.003	27.819
Appendicularians	5.300	4.435	0.662	11.169
Calanoides acutus	3.200	1.827	1.233	6.017
Oncaea sp.	2.933	1.310	1.048	4.745
Calanus simillimus	2.208	2.171	0.420	6.065
Pelagobia longirrata	1.129	1.184	0.000	3.752
Rhincalanus gigas	1.078	0.552	0.549	2.327
Microcalanus sp.	0.755	0.478	0.245	1.508
Calanus propinquus	0.518	0.636	0.066	1.974
Chaetognatha	0.427	0.367	0.095	1.225
Scolecithricella sp.	0.404	0.292	0.103	0.997
Polychaeta	0.280	0.523	0.000	1.274
Thysanoessa sp. sub/adults	0.271	0.119	0.147	0.495
Euchaeta antarctica	0.144	0.097	0.030	0.296
Clausocalanus sp.	0.129	0.196	0.000	0.586
Thysanoessa sp. calyptopis i-iii	0.113	0.115	0.001	0.279
Ostracoda	0.111	0.096	0.001	0.306
Clausocalanus laticeps	0.080	0.140	0.000	0.410
Pleuromamma robusta	0.048	0.078	0.007	0.239
Euphausia frigida calyptopis i- iii	0.044	0.041	0.001	0.099
Euphausia frigida sub/adults	0.021	0.023	0.003	0.070
Salps	0.016	0.030	0.000	0.089
Antarctomysis sp.	0.016	0.036	0.000	0.103
Euphausia frigida furcilia i - iv	0.015	0.020	0.001	0.061
Themisto gaudichaudii	0.012	0.020	0.000	0.060
Heterorhabdus sp.	0.012	0.008	0.001	0.024
Haloptilus sp.	0.011	0.011	0.001	0.029
Tomopteris spp	0.011	0.005	0.002	0.018
Siphonophora	0.009	0.016	0.000	0.042
Euphausia superba sub/adults	0.009	0.010	0.000	0.028
Euchirella rostrata	0.008	0.009	0.001	0.027
Racovitzanus sp.	0.006	0.007	0.000	0.021
Amphipoda	0.005	0.005	0.000	0.013
Euphausia superba calyptopis i- iii	0.004	0.006	0.000	0.019
Eucalanus sp.	0.004	0.004	0.000	0.011
Canadacia sp.	0.004	0.003	0.001	0.011
Ctenophora	0.002	0.003	0.000	0.008
Scaphocalanus sp.	0.002	0.001	0.000	0.003
Euaetideus australis	0.001	0.001	0.000	0.003
Aetideus sp.	0.001	0.001	0.000	0.003
Euphausia superba furcilia i - vi	0.001	0.001	0.000	0.003
Gadius sp.	0.001	0.001	0.000	0.003

Table 4. Mean percentage (standard deviation, minimum and maximum values) occurrence of the 45 taxa used in the intercruise comparison across all cruises and ranked in order of abundance.

Table 5. Depth distribution of four large calanoid species during austral summer 1926/27 and 1990 near South Georgia. Discovery data averaged across 13 hauls made in waters in excess of 750 m water depth. LHPR data taken from two hauls to ~800 m.

	Calanoides acutus	*Rhincalanus gigas*	*Calanus simillimus*	*Calanus propinquus*
Discovery 1926/27 Average Percentage in top 250 m (n=13)	64	41	91	87
LHPR hauls 1990 Average percentage in top 250 m (n=2) (see Ward et al., 1995)	59	96	99	91