



**MESOZOOPLANKTON OF
THE SCOTIA SEA:
PRESENT, PAST AND
FUTURE.**

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ABSTRACT

The potential impact of global warming on plankton populations and processes in the Southern Ocean is cause for concern. Greatest attention has concentrated on Antarctic krill, a keystone macroplankton species and currently the object of a commercial fishery. This thesis focuses on the mesozooplankton component of the zooplankton, in particular the Copepoda. These crustaceans are major secondary producers and are important dietary items for mesopelagic fish as well as being major recyclers of particulate carbon and nutrients. The balance between krill and copepods fundamentally influences the nature of ecosystem function, particularly with regard to carbon export and remineralization. In this synthesis of 18 years of research, summarised in eight papers, I address the question of whether there have been shifts in the distribution and community structure of mesozooplankton in the Scotia Sea over the last 70 years. Net samples obtained between 1995 and 2009 were compared with samples collected during the 1920s-1930s by the *Discovery Investigations*. Taking into account differences in net design between eras, no differences in overall abundances or community composition were initially apparent. Despite a median increase of 0.74°C in sea surface temperature since the 1930s, plankton distributions from contemporary sampling were geographically similar. However, further analysis showed that although ranked abundances were comparable between eras, three of the four biomass dominant copepods had increased in absolute abundance by ~20- 55% during contemporary times. Reasons for this are considered to be linked to changes within the food web, driven by decreasing krill abundance as a result of warming-induced habitat loss and the commercial exploitation of whales. Future investigations into spatial distributions and trophic overlap between krill and copepods, as well as renewed efforts in modelling the ecosystem effects consequent upon the harvesting of whales, are recommended.

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Paper 2120

Ward, P., Shreeve, R., Atkinson, A., Korb, B., Whitehouse, M., Thorpe, S., Pond, D. and Cunningham, N., (2006). Plankton community structure and variability in the Scotia Sea: austral summer 2003. *Marine Ecology Progress Series*, 309, pp.75-91.

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Paper 4.....154

Ward, P., Atkinson, A., Venables, H.J., Tarling, G.A., Whitehouse, M.J., Fielding, S., Collins, M.A., Korb, R., Black, A., Stowasser, G., Schmidt, K., Thorpe, S.E., and Enderlein, P. (2012b). Food web structure and bioregions in the Scotia Sea: a seasonal synthesis. *Deep Sea Research Part II: Topical Studies in Oceanography*, 59: 253-266.

Paper 5169

Ward, P., Meredith, M. P., Whitehouse, M. J., and Rothery, P. (2008). The summertime plankton community at South Georgia (Southern Ocean): Comparing the historical (1926/1927) and modern (post 1995) records. *Progress in Oceanography*, 78(3), 241-256.

Paper 6.....186

Ward, P., Tarling, G.A., Coombs, S.H., and Enderlein, P. (2012c). Comparing Bongo net and N70 mesozooplankton catches: using a reconstruction of an original net to quantify historical plankton catch data. *Polar Biology*, 35(8), 1179-1186.

Paper 7195

Tarling, G.A., Ward, P., and Thorpe, S.E. (2017) Spatial distributions of Southern Ocean mesozooplankton communities have been resilient to long-term surface warming. *Global Change Biology*. <https://doi.org/10.1111/gcb.13834>

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Ward, P., Tarling, G.A., & Thorpe, S.E., (2018). Temporal changes in abundances of large calanoid copepods in the Scotia Sea: comparing the 1930s with contemporary times. *Polar Biology* <https://doi.org/10.1007/s00300-018-2369-3>

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Most of my post-graduate career was spent studying zooplankton within the Southern Ocean, with a geographical emphasis on South Georgia and its links to the wider Scotia Sea. Over some 25 oceanographic cruises (1978-2014), my colleagues and I sought to characterise the biota, nutrient chemistry, important rate processes and their wider relationships with physics and season. We were very conscious of the vast legacy bequeathed us by the '*Discovery Investigations*'. Much of the groundwork essential for understanding the Southern Ocean was carried out by these pioneering scientists between the 1920's - 1950's which informed much subsequent work. The importance of the *Discovery Investigations* is routinely acknowledged in the literature and data collected has, in some fields, such as krill demography, plankton catches and oceanography, been extracted from field note-books and sorting sheets and digitised, or otherwise put in a form that safeguards and enables its future use.

I thank Dr Barry Heywood who gave me my first opportunity to work for British Antarctic Survey (BAS) in 1975 as his freshwater research assistant based on Signy Island. After 2 years south, I was appointed as a zooplankton biologist in BAS's newly created Offshore Biological Programme. Over the next 38 years I was fortunate to work alongside and collaborate with many committed and inspirational people, who made polar science intellectually challenging, globally relevant and above all fun. Especial thanks are due to my colleagues Angus Atkinson, Beki Korb, Rachael Shreeve, Geraint Tarling, Sally Thorpe and Mick Whitehouse from whom I learned so much. I also thank the various officers and crews of RRS *John Biscoe* and RRS *James Clark Ross* who facilitated our many field campaigns to the Southern Ocean, often under difficult conditions. Finally, I also thank my supervisors Carol Robinson (UEA) and Geraint Tarling (BAS) for encouragement and assistance along the way.

Acknowledgements of Cover Photographs

RRS James Clark Ross: Courtesy of the British Antarctic Survey

RRS Discovery: Courtesy of Cambridge University Press

RRS Sir David Attenborough: Courtesy of the Natural Environment Research Council

PUBLISHED PAPERS AND CO AUTHOR TESTIMONIES

Paper 1

Ward, P., Grant, S., Brandon, M., Siegel, V., Sushin, V., Loeb, V., and Griffiths, H. (2004). Mesozooplankton community structure in the Scotia Sea during the CCAMLR 2000 Survey: January-February 2000. *Deep Sea Research II*, 51: 1351-1367.

PW planned zooplankton sampling as complementary adjunct to multi-ship krill survey. MB provided physical oceanographic data and interpretation. PW sampled at sea onboard RRS James Clark Ross, sorted samples from all participating ships, and carried out data analysis and drafted paper. SG stored and handled data and with HG carried out GIS for figures. All commented.

I confirm that the above paragraph is a true reflection of the contribution of Peter Ward to this paper. Dr Volker Siegel, Institute of Seafisheries, Hamburg. 23rd May 2018



Paper 2

Ward, P., Shreeve, R., Atkinson, A., Korb, B., Whitehouse, M., Thorpe, S., Pond, D. and Cunningham, N., (2006). Plankton community structure and variability in the Scotia Sea: austral summer 2003. *Marine Ecology Progress Series*, 309, pp.75-91.

PW planned zooplankton survey and undertook sampling along with RS and AA. BK, MW and ST provided information on phytoplankton, nutrient chemistry and oceanography respectively. PW undertook zooplankton analysis. RS provided C:N data, DP provided fatty acid data for particulates. NC stored and retrieved data. PW drafted paper. All commented.

I confirm that the above statement is correct and is a true reflection of Peter Ward's contribution to this paper. Signed: M J Whitehouse 12th April 2018



Paper 3

Ward, P., Atkinson, A., and Tarling, G. (2012a). Mesozooplankton community structure and variability in the Scotia Sea: a seasonal comparison. *Deep Sea Research Part II: Topical Studies in Oceanography*, 59, 78-92.

PW conceived study. PW, AA and GT undertook zooplankton sampling. PW analysed zooplankton and provided information on abundance, biomass and community analysis. GT provided statistical analysis for catch comparison of net mesh sizes. PW drafted paper. All commented.

I confirm that the above paragraph is a true reflection of the contribution of Peter Ward to this paper.

Signed: Angus Atkinson 13th April 2018



Paper 4

Ward, P., Atkinson, A., Venables, H.J., Tarling, G.A., Whitehouse, M.J., Fielding, S., Collins, M.A., Korb, R., Black, A., Stowasser, G., Schmidt, K., Thorpe, S.E., and Enderlein, P. (2012b). Food web structure and bioregions in the Scotia Sea: a seasonal synthesis. *Deep Sea Research Part II: Topical Studies in Oceanography*, 59: 253-266.

PW undertook study and provided zooplankton data. Other authors provided summary data from their particular disciplines. PW drafted paper. All commented.

I confirm that the above statement is correct and is a true reflection of Peter Ward's contribution to this paper. Signed: M J Whitehouse 12th April 2018



Paper 5

Ward, P., Meredith, M. P., Whitehouse, M. J., and Rothery, P. (2008). The summertime plankton community at South Georgia (Southern Ocean): Comparing the historical (1926/1927) and modern (post 1995) records. *Progress in Oceanography*, 78(3), 241-256.

PW conceived study and compiled, assembled and analysed zooplankton and phytoplankton data. MM analysed oceanographic data and provided section outlining temporal changes. MW provided input on ocean warming and PR provided statistical analysis. Geraint Tarling undertook the PSI analysis. PW drafted paper and all commented.

I confirm that the above statement is correct and is a true reflection of Peter Ward's contribution to this paper. M J Whitehouse, 12th April 2018.

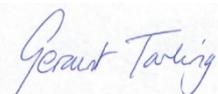


Paper 6

Ward, P., Tarling, G.A., Coombs, S.H., and Enderlein, P. (2012c). Comparing Bongo net and N70 mesozooplankton catches: using a reconstruction of an original net to quantify historical plankton catch data. *Polar Biology*, 35(8), 1179-1186.

PW conceived study and undertook field sampling and zooplankton analysis. GT provided statistical analysis which determined that the paired Bongo net samples could be treated independently. PW provided all other analysis. SC and PE provided input, material and constructed replica N70 net. PW drafted paper. All commented.

I confirm that the above statement is correct and is a true reflection of Peter Ward's contribution to this paper. G.A. Tarling 27th June 2018

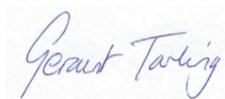


Paper 7

Tarling, G.A., Ward, P., and Thorpe, S.E. (2017) Spatial distributions of Southern Ocean mesozooplankton communities have been resilient to long-term surface warming. *Global Change Biology*. <https://doi.org/10.1111/gcb.13834>

GT and PW are joint first authors. PW conceived study, sourced historical samples and undertook all plankton sample analysis and data collation. GT conceived concept of community response (*C rel*) to temperature and undertook analysis between eras. ST sourced oceanographic data and provided interpretation between eras. GT lead on drafting manuscript PW and ST contributed sections. All commented.

I confirm that the above statement is correct and is a true reflection of Peter Ward's contribution to this paper. G.A. Tarling 27th June 2018

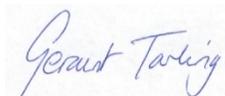


Paper 8

Ward, P., Tarling, G.A., & Thorpe, S.E., (2018). Temporal changes in abundances of large calanoid copepods in the Scotia Sea: comparing the 1930s with contemporary times. *Polar Biology* <https://doi.org/10.1007/s00300-018-2369-3>

PW conceived study, sourced historical samples and undertook all plankton sample analysis and data collation. GT recalibrated previous catch data from Ward et al. 2012, to account for copepod stage specific differences and applied to historical data set. He also carried out sensitivity analyses. ST input information on ocean warming and drafted Figure 1. PW drafted paper. All commented.

I confirm that the above statement is correct and is a true reflection of Peter Ward's contribution to this paper. G.A. Tarling 27th June 2018



GLOSSARY

Copepods: A major crustacean group whose life stages dominate mesozooplankton abundance and biomass. They are the dominant constituent of the plankton in every ocean generally comprising >70% by abundance.

Euphausiids: A group of shrimp-like crustaceans commonly referred to as krill. In the Southern Ocean the Antarctic krill (*Euphausia superba*), is a dominant macrozooplankton species and food for a number of dependent avian and mammalian predators such as penguins, seals and whales.

Ocean acidification: Oceans absorb carbon dioxide (CO₂) from the atmosphere which reacts with seawater to form carbonic acid. As atmospheric levels of CO₂ increase in response to global warming, the acidity of seawater increases. As a result, organisms with calcareous shells are in danger of incurring damage to their skeletons. Ocean acidity is estimated to have increased by ~30% in the last 200 years

Phytoplankton: Generally single celled plants that produce complex organic compounds from simple substances present in their surroundings via the process of photosynthesis utilising energy from sunlight; a process termed **Primary Production**.

Plankton: Collectively the bacteria (bacterioplankton), plants (phytoplankton) and animals (zooplankton) suspended in the ocean and generally considered to be at the mercy of ocean currents. The term derives from the Greek 'planktos' meaning wanderer or drifter.

Salps: Gelatinous zooplankton belonging to a group known as tunicates. Individuals may be several centimetres in length and, by virtue of asexual reproduction or budding, they can quickly form chains of individuals and constitute dense swarms. It has been suggested that recent declines in krill abundance in the Southern Ocean, have been accompanied by salps extending their range.

Secondary Production: The amount of animal biomass that is produced in a given area over a given time period, usually expressed in gm⁻²yr⁻¹.

Stenothermy: A condition which allows animals to only survive within a small temperature range c.f. eurythermy where organisms can exist over a wide temperature range.

Zooplankton: A diverse group of animals ranging in size from large gelatinous forms such jellyfish to small protozoans. Collectively, they exhibit a variety of trophic

behaviours from herbivory and omnivory through to carnivory and are termed **Secondary Producers**. It is convenient to group zooplankton into the following size categories:

Macrozooplankton: Zooplankton >2 -20 cm, includes organisms characterized by very different size, features, and behaviour such as euphausiids (krill), amphipods, and smaller jellyfish.

Megaplankton: Zooplankton > 20 cm, includes large medusa, salps and larger euphausiids.

Mesozooplankton: Zooplankton 0.2-2.0 cm includes crustacean organisms such as copepods and ostracods as well as pteropod molluscs and chaetognaths.

Microzooplankton: Zooplankton 20–200µm includes large protozoans, foraminiferans and tintinnids as well as crustacean nauplii. They are regarded as major grazers of phytoplankton.

CRITICAL ANALYSIS

CHAPTER 1: INTRODUCTION

Purpose

This critical analysis is an assessment of mesozooplankton abundance and distribution within the Scotia Sea (Southern Ocean) during contemporary times and during the period of the *Discovery Investigations*. It is based on an analysis of samples taken with a variety of nets during research cruises between 2000 and 2009 and those undertaken by *Discovery Investigations* during the 1920s and 1930s.

Following an inter-comparison of the catching ability of the two main nets used to collect samples, a paired Bongo net during contemporary times and a N70 ring net during the *Discovery Investigations*, calibration factors were determined and applied to *Discovery* data, allowing a temporal comparison over the wider Scotia Sea to be made. Sea surface warming of the Scotia Sea that has occurred between the two eras was also assessed to see whether it has had measurable effects on the contemporary distribution and abundance of mesozooplankton.

Structure

This thesis starts with a brief historical overview of the timeline of oceanographic research in the Southern Ocean during the 20th century, followed by a chapter setting the Scotia Sea into the larger context of the Southern Ocean in terms of hydrology, sea-ice and primary and secondary production. My research on mesozooplankton is then described, and comparisons are made between the two eras. There follows a discussion of recent environmental changes within the Southern Ocean, notably warming and the commercial exploitation of living resources that have occurred during the last century. Against this background, I then present an assessment of changes within the mesozooplankton to date, based on my own research, and consider those likely to occur in future.

CHAPTER 2: BIOLOGICAL OCEANOGRAPHY IN THE SOUTHERN OCEAN DURING THE 20TH CENTURY

Background to *Discovery Investigations*

The Atlantic sector of the Southern Ocean has been the subject of concerted oceanographic investigation for close on 100 years and is arguably one of the best-studied areas in the Southern Ocean. Prior to this, marine research was, initially at least, largely opportunistic and curiosity driven, mainly carried out by exploratory expeditions such as the Belgian and Scottish expeditions of 1897-1899 and 1902-1904 respectively. The advent of commercial whaling and sealing, in what was the Falkland Island Dependencies, in the late 19th and early 20th centuries fundamentally changed this situation. Walton and Bonner (1985) provided a succinct overview of the early history of scientific exploration in Antarctica and the increase in knowledge as a result of exploitation.

The International Council for the Exploration of the Sea (ICES) was established in 1902 as a response to the development of the fishing industry and had provided a great stimulus to marine research which could be used to sensibly underpin any necessary regulation (Hardy 1967). Against this background, concern over the scale of whale exploitation in the south led to government controls including restricting the number of whale catchers, banning the killing of mothers and calves and imposing a tax on whale oil. Some of this money was used to finance scientific investigation to further underpin future legislation if needed.

The idea of the *Discovery Investigations* was thus conceived in the early part of the 20th century, although planning for them was delayed by the advent of World War I and the programme proper commenced in the 1920's. The *Discovery Investigations* ran in the 1920s-1930s and again briefly in the early 1950s. While ultimately they did little to help the plight of the whale (commercial whaling in the Antarctic ceased for economic reasons in the 1970s), they provided the basis of much of what we know about the Southern Ocean today in a series of reports covering 37 volumes and 13,000 pages. It cannot be overstated how important the *Discovery Investigations* were in providing the scientific framework and basis for understanding the physics

and major elements of the biota of the Southern Ocean, which future generations of oceanographers have built upon. Many of the key questions we still grapple with, for example the role of micronutrients in promoting phytoplankton growth and elements of krill population biology and distribution were formulated by these early researchers (Hart 1942; Marr 1962; Mackintosh 1972, 1973).

Whilst the *Discovery Investigations* provided descriptions of plankton communities occurring around South Georgia (Hardy and Gunther 1935), the large-scale view was necessarily built up of snapshots obtained from multiple cruises in different years. For example, an initial view of the South Atlantic sector, based on 600 samples collected during 1927-1931 in the top 100m of the water column, emphasised the distribution of warm and cold water plankton and the spatio-temporal variability in its richness (Mackintosh 1934). Many of the major features recognised today were first disclosed by this analysis, notably the presence of a warm water community to the north of the region, scarce plankton in the region of the Antarctic Peninsula and a zone enclosing the line of the confluence of Bellingshausen and Weddell Sea fauna. The *Discovery Investigations* plankton data continued to be published in a series of reports through the latter part of the 20th century, often focussing on the ecology of single species (e.g. Baker 1954, 1959; David 1958; Andrews 1966; Kane 1966).

Post *Discovery*

Extensive Russian work during the 1960s and 1970s carried on alongside commercial exploitation of fish stocks, notably around South Georgia, and provided further information on plankton distributions, life cycles and oceanography (e.g. Voronina 1966, 1968; Voronina and Naumov 1968; Vladimirskaya 1968).

The British Antarctic Survey (BAS) commenced offshore pelagic research during the late 1970s, along with many other current Antarctic operators, at a time when interest in krill research was resurgent due to recognition of its potential as a raw material for producing fish meal and for direct human consumption (Everson 1977). The establishment of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) in 1980 was a multi-lateral response to concerns that unregulated increases in krill catches in the Southern Ocean could be detrimental for

Antarctic marine ecosystems, particularly for seabirds, seals, whales and fish that depend on krill for food. Figure 1 depicts the schematic foodweb.

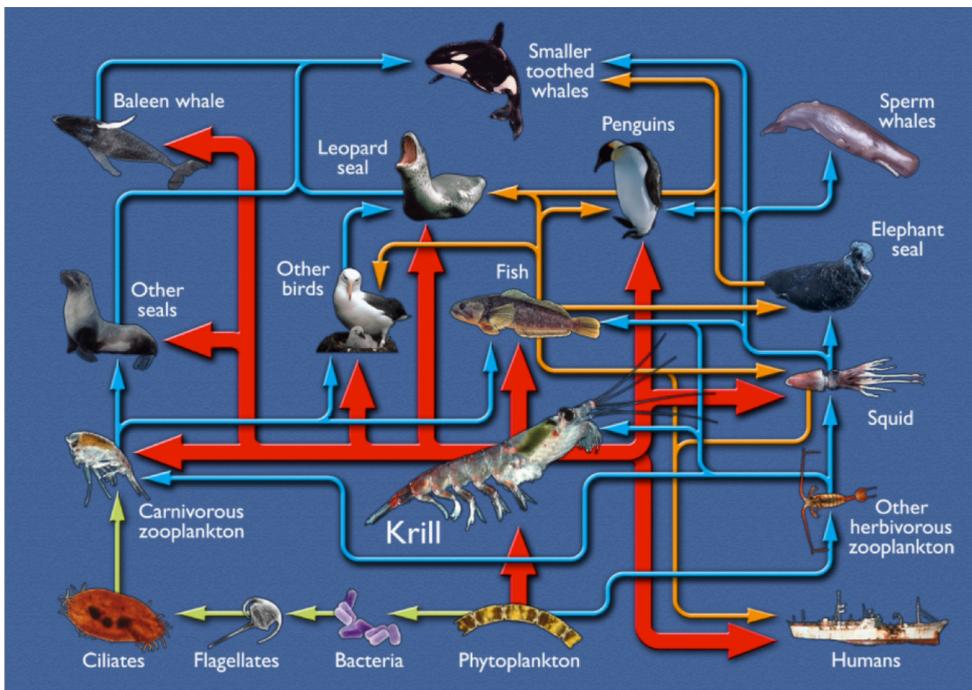


Figure 1: Schematic food web for the Southern Ocean (courtesy of British Antarctic Survey)

This Convention stimulated fresh thinking about fundamental issues relating to ecosystem structure and function and the scales over which processes occur (Smetacek et al. 1990; Tréguer and Jacques 1992; Murphy et al. 1998) and conservation biology more generally. As a result of the strong international interest in krill stocks, the BIOMASS programme (Biological Investigations of Antarctic Marine Systems and Stocks) was conceived and generated the First and Second Biological Experiments (FIBEX and SIBEX): field programmes which focussed on synoptic estimates of krill biomass and the dynamics of its distribution in the Atlantic and Indian Ocean sectors and Antarctic Peninsula respectively (El Sayed 1994). Other international programmes such as JGOFS (Joint Global Ocean Flux Study) and GLOBEC (Global Ocean Ecosystem Dynamics) both had Southern Ocean components and CCAMLR 2000, a multi-national multi-ship study aimed to provide a synoptic view of oceanography, zooplankton, krill and higher predator biomass and distribution in the Scotia Sea and waters adjacent to the Antarctic Peninsula.

Whilst krill was the major focus of these programmes, research on meso- and macro-zooplankton continued apace, elaborating lifecycles of copepods (Marin 1988; Atkinson 1991; Schnack-Schiel and Hagen 1994, 1995; Atkinson et al. 1997; Ward et al. 1997; Schnack-Schiel 2001), lipid biochemistry of plankton (Kattner and Hagen 1995; Hagen et al. 1996; Ward et al. 1996) and rate processes, particularly within the Research on Antarctic Coastal Ecosystem Rates (RACER) program (Huntley et al. 1991). At the same time, community studies over various scales were also being carried out, both within the Atlantic sector (Boysenn-Ennen and Piatkowski 1988; Piatkowski 1989; Atkinson et al. 1990; Boysenn-Ennen et al. 1991; Atkinson and Sinclair 2000), the Indian Ocean sector (Pakhomov et al. 2000) and also the Australian sector, where Hosie (1994) and Hosie et al. (1997) elaborated the distribution of macroplankton in Prydz Bay as did Chiba et al. (2001) on a hitherto unprecedented scale between latitudes 90° and 160°E. During this period, seminal works also appeared which linked physical and biological processes to species biogeographic distributions (Hempel 1985; Tréguer and Jacques 1992; Longhurst 1998).

Renewed interest in the plankton collections made by the *Discovery Investigations* as a valuable resource arose as the nature of their depth resolved samples and extensive seasonal and spatial coverage was appreciated. Thus, Atkinson (1991) and Atkinson and Sinclair (2000), used them to elaborate the seasonal distribution and lifecycles of copepod species within the Scotia Sea and determined zonal distribution patterns, while Mackey et al. (2012) used macroplankton data to model the effects of increasing temperature on distributions.

Today, the Southern Ocean is fully integrated into the study of earth system science and, with the recognition of the feedbacks and links between oceans and atmosphere, much of the recent focus, as elsewhere, is on the putative impacts of global warming and acidifying oceans (McNeil & Matear 2008; Flores et al. 2012; Meijers 2014). CCAMLR continues to oversee the conservation of Antarctic marine ecosystems and practises an ecosystem-based management approach. This allows commercial harvesting as long as it is carried out in a sustainable manner and takes account of the effects of fishing on other components of the ecosystem.

<https://www.ccamlr.org/en/organisation/convention>.

It is against this background that the work presented in this thesis took place. Whilst the broad distribution patterns of plankton were known from the *Discovery Investigations* (Mackintosh 1934; Hardy and Gunther 1935; Baker 1954), many subsequent studies have been limited in both seasonal and geographic coverage and the composite nature of others undoubtedly colour the results. Development of regional oceanographies (Deacon 1933, 1937; Foster 1981; Foster and Middleton 1984; Orsi et al. 1995) allowed ecological zonation to be set in a physical context and the advent of the collection of remotely sensed data in the 1970s was also critically important in this respect (Longhurst 1998). Thus the ability to observe the seasonal development of phytoplankton blooms and the advance and retreat of sea-ice became powerful tools, allowing real-time interpretations of structure and community development (Comiso et al. 1993; Cavalieri et al. 2003; Korb et al. 2004). As I show in later chapters, *Discovery* samples have allowed a window into the past and comparison with contemporary collections, which separated by some 60-70 years, lends a valuable perspective to the debate on the response of plankton and the wider marine ecosystem to a changing climate.

CHAPTER 3: THE SCOTIA SEA WITHIN THE SOUTHERN OCEAN

Preamble

Any discussion of the biogeography of Antarctic zooplankton is intimately connected to the physical structure of the Southern Ocean and its water masses. In order to understand how zooplankton are distributed, we need to be aware of how the medium in which they exist is organised. While this is not the primary purpose of this thesis, it is appropriate to elaborate the main features of the Southern Ocean at least insofar as they affect the Scotia Sea, which is the geographic focus of this study (Figure 2).

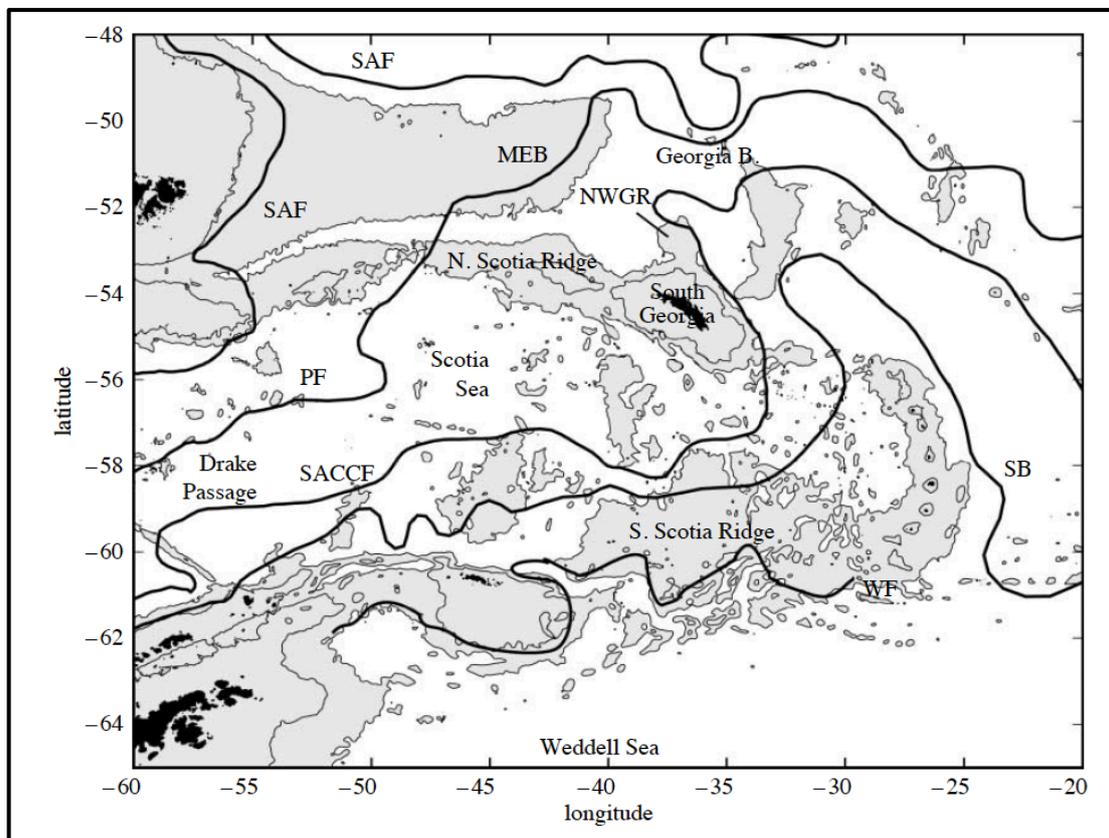


Figure 2: The Scotia Sea and surrounding areas showing the general position of the major frontal systems in relation to bottom topography. SAF, sub-Antarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Front; SB, Southern ACC Boundary; WF, Weddell Front; MEB, Maurice Ewing Bank; NWGR, North West Georgia Rise, Georgia B. Georgia Basin (From Murphy et al. 2007a).

The Scotia Sea is situated in the Atlantic sector of the Southern Ocean within the Antarctic Circumpolar Current (ACC) and extends some 2000 km eastwards beyond

Drake Passage to its easternmost edge formed by the Scotia Arc (Figure 2). It is bounded to the south by the Weddell Gyre and to the north by the North Scotia Ridge, a distance of ~750 km. The ACC flows through Drake Passage and traverses the region in a NE direction before crossing the Scotia Arc that rises from depths of around 3000–5000 m as a chain of islands extending from the Antarctic Peninsula to the tip of South America.

Hydrology

The first comprehensive accounts of the hydrology of the Southern Ocean were published by Deacon (1933, 1937) who described the main features of the circulation. The Southern Ocean is unique in having a circulation unlimited by land masses and thus forms a continuous body of water flowing around the Antarctic continent and hence the globe. This is the Antarctic Circumpolar Current (ACC), the largest ocean current in the world at ~20,000 km in length. Its northern boundary is generally taken as the sub-tropical front (STF), south of which the eastwards-flowing circulation is driven by strong westerly winds. In this way, the ACC links the Atlantic, Indian and Pacific Oceans and transports heat, salt and nutrients from one to the other. A series of oceanic fronts or discontinuities lie within the current and partition it into zonal bands (see Longhurst 2010 for a concise overview). These fronts are associated with narrow bands or filaments of faster flowing water embedded in the relatively slower flowing body of the ACC. The jets are generally continuous, although they can form various branches steered by topography (Sokolov and Rintoul 2009a, 2009b). The majority of flow is associated with these fronts (Gille 1994) although meridional eddy activity is also an important transport mechanism (Rintoul et al. 2001; Hogg et al. 2008).

The ACC has a number of water masses associated with it (Figure 3). The surface layers extend down to around 250 m below which a body of Circumpolar Deep Water (CDW) is found overlying Antarctic Bottom Water which is formed near the continent. Although plankton samples described in this thesis were taken from the overlying surface waters, a proportion of the plankton seasonally migrate into the CDW to overwinter. As such, this has implications for distribution and population dynamics, which will be discussed later in this thesis. South of the productive

southern edge of the STF lies sub-Antarctic surface water (SASW), separated from Antarctic surface water (AASW) proper by the sub-Antarctic front and the Polar Frontal Zone (PFZ) (Whitworth 1980). Because of the presence of ice cover in winter, the AASW is relatively less saline and has a pronounced temperature minimum in the top 200 m during summer, termed the winter water layer. The southern edge of the PFZ is bounded by the Antarctic Polar Front (APF) at which point the AASW is subducted below the SASW, the depth of the temperature minimum exceeds 200 m and water flows north forming the underlying sub-Antarctic Intermediate water. Polewards, the southern limit of the ACC is taken to be the region in which westerly winds give way to easterlies close to the Continent at around 65°S. Here the warm-deep water is brought to the surface in a zone of divergence and is entrained into the surface mixed layer.

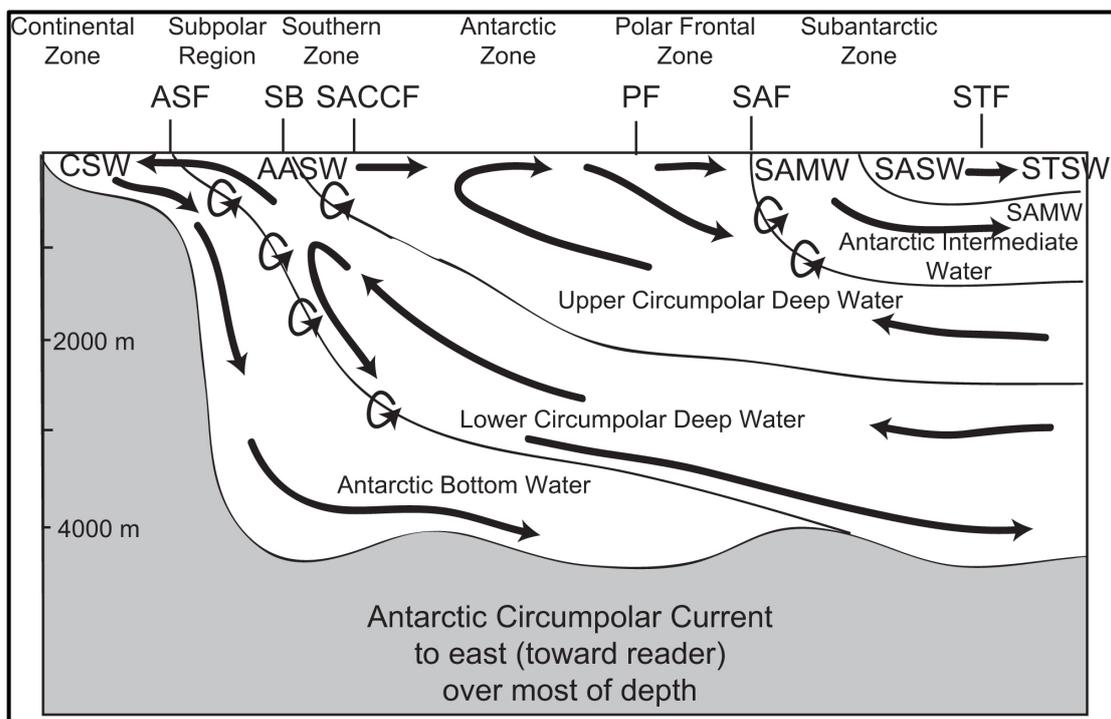


Figure 3: Schematic two-cell meridional overturning circulation in the Southern Ocean. An upper cell is primarily formed by northward Ekman transport and southward eddy transport in the Upper Circumpolar Deep Water layer. A lower cell is primarily driven by dense water formation near the Antarctic continent. Taken from Talley (2011).

Continental Shelf Water (CSW), Antarctic Surface Water (AASW), Subantarctic Mode Water (SAMW), Subantarctic Surface Water (SASW), Subtropical Surface Water (STSW), Antarctic Slope Front (ASF), Southern Boundary (SB), Southern ACC Front (SACCF), Polar Front (PF), Subantarctic Front (SAF), and Subtropical Front (STF).

The corresponding surface flow next to the continent, termed the Antarctic Coastal Current (ACC), is westwards and forms the southern and western limbs of the Weddell Gyre. In the Scotia Sea, the Weddell Scotia Confluence separates the Weddell Gyre from the ACC and is formed from a mixture of the Weddell Gyre, ACC and shelf waters from the Antarctic Peninsula (Whitworth et al. 1994). Orsi et al. (1995) reviewed all historical data and redefined the southern limits of the ACC as being the point at which the density and dissolved oxygen characteristics of Upper CDW shoal above 200 m and are no longer apparent to the south. This was termed the Southern Boundary of the ACC (SBACC).

Orsi et al. (1995) also identified a further front, embedded within the flow of the ACC which they termed the Southern Antarctic Circumpolar Current Front (SACCF) which, in places, lies close to the Southern Boundary. This is the case in the western Scotia Sea, near the Antarctic Peninsula where interaction between the two fronts is a possibility (Brandon et al. 2004). Downstream, in the central and eastern Scotia Sea, the fronts are separated by over 300 km (Thorpe et al. 2004).

The Scotia Sea (Figure 2) is the main focus of this study. It extends from 20 to 65°W, is meridionally around 1000 km wide and is bounded to the south by the Weddell Gyre. Immediately downstream of Drake Passage, the ACC is steered topographically by the Scotia Arc, its associated seamounts and shelves and this and the outflow of water from the Weddell Sea accounts for an element of northwards flow in what is otherwise a predominantly eastwards movement.

Sea-Ice

Seasonal sea-ice presently covers ~40% of the Scotia Sea each winter, fed mainly from the Weddell Sea and driven northwards by ocean currents and surface winds (Murphy et al. 1998; Harms et al. 2001; Parkinson 2002, 2004). The maximum northward extent usually occurs during September or October and by February-March the ice-edge has usually retreated to its minimum extent and is located entirely within the Weddell Sea (Figure 4). The retreat in spring usually occurs earlier in the east of the region (Oct-Nov) than the west, which can remain ice covered until late in the spring (Nov-Dec). However, timing of both advance and retreat shows significant

inter-annual variation and is related to changes in air temperatures, wind speed and direction reflecting regional atmospheric dynamics (Murphy et al. 2007a). The mean maximum winter extent of the ice-edge is thought to be broadly coincident with the summer position of the SBACC, although again there can be considerable variation.

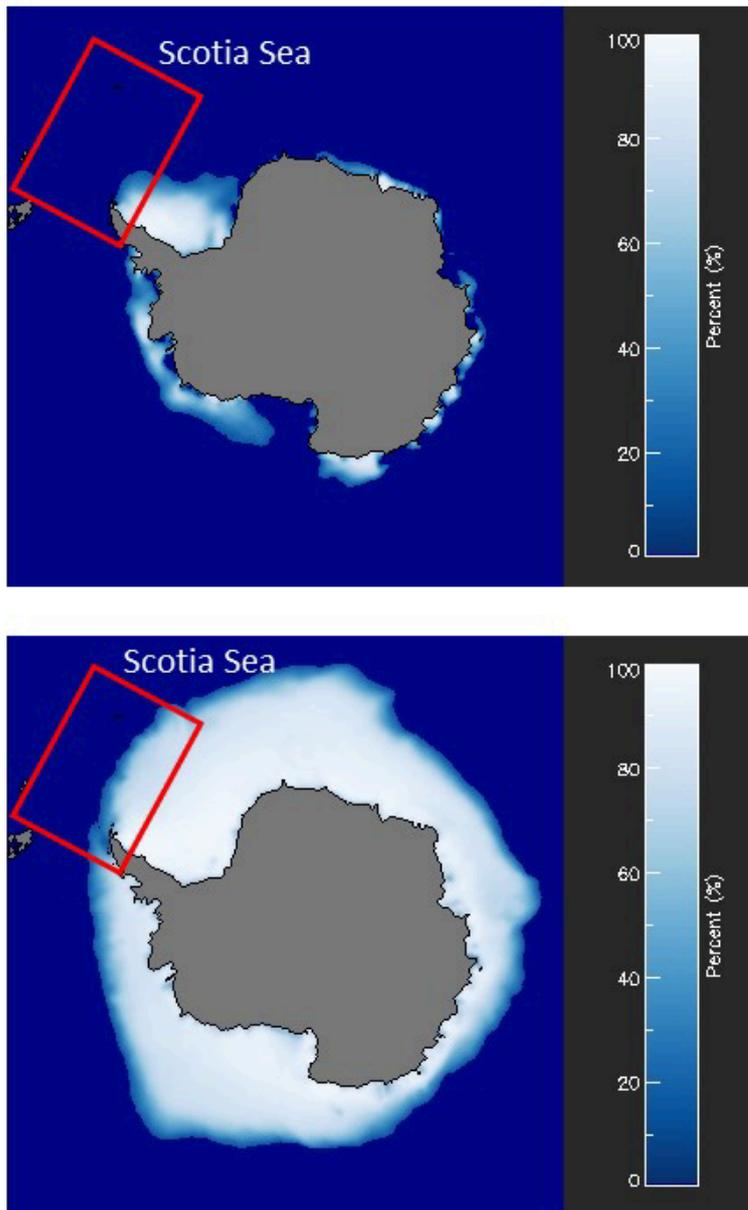


Figure 4: Mean sea-ice concentration around Antarctica 1979-2015. Top panel sea-ice minimum extent February, lower panel sea-ice maximum extent September. Taken from Stroeve, J. and W. Meier. 2017. *Sea Ice Trends and Climatologies from SMMR and SSM/I-SSMIS, Version 2*. Position and approximate extent of the Scotia Sea outlined in red. [https://daacdata.apps.nsidc.org/pub/DATASETS/nsidc0192_seaice_trends_climo_v2/monthly-climatology/browse/]. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center. doi: <http://dx.doi.org/10.5067/EYICLBOAAJOU>. [accessed 09/11/2017].

In many areas, the retreat of sea-ice is rapid and mainly wind driven although, in areas where it retreats slowly, the upper water column can be stabilized by melt water. The ensuing shallow surface mixed layers coupled with increasing light penetration are often the focus for ice edge blooms (Saukshaug and Holm Hansen 1984; Smith et al. 2008; Park et al. 2010). Sea ice cover is highly variable and, based on shipboard observations, it has been suggested that it declined from the mid-1950s to ~1970 (de La Mare 1997). Subsequently, despite reported ocean warming and increased air temperatures over much of the Southern Ocean (Meredith and King 2005), ice cover has recently increased (Zwally et al. 2002; Parkinson 2004) although variations within sectors have been observed (Stammerjohn et al. 2008). Sea-ice growth in the Weddell sector has shown a positive trend, $+1.4 \pm 0.9\%$ (decade)⁻¹ but it has been negative in the Bellingshausen and Amundsen Sea, $-9.7 \pm 1.5\%$ (decade)⁻¹ (Zwally et al. 2002). This is somewhat counter-intuitive given the warming trends of air and ocean, although shifting weather patterns and increased snow fall over the Southern Ocean are thought to be responsible, as well as changes in wind driven ice advection (Holland and Kwok 2012, Holland 2014). In September 2014, the maximum ice extent of the satellite era was recorded. <https://www.nasa.gov/content/goddard/antarctic-sea-ice-reaches-new-record-maximum>

Primary production within the Southern Ocean

Perhaps the most striking feature of the Southern Ocean is the extreme seasonality. At 60°S, plant growth is limited from May to August (the austral winter) due to lack of irradiance. Increasing daylight in spring and stratification of the upper water column due to insolation or ice melt permits growth where sufficient nutrients are available (Boyd 2002).

For many years the high nutrient, low chlorophyll (HNLC) status of much of the Southern Ocean was deemed a paradox (Hart 1934). Nutrient levels remained high, yet phytoplankton growth was often negligible. Drawing on findings of trace element experiments carried out in the early 20th century, Hart (1942) suggested that, among other factors controlling phytoplankton growth, micronutrients such as iron and manganese, particularly with respect to neritic waters, might be important. The advent

of remote sensing in the 1970s advanced knowledge by disclosing spatial and temporal patterns of temperature, sea-ice cover and phytoplankton growth (from surface expressions of chlorophyll) on hitherto unprecedented scales (Hooker et al. 1992, Hovis 1981). This, coupled with biogeochemical studies looking at algal growth dynamics conducted during numerous mesoscale field campaigns, focussed the search for environmental factors controlling phytoplankton growth. Seminal studies by Martin and co-workers (Martin et al. 1990) established the iron hypothesis which proposed that, during glacial periods in the Southern Ocean, greater input of dust-derived iron led to enhanced uptake of nutrients and a drawdown of atmospheric CO₂. Trace element studies (de Baar et al. 1995; Boyd et al. 2000; Blain et al. 2001) have proliferated in the last 20-25 years and studies such as the Southern Ocean Iron Release Experiment (SOIREE) and the Iron Experiments (EISENEX) (Assmy et al. 2007) and LOHAFEX (Boyd and Ellwood 2010; Martin et al. 2013) have found iron limitation to be widespread.

Within the Atlantic sector, de Baar et al. (1995) indicated that, iron levels were considerably higher in the core of the APF remote from land (6°W), than in HNLC waters to the south and were associated with a sub-surface spring bloom. Natural fertilization has been shown to be important with sedimentary sources of iron present at shelf edges and deep topographical features, where interactions with ocean currents promote upwelling from bottom sediments into the euphotic zone (Blain et al. 2008; Park et al. 2010; Morris & Charette 2013). In addition, aeolian sources (Cassar et al. 2007) and the release of glacially bound iron in melting icebergs (Smith et al. 2007; Raiswell et al. 2008) are all considered potentially important in promoting primary production. Algal physiology in relation to trace element uptake and limitation remains a sharply focussed area of research (Pollard et al. 2009; Boyd and Ellwood 2010; Hassler et al. 2011) although great uncertainties still remain with regard to macronutrient stoichiometry, bioavailability of iron and its retention in surface waters.

Despite the existence of diverse species of phytoplankton in the Southern Ocean, relatively few are thought to play a critical role in biogeochemical processes (Smetacek et al. 2004; Queguiner 2013). In low productive systems, most of the primary production and biomass is in the smaller size fractions (pico- and nano-

plankton) that contribute to the recycling microbial web (Korb and Whitehouse 2004). Biomass tends not to accumulate even under favourable growth conditions, as grazers such as ciliates and dinoflagellates appear to keep pace with their food. Under iron-replete conditions, phytoplankton biomass is higher and cells are bigger, although blooms tend to be dominated by few species such as members of the genera *Thalassiosira*, *Chaetoceros*, *Rhizosolenia*, *Proboscia*, *Corethron* and *Fragilariopsis* (Priddle et al. 1986; Smetacek et al. 2004). It is these species that characterise the short food chains that lead via krill to higher predators. Highly silicified species of phytoplankton such as *Fragilariopsis kerguelensis*, *Thalassiothrix antarctica*, *Corethron pennatum* and other pennate species often occur in high abundance in the PFZ and APF and contribute greatly to the siliceous ooze characteristic of the seafloor underlying the ACC (Zielinski and Gersonde 1997).

Recently, Antarctic krill (*Euphausia superba*), an important grazer of phytoplankton, has been identified as an important recycler of iron (Tovar-Sanchez et al. 2007, Schmidt et al. 2016). Clearly in such a highly seasonal environment, and where seasonal ice cover is significant over a large area, other factors such as irradiance, upper water column stability and levels of macronutrients (particularly silicate) and rates of recycling have all been identified as important for phytoplankton growth. For a comprehensive review of phytoplankton research in the Southern Ocean up to the early part of this century see Boyd (2002) and for a resumé of the main findings of mesoscale iron addition experiments see de Baar et al. (2005) and Boyd et al. (2007). The most recent review by Tagliabue et al. (2017) emphasised the uncertainties in our understanding of the dynamics of iron pools and also the linkages to physical, chemical, biochemical and ecological processes.

Scotia Sea

The south-west Atlantic Ocean, of which the Scotia Sea is a part, is recognised as one of the most productive within the ACC. Examination of remotely sensed images shows that, during austral spring and summer, some of the most notable chlorophyll blooms observed within the Southern Ocean occur along the coast of the Antarctic Peninsula and also within the Scotia Sea associated with the island arc of the Scotia ridge (Figure 5).

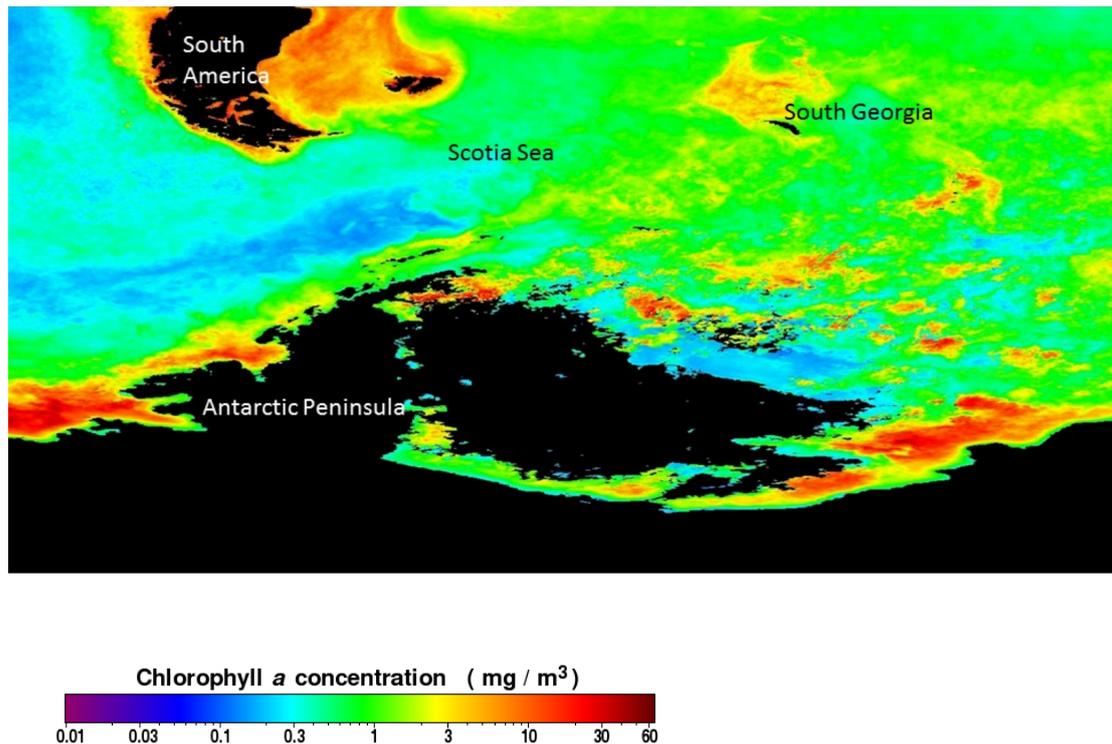


Figure 5: Composite satellite image of the Scotia Sea during austral summer.

<https://oceancolor.gsfc.nasa.gov/data/10.5067/AQUA/MODIS/L3B/CHL/2014/>.

Despite false colour images tending to show the central Scotia Sea as having low concentrations of chlorophyll, recent research has demonstrated that levels can also be substantial in the land-remote central regions (Whitehouse et al. 2012). These authors emphasise the great inter-annual variability of bloom formation in areas such as the central Scotia Sea and speculate that its origins may lie with advection of iron from the Peninsula downstream via eddies associated with the Shackleton fracture zone. Thompson and Youngs (2013) demonstrated that, for much of the time, the SACCF partitions regions of high chlorophyll biomass between itself and the APF to the north, although occasionally this breaks down in January during certain years when biomass can be high on both sides.

A comprehensive review by Park et al. (2010) noted that the Scotia Arc forms a barrier to the ACC on its northern, southern and eastern edges. This complicates the oceanography and influences primary production in various ways. The interaction of bottom topography with the ACC creates regions of mixing and, with the upwelling of limiting nutrients, high productivity can result (Korb et al. 2004; Park et al. 2010;

Thompson and Youngs 2013). This spatial and temporal variability allowed Park et al. (2010) to partition the Atlantic sector into 8 compartments each of which was investigated to identify the seasonality and intensity of bloom occurrence. Their analysis looked at patterns of variance in satellite sensed Chl *a* concluding that the regular seasonal blooms only explained ~38% of the variability in an 11 year data set.

Regular bloom occurrence comprised December blooms in the northern Drake Passage region, November blooms in the southern Drake Passage associated with a retreating ice edge and along the SACCF and SBACCF and late season blooms in the northern Scotia Sea. Elsewhere in the South Atlantic, blooms were seasonally irregular. Collectively these 8 modes of variability explained 60% of the variance of monthly Chl *a* concentrations. Patterns were geographically consistent and allowed potential causes of variability to be examined within the 8 regions. Chl *a* was classified on the basis of temporal occurrence and standing stock. For example, the Georgia Basin (Chl *a* >3 mg m⁻³), where blooms can persist for 4-5 months, can be contrasted with spring blooms in the SACCF off the west Antarctic Peninsula (WAP), which are brief.

Only in Drake Passage was strong seasonality seen, with low or no regular seasonality seen over much of the remaining area. Such variability may have many and differing causes, depending on factors such as geostrophic flow, ice cover and eddy formation and incursion through the region. In regions of ice cover, melting can stabilise the water column resulting in spring ice edge blooms, although these are not always observed and may also temporally lag ice retreat by several weeks. Deep winter mixing of the upper mixed layer was only observed in Drake Passage, which entrained limiting nutrients into near surface waters ready for spring utilization. Elsewhere, the depth of winter mixing was <150 m and was seen as insufficient to provide nutrients, particularly iron, as the ferrocline has been reported to lie at ~200m (Loscher et al. 1997). Kahru et al. (2007) focussed on eddies within the Scotia Sea and their propensity to be responsible for increased productivity, particularly within the SACCF. It has been suggested that increased winds will increase eddy activity and pole-ward heat flux (Meredith and Hogg 2006; Hogg 2008, Hogg et al. 2015). However the response of the ACC to increased wind-stress is currently under debate

and atmospheric anomalies may under certain circumstances either increase or have no effect on eddy kinetic energy (Langlais et al. 2015)

Zooplankton and secondary production

The diversity of plankton in the Southern Ocean is generally lower than elsewhere in the South Atlantic. Whilst most major taxonomic groups are present, diversity for many of these peaks in the subtropical and equatorial waters to the north, falling sharply further south, particularly south of the APF. However, this is not a smooth latitudinal decline and the transition zone between the subtropical gyre and the sub-Antarctic province located at ~30°-40°S is a region where expatriation of warm and cold water species occurs (Boltovskoy et al. 1999). In the tropics and subtropics, production cycles are of generally low amplitude, continue through the year, and primary and secondary production are closely coupled. This leads to a retentive system in which diversity is characteristically high (Conover 1979; Longhurst and Pauly 1987).

In cold temperate and in Polar regions, production and consumption become increasingly uncoupled and, here, diversity is lower and variance higher (Woodd-Walker et al. 2002). There is also an inverse correlation between body mass and habitat temperature. Larger plankton occur in colder waters and this is reflected in increased biomass relative to tropical and subtropical waters (Ikeda 1985). However because of metabolic scaling and warmer waters, higher community metabolism is seen in the tropics. In the Southern Ocean, the plankton is characteristically stenothermal as the functional specialization to permanently low temperatures implies reduced tolerance of high temperatures as a trade-off (Pörtner et al. 2007). The net result of low temperature and pronounced seasonality is a reduction in plankton abundance in the most southerly waters, where extended development and multi-year life-cycles are apparent (Marin 1988; Chiba et al. 2001; Mackey et al. 2012). In the more northerly waters of the ACC, a greater diversity of warmer water- and more generally distributed species leads to higher abundance.

It was recognised early on in the *Discovery Investigations* that plankton species distributions were, on the whole, circumpolar (Baker 1954) and showed strong

relationships with temperature (Mackintosh 1934). This has been broadly confirmed by more recent authors (e.g. Pakhomov and McQuaid 1996; Mackey et al. 2012). Over the last 20 or so years, numerous studies have defined Southern Ocean plankton communities. These have given a near consistent view of epipelagic communities which are bounded by the physical transitions and discontinuities often found at frontal zones (Hosie 1994; Errhif et al. 1997; Pakhomov et al. 2000; Takahashi et al. 2010; Ward et al. 2003, 2006).

For a long time the Antarctic Convergence, now commonly referred to as the Antarctic Polar Front (APF) was seen as an important, if not the most important, feature for defining plankton distributions in the Southern Ocean and was generally thought to isolate the Antarctic fauna from the sub-Polar waters to the north. Its position was thought to be fairly constant (see Deacon 1982) and, within the Scotia Sea, it is largely steered by bottom topography (Moore et al. 1999). Recently, Freeman and Lovenduski (2016) determined an average gradient intensity of 1.7°C per 100 km with a range of 1.4-2.3°C per 100 km across the APF. Thus the average change in temperature is abrupt and significant. However, while the APF was at one time seen as a barrier to some species, such as the chaetognath *Sagitta gazellae*, which had measurably different populations on either side (David 1955), Mackintosh (1960) found that many other species could be found on both sides. Subsequent research has shown that, for many plankton species, the APF is coincident with discontinuities in distribution rather than forming a barrier and in many cases abundances are elevated in its proximity (Atkinson and Sinclair 2000; Pakhomov et al. 2000; Dubischar et al. 2002), in part due to a retentive circulation (Pollard et al. 2002)

Within the macrozooplankton, the euphausiid *Euphausia superba*, or Antarctic krill, is certainly the best known species. Its high biomass and central role in foodwebs, particularly those linking primary production to higher predators is well documented (e.g. Smetacek and Nicol 2005; Murphy et al. 2007a; Flores et al. 2012). Gelatinous macrozooplankton, in particular salps (*Salpa thompsoni*), can also be regionally dominant and the response of both these species to a warming Southern Ocean is of great interest, as the balance of the two has the potential ability to significantly alter carbon flux (Le Fevre et al. 1998; Pakhomov et al. 2002; Atkinson et al. 2004).

As in other oceans, copepods dominate the total mesozooplankton across most of the Southern Ocean, in terms of biomass, abundance, grazing activity and secondary production. They typically comprise >75% of biomass and are only exceeded by krill or salps in some sub-regions in some years (Atkinson et al. 2012). In common with many other taxonomic groups, endemism within the Southern Ocean Copepoda is high. Park and Ferrari (2009) noted that all 8 coastal species belonging to the genera *Drepanopus*, *Paralabidocera* and *Stephos* are endemic and, of 184 deep-water species, 50 originally described from the Southern Ocean have not been found elsewhere. Many of the endemic species have been relatively recently described from under-sampled bathypelagic/abyssal and hyperbenthic environments which suggests that there are likely to be more new species described once these habitats are more fully investigated.

Most studies have however addressed the large species that dominate biomass, such as *Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus* and *Metridia gerlachei*. These species inhabit surface waters during spring and summer when they reproduce. Later in the season, lipid-rich stages may enter a state of diapause where metabolism is greatly reduced and the animals descend to depth to overwinter (Ommanney 1936; Andrews 1966; Atkinson 1991). Smaller taxa such as the *Oithonidae*, *Oncaeiidae* and small calanoids such as *Ctenocalanus citer* and *Microcalanus pygmaeus* have latterly received more attention and their importance in energy flow and recycling is beginning to be appreciated (Schnack-Schiel and Mizdalski 1994; Metz 1996; Atkinson 1998; Dubischar et al. 2002; Ward and Hirst 2007; Pond & Ward 2011).

CHAPTER 4: MESOZOOPLANKTON IN THE SCOTIA SEA: THE PRESENT 1

Basin-scale synoptic surveys

The CCAMLR 2000 survey (Watkins et al. 2004), the first multinational, multi-ship survey in the Southern Ocean since 1979/80, was planned to cover 15 degrees of latitude and 50 degrees of longitude and provide an opportunity to sample within the Atlantic sector on what approximated to a basin scale. Under normal circumstances, a synoptic view of this scale would have been difficult to achieve without temporal aliasing but the 4 ships involved completed the survey in only 29 days. I was successful in lobbying at the cruise planning stage to include mesozooplankton within this survey's remit.

The resulting 123 rectangular mid-water trawl (RMT1; 1m², 330 µm mesh) samples taken between January 11th – February 11th 2000, provided a synoptic basin-scale view of plankton distribution which is described in **Paper 1** (Ward et al. 2004). The approach adopted was to use the multivariate package PRIMER 5 (PRIMER-E Ltd 2000; Clarke and Warwick 2001), to elucidate mesozooplankton community structure and its relationship, if any, with water mass distribution. Abundance data were pooled within species, reducing the data set from 120 to 77 taxonomic categories. These data were log transformed and a matrix created that used all species that contributed $\geq 4\%$ of the total abundance at any one station to reduce the importance of rarer taxa. This further reduced the data set to 31 taxa. Two main groups of stations were disclosed by nearest neighbour clustering, the first located in the northern part of the ACC and the second further south, the border between the two running broadly along the line of the Weddell Front and the SBACC. Stations belonging to the latter group were also found west of the Antarctic Peninsula and around the South Sandwich Islands, suggesting a cold water influenced community. Four minor groups were geographically consistent with waters around the South Shetland Islands and in water influenced by the Weddell Scotia Confluence. Overall, median abundance was ~6-7 times higher in the more northerly of the two main groups. In terms of species occurrence, the dominant taxa across all groups was the Copepoda, accounting for

>90% of total counts within the two major groups, but only between 53- 75% for remaining groups where larvae of *Euphausia superba* were more prominent.

Although this study was a synoptic view of plankton distribution during the austral summer, its unprecedented scale allowed consideration of a number of different habitat zones within the Atlantic sector, from the northern seasonally ice-free waters extending up towards the APF to the southern edge of the ACC where it abuts the Weddell Gyre and where sea-ice cover is variable but present for a mean duration of ~160 days (SD 57 days) up to 1992 (Murphy et al. 2007a). Other community studies were reviewed, generally finding that the data derived from this large-scale study were in agreement, particularly with regard to the presence of neritic communities around the tip of the Antarctic Peninsula which were relatively impoverished in species abundance (Mackintosh 1934; Jazdzewski et al. 1982; Mujica and Torres 1982).

The analysis was rerun using a dataset that was more finely taxonomically resolved, using unpooled ontogenetic species stages. In this ordination, a group of stations intermediate in character was identified south of the SACCF, between the two largest groups of the reduced ordination. An analysis of similarity (ANOSIM) was carried out to test the congruence of community structure with water masses. Stations were classified according to where they lay in relation to the main frontal positions. The main boundary appeared to be the Weddell Front which separated plankton within the main body of the ACC from the Weddell Gyre. It appeared to reflect an important disjunct in the age distribution and abundance of copepods (where overwintered stages were found to the south, compared to a new generation further north), rather than taxonomically distinct communities. There was a generally poor fit found in relation to the position of the SACCF which appeared to have little importance in this study as a community boundary. In essence, this study showed that over most of the oceanic region, a single community existed although with variations, largely in terms of phenological development of species and the mass occurrence of patchily distributed organisms such as krill larvae. This, in many ways, supports the faunistic divisions proposed by Mackintosh (1934) who emphasised that boundaries were not geographically fixed and noted the strong structuring effect that pack-ice distribution and temperature have on zooplankton communities.

Paper 2 (Ward et al. 2006) built on this information and described community structure and variability in the Scotia Sea during another large-scale survey (JR82) undertaken during Jan –early Feb 2003 as part of the UK’s Southern Ocean GLOBEC initiative. The main aims of this initiative were to study large-scale population processes among krill and copepods in the Scotia Sea. A total of 61 stations were worked during the course of the cruise and, at all stations, a motion compensated Bongo net (0.61 m dia) equipped with a 200 μm mesh was deployed to 400 m and hauled vertically to the surface. Additionally, a Longhurst-Hardy Plankton Recorder (LHPR) was deployed at 8 stations to 1000 m and towed obliquely to the surface. The LHPR was programmed with a gauze advance time of 90 sec^{-1} which resulted in an ascent profile containing 45-60 patches with a depth resolution of ~ 20 m. Female *Calanoides acutus* and *Rhincalanus gigas* were isolated from Bongo net cod ends and incubated for 24 hours to establish egg production rates (EPRs) and investigate population processes. Carbon mass (C mass) determinations were carried out on various stages of the dominant copepod species. The results of this survey confirmed the previous investigation **Paper 1** (Ward et al. 2004), insofar as the various groups of zooplankton could be viewed as belonging to a single community, albeit one with regional differences in phenological development. This was reflected in the fact that latitude was the strongest single environmental correlate, with the community pattern mirroring the gradient in production which commences earlier in the northern part of the ACC during spring and summer. Surface chlorophyll was a weaker correlate of community pattern which is somewhat paradoxical given that the C mass of species stages measured and overall zooplankton abundance relate positively to measures of food biomass and quality.

However, while most species are present across the whole ACC they frequently have different centres of abundance, reflecting ranges, relationships with temperature and different behaviours. The strong positive relationships between indices such as carbon mass, EPRs and plankton abundance, with food related indices such as phytoplankton size, amounts (particulate organic carbon) and quality (total fatty acids), as well as water column nutrient levels (a proxy for past production; see Ward et al. 2007) suggested the importance of bottom up factors on mesozooplankton communities. Food limitation is therefore a major control, particularly in iron-limited regions (Smetacek et al. 2004).

There is no doubting the importance of sea-ice cover as a control on production processes in the Scotia Sea and this can reduce primary production and the ability of zooplankton to reproduce and develop at optimal rates. A receding ice edge can however have the opposite effect, by increasing water column stabilisation and promoting phytoplankton development, leading to copepod recruitment (Atkinson and Shreeve 1995; Burghart et al. 1999). Stage composition of *Calanoides acutus* and median population depth were consistent with an overwintered population being present in the southern part of the Scotia Sea with many females exhibiting high EPRs. In contrast, at the northern-most stations, population structure was commensurate with a new generation, the later stages of which were beginning a seasonal descent to overwinter. Based on current knowledge of development rates of *C. acutus* (Shreeve et al. 2002), an approximate 3 month difference in population age is indicated across the ~1000 km of the Scotia Sea, north to south.

Data from 2003 were compared with those obtained in 2000 and with an earlier study in the same region during summer 1981 (Brinton, 1985; Marin 1987). Satellite images indicated that during 1981, monthly ice-edge positions were close to the long-term average as ice retreated across the Scotia Sea from its northerly extent in September 1980 to a minimum in February 1981. During 2000 and 2003, the rates of ice retreat were largely indistinguishable from the mean until, in the case of 2003 (Cruise JR82), the retreat slowed and the region did not become ice-free until March, a month later (Figure 6).

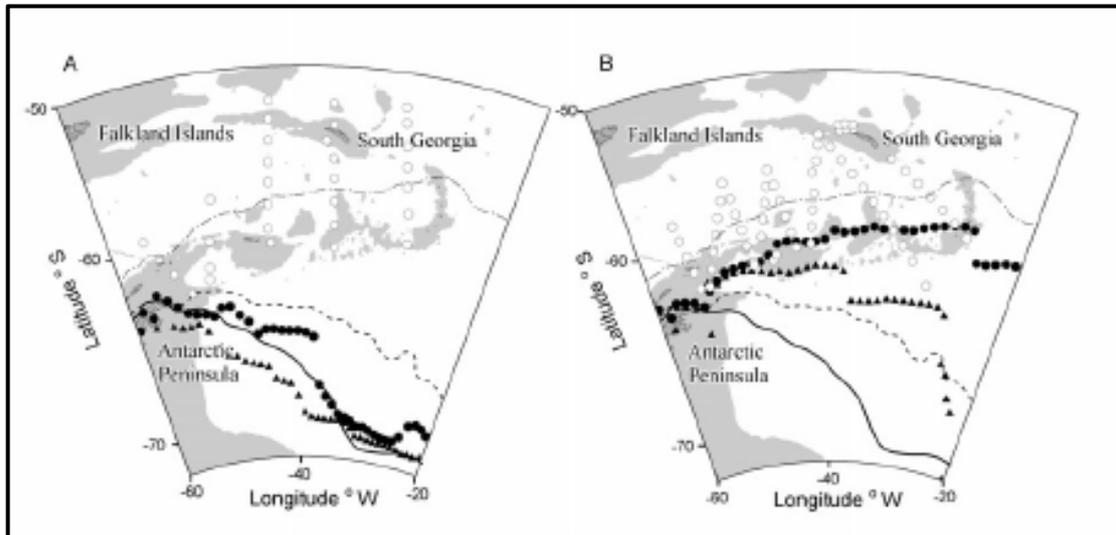


Figure 6: Mean positions of 15% ice edge during January and February 2000 (panel A) and 2003 (panel B) in relation to 25 yr monthly mean position. The pecked line represents the 25 yr average position during January and the solid line February. Filled circles are actual positions during January, filled triangles position during February. In both panels 25 yr average for August is shown as most northerly broken line.

Both seasons (1980/1981 and 1999/2000) in which the ice retreated in line with the 25 year mean were characterised by large numbers of krill larvae and a spring generation of copepods throughout the Southern Scotia Sea. In contrast, during 2002/2003 the existence of an overwintered (pre-recruitment) generation was noted until late into the summer as well as low numbers of krill larvae in regions where intense spawning normally takes place (Spirodonov 1985). A bloom to the east along the line of the retreating ice-edge was however coincident with higher EPRs of *C. acutus* and a shallower median population depth, than at comparable latitudes further west.

Viewing the findings of these two large-scale cruises together, it was concluded that while community structure and distribution were broadly similar, considerable variability in the production and development of zooplankton populations was seen. This appeared to be largely due to variation in the timing of sea-ice retreat over the summer period. Based on satellite data, Smith & Comiso (2008) also found that primary production was, to a large extent, determined by ice dynamics and with no sustained phytoplankton blooms occurring in waters >1000 m. While there is intense seasonal variability in many of the physical and biological properties of the Southern

Ocean, it was concluded that quantifying the impact that sea-ice dynamics has on production cycles will be an extremely important part of understanding community structure and function. Since these papers were published, the impacts of sea-ice on the community structure and the population dynamics of krill, other macrozooplankton and mesozooplankton, have been further explored (Flores et al. 2011; Hunt et al. 2011; Saba et al. 2014; David et al. 2017). Latterly, the role of ice algae in sustaining zooplankton populations has been investigated (Kohlbach et al. 2017; Schmidt et al. 2018).

Paper 2 was published in 2006, at a time when the importance of relationships between plankton and ocean-atmospheric forcing were being recognised and explored, notably in the North Atlantic (e.g. Planque and Taylor 1998; Beaugrand et al. 2002; Beaugrand and Ibanez 2002) and North Pacific (Brodeur and Ware 1992; Francis et al. 1998; McGowan et al. 1998). Likewise in some areas of the Southern Ocean, notably the west Antarctic Peninsula (WAP), where time series of sampling and observation are now approaching 25 years. It is here that modes of climate variability, like the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO), which interact with ocean processes over sub-decadal scales and their impacts on the flora and fauna are beginning to be teased apart (Loeb et al. 1997, 2009; Steinberg et al. 2015). This is explored more fully in Chapter 7.

CHAPTER 5: MESOZOOPLANKTON IN THE SCOTIA SEA: THE PRESENT 2

Seasonal Dimension

A series of 3 cruises carried out in October- December 2006 (Spring), January-February 2008 (Summer) and March-April 2009 (Autumn) allowed a seasonal investigation of mesozooplankton abundance, biomass and community structure to be undertaken. Collectively these cruises comprised the field element of the BAS Discovery 2010 programme, investigating spatial and temporal variability along a north-south transect located in the central Scotia Sea (Tarling et al. 2012). **Paper 3** (Ward et al. 2012a) and **Paper 4** (Ward et al. 2012b) used data collected during these cruises from stations along a transect extending from the South Orkneys at the base of the Scotia Sea up into the APF. **Paper 3** (Ward et al. 2012a) focussed on mesozooplankton and offered a seasonal comparison of abundance and biomass as well as community structure and variability. **Paper 4** (Ward et al. 2012b) provided an analysis of food-web structure and bioregionalisation using data from numerous cruise sub-disciplines such as nutrient chemistry, phytoplankton cell counts, acoustics, and mesopelagic fish biology as well as meso- and macro-zooplankton. Spatial variation across the Scotia Sea was described and the relative roles of frontal zones and ice cover in establishing observed patterns was discussed.

Net sampling was carried out using the previously described motion compensated Bongo net equipped with 100 and 200 μm nets. Additionally a smaller 0.18m dia. paired Bongo net with 53 μm mesh was deployed at each station. The emphasis in **Paper 3** was primarily an assessment of abundance and biomass by season rather than community structure, as the samples were restricted to a repeated transect. However, sampling disclosed that across all three seasons the same basic division of stations was apparent. A southern group was characterised by uniformly lower plankton abundance and biomass than a northern group in all seasons. The boundary between the two groups was broadly coincident with the SACCF (Ward et al. 2012b **Paper 4**). With a few exceptions, most taxa were widely distributed across the Scotia Sea and the consistently higher mesozooplankton abundance in Group 2 was reflected

in the abundances of *Oncaea* spp., *Oithona similis*, *Ctenocalanus citer* and *Metridia* spp. Some species were present in all seasons at broadly similar densities e.g. chaetognaths and ostracods whereas others were particularly abundant during one or more cruises e.g. appendicularians (summer) *Pelagobia longicirrata* (spring and summer) suggesting spring/summer recruitment, whereas *Euphausia superba* calyptopes were only seen in autumn and almost exclusively in the southern Group 1.

In this study (**Paper 3**), metazoan densities up to 8,800 individuals m^{-3} were recorded in the 53 μm nets from stations within Group 2, but 20 litre water bottle casts in the surface 100 m produced estimates of up to 40,000 individuals m^{-3} . Estimated ratios between the different meshes employed using median abundances were 1.71 for the 53 μm nets compared to the 100 μm nets and 5.9 for the 53 to 200 μm nets (Figure 7).

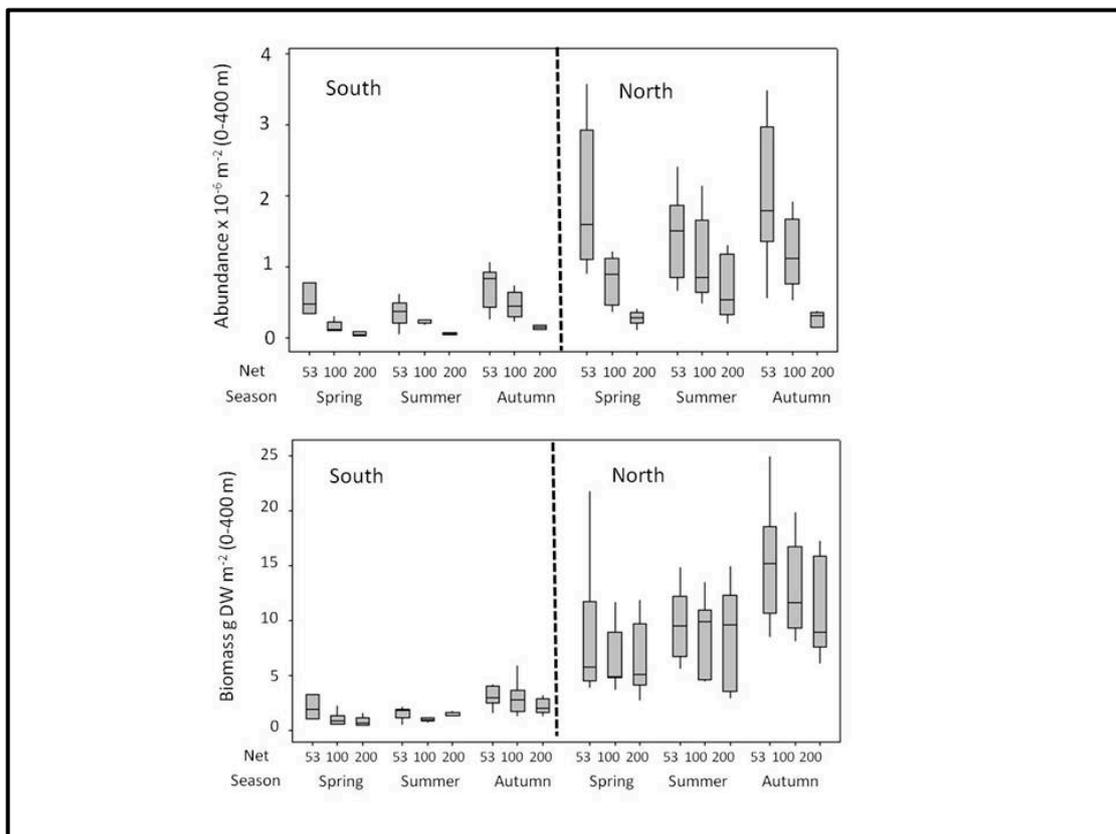


Figure 7: Boxplots of mesozooplankton abundance and biomass captured by 53, 100 and 200 μm mesh Bongo nets. Data shown on plot are median (line within box), Q1-Q3 (box ranges) and whiskers representing upper limit = $Q3 + 1.5(Q3 - Q1)$ and lower limit = $Q3 - 1.5(Q3 - Q1)$. Data are presented in relation to net mesh, season and station group (north and south) as determined by cluster analysis.

Biomass patterns contrasted with those of abundance insofar as there were no consistent differences between nets within Group 1 stations although autumn values across both groups were highest. Median biomass values were ~5-6 times higher in Group 2 in all seasons. Our data indicated that mean net abundances for the 100 μm nets averaged 58% of the 53 μm nets and 17% for the 200 μm nets. In terms of biomass, estimates were closer with the 100 μm nets averaging 99% of the 53 μm nets and 70% for the 200 μm nets. Use of fine mesh nets is challenging the view that the Southern Ocean is dominated by large secondary producers and short food chains. The contribution of small secondary producers to abundance and biomass was clearly seen in this study and their importance as grazers and recyclers has also been recognised (Dubischar and Bathmann 1997; Atkinson 1998).

Data-sets collected during the 3 cruises comprising nutrients, phytoplankton cell counts, meso-and macrozooplankton, fish and acoustic data were subsequently used to investigate food web structure and identify bioregions in **Paper 4** (Ward et al. 2012b). Various schemes have been used to partition the Southern Ocean into functionally distinct sub-units so as to facilitate ecosystem modelling, management and conservation (Grant et al. 2006). For example, Hempel (1985) considered that three distinct zones are present: the ice-free zone of the ACC dominated by copepods, salps and small euphausiids, the seasonal pack-ice zone of the East Wind Drift and areas of adjacent fronts and eddies in which Antarctic krill is dominant, and the permanent sea-ice zone near the Antarctic continent and its ice shelves where zooplankton biomass is low and predators are scarce. An alternative scheme based on phytoplankton and nutrient dynamics, proposed by Tréguer and Jacques (1992), defined 4 zones, similar to those of Hempel (1985), including the well mixed, permanently open, ocean zone (POOZ) and the seasonal sea-ice zone (SIZ) in which seasonal stratification near the receding ice edge is seen. Two zones of minor extent include the PFZ, where eddy activity is characteristic and the productive and coastal and Continental shelf zone. Finally, based on ocean colour satellite imagery and knowledge of the response of planktonic algae to physical forcing, Longhurst (1998, 2010) defined 4 zones, the south subtropical convergence province, the sub-Antarctic province (including the PFZ), the Antarctic province akin to the seasonal ice zone of

Tréguer and Jacques (1992) and the Austral Polar province much of which lies polewards of the Antarctic Circle.

The utility and robustness of a bioregional approach in the Scotia Sea was tested using biological and physical data from the three seasonal cruises. The transect spanned the POOZ and the PFZ to the north as well as the SIZ to the south and, although sampling took place across three seasons at different spatial scales and taxonomic resolutions, cluster analysis indicated consistent spatial divisions across a wide range of physical and biological data. Using physical and chemical data, (nutrient, temperature and ocean depth), two groups were distinguished which separated along the line of the SACCF. Biological data strongly supported this physical realisation, reinforcing the view that functionally different foodwebs exist on either side of the frontal zone. Given the findings in previous studies, whereby many species are widespread across the Scotia Sea, it should be emphasised that key organisms such as krill and salps may be common either side of the front, although may have different trophic roles. Krill are efficient at transferring carbon to a wide range of apex predators and episodically export faecal material to depth, whereas the salps are microphagous and could potentially contribute most to flux, especially in offshore waters (Le Fèvre et al. 1998).

Outside the Atlantic sector, the SACCF is not generally recognised as being coincident with significant faunal discontinuities. There is little evidence that it constrains the movement of krill or other zooplankton, either at the surface or at depth. Similarly, although primary production is higher in the northern part of the Scotia Sea, it is probably insufficient to underpin the 2-9 fold differences in abundance and biomass either side of the SACCF. There is a significant temperature gradient of $\sim 4^{\circ}$ - 5° C across the meridional extent of the Scotia Sea. Temperature effects on plankton are complex, influencing processes at a number of levels of biological organisation from whole organism mortality (Ward and Hirst 2007; Kiørboe and Hirst 2008) down to sub-cellular processes (Pörtner 2006). The southern part of the Scotia Sea is under the influence of seasonal ice cover which affects production, particularly if ice persists, and hence will exacerbate seasonal differences. The northern boundary of the ice-edge in the Scotia Sea is broadly coincident with the

SBACC at the point where it was crossed by the transect, but the marginal ice zone, where dilution effects are measurable, can extend up to 250 km beyond this.

Within the Southern Ocean, plankton diversity decreases from warmer to colder waters (Chiba et al. 2001), reflecting the fact that truly polar species are fewer in number and stenothermal. Further north there will be a wider mix of warmer water and more widely distributed species. In the southern parts of their ranges, some species such as *Calanoides acutus* and *Rhincalanus gigas* characteristically have 2-year life cycles, being unable to complete them in a single year (Marin 1988; Atkinson et al. 1997; Ward et al. 1997). Others, such as *Oithona similis*, have reduced fecundity at low temperatures because of increased egg hatching and development times.

The bioregional approach has also been explored for other faunal groups including benthic ones (Clarke et al. 2009), where small changes in seabed temperature corresponded well with spatially distinct communities of gastropods and bivalves. Koubbi et al. (2011) examined the distribution of myctophid fish in the Indian Ocean and defined up to 12 groups, many of which were separated by frontal features. The utility of such eco-regions remains to be seen, but such science-based approaches are clearly important in the process of identifying potential marine protected areas (Koubbi et al. 2016; Brooks et al. 2016).

In the preceding two chapters, I have set out the results and major findings from a number of large scale surveys undertaken across the Scotia Sea. This ‘contemporary’ data series has focused largely on the mesozooplankton, in particular copepods and discussed some of the factors that might influence their spatial and temporal distributions. The abundances and spatial distributions disclosed by these surveys, among others, form the basis for a comparison with historical data drawn from *Discovery Investigations* in the next section of this thesis.

CHAPTER 6: MESOZOOPLANKTON IN THE SCOTIA SEA: THE PAST

Discovery vs Contemporary

In the following section, the results and discussion of an investigation to compare the abundance and distribution of mesozooplankton during the 1920's and contemporary times, (1995-2005) are outlined (Ward et al. 2008 **Paper 5**). The study, centred on the island of South Georgia, in the north-east Scotia Sea, was based on historical data collected by *RRS Discovery* and *William Scoresby* during their 1926/27 surveys and BAS data collected as part of on-going investigations into the regional marine ecosystem. Data on *Discovery* zooplankton abundances were presented in the appendices of Hardy and Gunther (1935) and, although only representing one season, provided an opportunity to review whether the distribution patterns around South Georgia were similar to those seen in recent sampling. Some taxonomic issues had to be addressed, primarily the likely misidentification of *Oithona similis* as *O. frigida* in the original *Discovery* surveys and a number of other inconsistencies relating mainly to outdated nomenclature.

Discovery zooplankton data had been collected using a vertically hauled ring-net of 0.7m dia. fitted with various imperial mesh sizes (see Kemp et al. 1929). Equivalent metric sizes are a mouth panel of 5 mm knot to knot and two other panels of ~440 μm and ~195 μm respectively (see Ward et al. 2012c **Paper 6**). Contemporary samples were collected with a motion compensated Bongo net equipped with a 200 μm mesh. Phytoplankton samples during *Discovery* era were taken with a 50 μm mesh net vertically hauled from 50 m to surface.

Oceanographically, surface waters were ~1°C colder during the *Discovery* survey era than during the contemporary era, consistent with a decadal warming trend in this part of the Southern Ocean (Whitehouse et al. 2008). In other respects, circulation patterns appeared similar between eras and no large-scale differences in the position of frontal zones were detected. Phytoplankton counts and zooplankton data (both *Discovery* only) were input into a species by station matrix and analysed using routines within the PRIMER statistical package. Both groups exhibited patterns of distribution that were consistent with contemporary findings. The comparison of zooplankton

abundance data was initially restricted to BAS stations lying within 40 km of the original *Discovery* station positions to allow for spatial variation. Nonetheless, large inter-annual variations in zooplankton abundance were still apparent which meant that, despite having the lowest zooplankton abundance across all years, data from 1926/1927 fell within the range displayed by contemporary data. It should be noted that, at this time, no allowance could be made for differences in the filtration characteristics of the nets used. A percentage similarity index (PSI) analysis was also carried out (Figure 8), which showed that, despite inter-annual variability, there was little difference in zooplankton composition between eras.

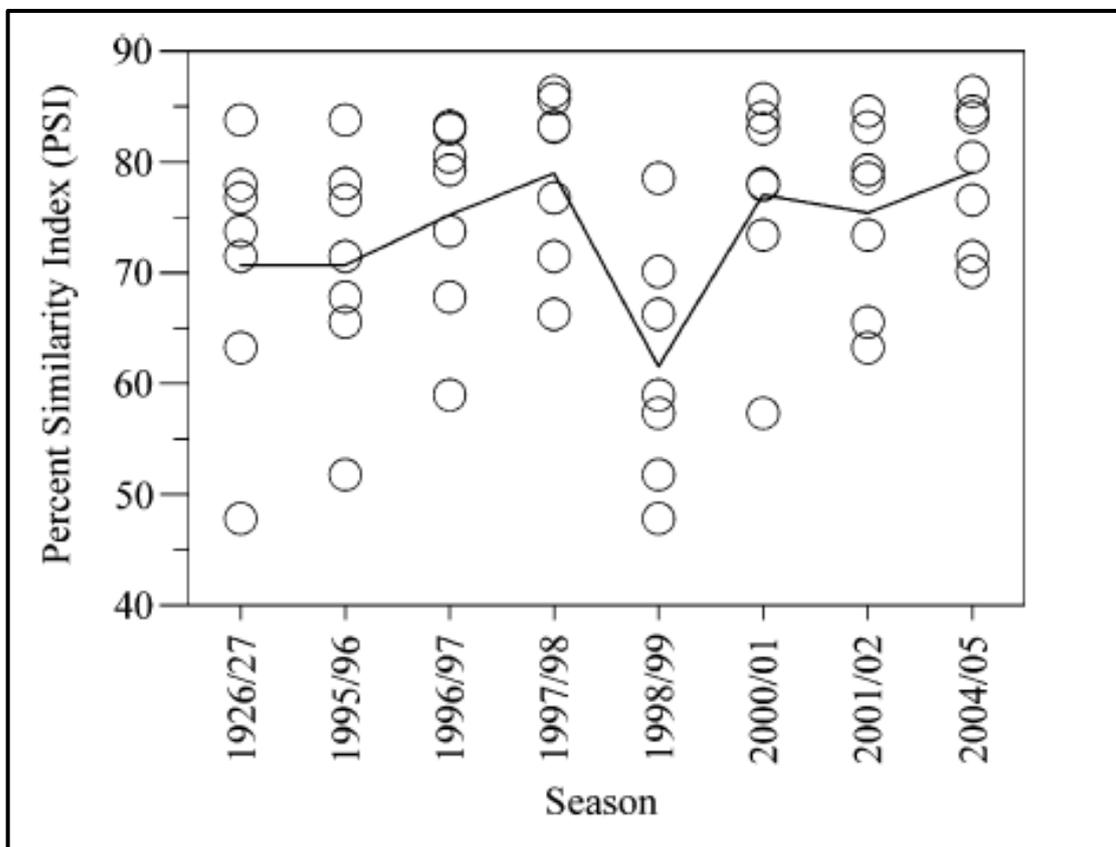


Figure 8: Percentage Similarity Index (PSI) based on a common matrix of 45 taxa taken from N70V(Season 1926/27) and Bongo nets (remaining seasons). Open circles represent PSI comparisons for that year and every other year in the series. Solid line is the mean across all comparisons.

In fact, the season most different from the others was 1998/99 in which the thecate pteropod *Limacina* spp. was extremely abundant. No long-term differences in these data were apparent from the analysis, although more subtle changes in species composition could not be ruled out.

Net calibration

One of the major issues with the potential to confound any comparison between eras is the use of different nets. In the case of the *Discovery Investigations*, the N70V, a ring net of 0.7m dia. comprised of three different mesh sizes, was commonly used and generally fished through six depth horizons from 1000 m-surface. The contemporary net used was a paired motion compensated Bongo net with the diameter of each net being 0.61 m and equipped with a uniform 200 μm mesh. This has usually been deployed between 200 m and the surface although for some cruises it was 400 m to surface. Plankton nets are known to be highly selective (Hernroth 1987; Nichols and Thompson 1991; Ward et al. 2012a **Paper 3**; Makabe et al. 2012; Antacli et al. 2014). In order to be able to standardize data caught by nets with differing filtration characteristics, a replica N70 net was constructed, based on the original plans in Kemp et al. (1929) and a cruise was spent fishing the two alongside each other to facilitate a comparison (Ward et al. 2012c **Paper 6**). Results clearly indicated that any comparison between contemporary and historical samples would require size related differences in plankton composition to be taken into account, as Bongo net catch abundance was ~ 3 times greater than the N70 and ~ 4 times greater when only copepod instars ≤ 0.5 mm body length were considered. Differences in catch ratio and species composition (% copepods) were also found with increasing Chl *a* concentrations. Both declined with increasing Chl *a*, although there was no difference in slope between % copepods and Chl *a*, caught by either net, there was a significant difference in elevation ($p < 0.001$).

Having established a difference between the two nets empirically (Figure 9), it became possible to carry out a quantitative assessment of mesozooplankton distribution, abundance and species composition between the two eras. Following the above corrections for net filtration differences, the adjusted abundance values for the *Discovery* cruise of 1926/1927 lay more closely within the range of abundances determined from the post-1995 samples although still somewhat at the lower end. Likewise, when the PSI analysis was re-run, no changes from the original were seen.

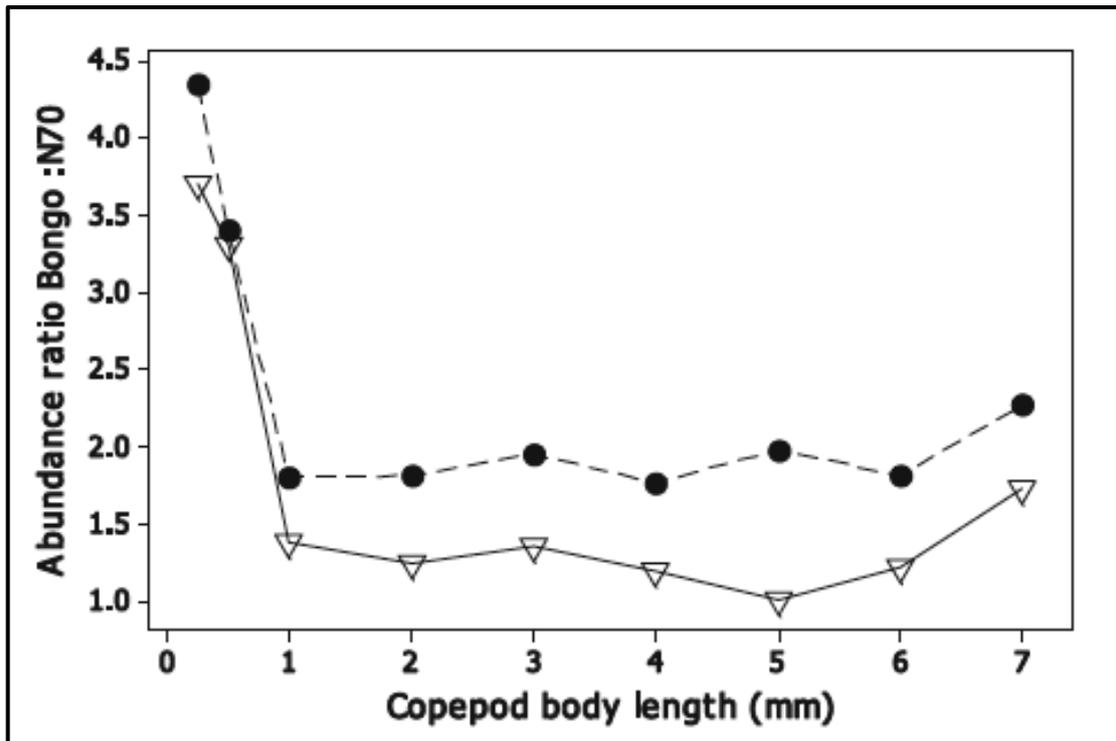


Figure 9: Mean Bongo:N70 copepod catch ratio in relation to body length. Pecked line with solid circles is low Chl a (<2 mg m⁻³), solid line with inverted triangles is high Chl a (>2 mg m⁻³).

In the final two papers discussed within this thesis, this comparative approach is extended to a series of net hauls taken from the wider Scotia Sea during *Discovery* times and also from contemporary cruises. However before discussing this in detail, Chapter 7 outlines the warming trends that have been apparent in the Southern Ocean since the start of routine measurements undertaken by the *Discovery Investigations* in the 1920s. This emphasizes some of the driving environmental processes that may have the potential to underlie any changes apparent in the plankton data. These of course are not simply restricted to physical processes. The Southern Ocean food web has been deeply perturbed in the last 100 or so years as a result of the commercial exploitation of stocks of seals and whales (Laws 1977, 1985; Hill et al. 2006; Trathan and Agnew 2010) and the long-term ramifications of this are only beginning to be explored.

CHAPTER 7: RECENT CHANGES WITHIN THE SOUTHERN OCEAN

Evidence for warming

Over the last 20-25 years the scientific literature has addressed at great length, one of the most challenging environmental issues mankind has faced in recent times, global warming. Both on land and in the oceans, warming has the potential to perturb ecosystems to the point where equilibrium changes and intrinsic qualities of structure and function begin to shift, change and break down (Walther et al. 2002; Walther 2010). In terrestrial environments agricultural practices may be seriously impacted and likewise, in the oceans, so may commercial fisheries. As one of the major aims of this thesis is to make a comparison between contemporary plankton abundance and distribution in the Scotia Sea with historical data, it is appropriate to review the evidence for warming in the Southern Ocean and to look at likely impacts.

That the world ocean is warming is beyond doubt (Levitus et al. 2000), yet its effects on the world's largest ecosystem, the marine pelagic realm, are largely unknown. Sea-surface temperature time series for the last 100 years show two periods of warming, the first in the 1920s-1940s followed by a period of cooling and then again in the 1970s. On a global scale, this warming trend implies that the ocean has gained heat from the atmosphere over the last 50 to 70 years (the maximum extent of most time series). Much of our current understanding of the mechanisms underlying warming and its effect on the marine environment has been gleaned from studies in the northern hemisphere which 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 (Fromentin and Planque 1996; Planque and Fromentin 1996; Taylor et al. 2002). Fluctuations resulting from changes in large-scale climate patterns such as the North Atlantic Oscillation (NAO) may be seen as a proxy for regulating forces in aquatic and terrestrial ecosystems (Stenseth et al. 2003). Evidence suggests that such climatic fluctuations influence 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).

The Southern Ocean is no exception to this trend and, from the 1930s through to the 1990s, warming has been detected throughout the upper 1000 m, principally within the ACC (Gille 2002, 2008). West of the Antarctic Peninsula, surface waters increased $>1^{\circ}\text{C}$ between 1951 and 1998 (Meredith and King 2005) associated with increased stratification in the upper layers and salinification caused by changes in sea-ice production (Turner et al. 2014). Within the Scotia Sea, warming around South Georgia has been documented over the last 80 years that is greater than that determined in the main body of the ACC. Within the surface 100 m, increases of $\sim 0.9^{\circ}\text{C}$ in January and as much as $\sim 2.3^{\circ}\text{C}$ in August have been detected (Whitehouse et al. 2008).

Atmospheric warming over the Antarctic continent has not been uniform. Surface temperature trends show significant warming across the Antarctic Peninsula and, to a lesser extent, West Antarctica since the early 1950s, with little change across the rest of the continent. The largest atmospheric warming trends occur on the western and northern parts of the Antarctic Peninsula. Vernadsky Station (65.48 S, 64.48 W) has experienced the largest statistically significant ($<5\%$ level) trend of $+0.53^{\circ}\text{C}$ per decade for the period 1951 – 2006, with winter temperatures increasing by $+1.01^{\circ}\text{C}$ per decade from 1950 – 2011 (Turner et al. 2014). The 100-year record from Orcadas on Laurie Island, South Orkney Islands, shows warming of $+0.20^{\circ}\text{C}$ per decade (Turner et al. 2005). Here, there is also a high correlation during the winter between sea ice extent and surface temperatures, suggesting more sea ice during the 1950s - 1960s and a reduction since then. Most recently Turner et al. (2016) documented cooling at the Antarctic Peninsula since the 1990's, suggesting that large natural decadal scale variability may underlie the overall trends seen since the 1950s.

Mechanisms of warming

Changes in the large-scale circulation of the atmosphere appear to underlie Southern Ocean warming, in particular the Southern Annular Mode (SAM) which is the dominant mode of extratropical variability in the southern hemisphere (Sen Gupta et al. 2012). It is a circumpolar pattern of atmospheric mass displacement in which intensity and location of the gradient of air pressure between mid-latitudes (high

pressure) and the Antarctic coast (low pressure) change in a non-periodic way over a wide range of time scales (Turner et al. 2014). The SAM has become more positive in the last 50 years, as pressure has dropped around the coast of the Antarctic and increased at mid- latitudes. Since the late 1970s, this change has increased westerly winds over the Southern Ocean by 15-20% (Korhonen et al. 2010; Turner and Marshall 2011) and moved them south by 1-2° of latitude. As a result, a deepening of the Amundsen Sea Low has occurred, with consequent effects on temperature and sea ice in the coastal region of West Antarctica as stronger westerly winds bring warm maritime air masses across the northern Antarctic Peninsula to the ice shelves on the eastern side. The increased warming is thought to have contributed to the recent collapse of the northern sections of the Larsen ice-shelf (Marshall et al. 2006). It has been suggested that the SAM also changed in response to the development of the Antarctic ozone hole in the Austral spring (Thompson et al. 2011) as well as local sea-ice loss (Turner et al. 2013).

ENSO events have also been highlighted as significant forcing agents of ecosystem change (Stenseth et al., 2002, 2003; Smith et al. 2003). ENSO is known to have a particularly strong influence on the Southern Ocean in the southern and south-east 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). Clem and Fogt (2013) suggested that both SAM and ENSO have a spatial dependency with regard to the impacts they have on the Antarctic Peninsula. Relationships with ENSO and Antarctic Peninsula climate are persistent and significant across the western Peninsula, while relationships with the SAM are persistent and significant across the north-eastern Peninsula.

Impacts of warming

The duration, extent, and seasonality of sea ice are among the principal physical determinants of variability in Polar ocean ecosystem dynamics, particularly in coastal Antarctic marine ecosystems (Ducklow et al. 2013). Since the advent of satellite observations in 1979, sea-ice extent in the Southern Ocean has increased slightly overall, although regional differences have been marked. In the WAP and southern Bellingshausen Sea regions over the period 1979-2004, Stammerjohn et al. (2008)

determined that sea ice is retreating 31 ± 10 days earlier and advancing 54 ± 9 days later, although the opposite trend is being experienced in the western Ross Sea region, where sea ice is retreating 29 ± 6 days later and advancing 31 ± 6 days earlier. These variations have been linked to ENSO and SAM variability causing changes in wind patterns and a deepening of the Amundsen Sea low (Turner et al. 2009, 2014) as well as changes in temperature (Jacobs and Comiso 1997) and patterns of sea-ice advection (Holland and Kwok 2012). At the WAP, longer periods of ice-free conditions in summer means that atmospheric warming will also contribute more to sea-ice changes acting as a positive feedback to enhance and sustain the rate of warming and sea ice retreat (Meredith and King 2005).

Spatial and temporal variability may obscure detection of ecological trends through discrete sampling. The absence of extensive time-series throughout much of the Southern Ocean also means that it is difficult to detect, and therefore predict, how long-term change might influence plankton dynamics. Relatively few studies on the impacts of warming on the pelagic biota of the Southern Ocean have been carried out. Most of these have taken place at the WAP, where time-series observations are now approaching 25 years. The general applicability of these findings to the greater part of the Southern Ocean is as yet unclear, as the extreme variability found at all levels of ecosystem organisation means that making predictions can be misleading if based on short term studies of a small number of species (Clarke et al. 2007).

Case Studies

At the WAP, plankton observations, as part of the Palmer Antarctica Long Term Ecological Research (PAL LTER), have been on-going since 1993. Here sea-ice cover has declined by as much as 90 days (Stammerjohn et al. 2008) and satellite colour imagery has shown that phytoplankton blooms declined by up to 90% in 1998–2006 compared with 1978–1986 (Montes–Hugo et al. 2009). Further south, sea-ice loss opened up new areas of the ocean for phytoplankton growth (Montes–Hugo et al. 2009) so, paradoxically, both decreasing phytoplankton blooms in the north and increases in the south are a response to a warming climate (Obryk et al. 2016).

Steinberg et al. (2015) investigated population abundances of a number of macrozooplankton species and found significant relationships over time with sea-ice, chlorophyll, temperature and climate modes such as the SAM and ENSO. Many environmental factors were found that explained temporal variation in abundances. A combination of atmospheric indices (+SAM - ENSO (La Niña)) that favoured low sea-ice extent, cyclonic atmospheric circulation, and increased frequency of warmer NW winds extending further polewards favoured species such as salps, the pteropod *Limacina* and the polychaete *Tomopteris* but not the ice associated euphausiid, *Euphausia crystallorophias*. In contrast, the opposite circumstances; (-SAM +ENSO (El Niño)), favoured anticyclonic atmospheric circulation, cold southerly winds over the WAP, greater sea-ice sea extent and potentially colder surface waters. Negative associations were then apparent with all of the aforementioned species except *E. crystallorophias* which was positively associated with such conditions. Some species such as *E. superba* and *Thysanöessa macrura* appeared to be under bottom up control and were more closely tied to primary production. Many of the associations were multi-factorial including links to ENSO and SAM and could be either coincident or have lagged delays of up to 1-2 years particularly in the case of *E. superba*, a long-lived species. There was also a suggestion in the data that carnivorous zooplankton increased over time potentially exerting greater top-down control.

At the northern Antarctic Peninsula, the findings of Loeb and Santora (2012), supported the role of multi-year atmospheric-oceanic processes associated with ENSO, affecting the population dynamics of *Salpa thompsoni*. Population increases appeared to be initiated during the reversal from La Niña to El Niño conditions within the multi-year ENSO cycle. Similarly, the balance between salp-dominated coastal zooplankton assemblages and copepod-dominated oceanic zooplankton assemblages also varied depending on the relative influences of Weddell Sea and oceanic waters (Loeb et al. 2010). Fluctuations were associated with latitudinal movement of the SACCF driven by ENSO variability. Decreased north-west winds and equatorward movement of the ACC allowed Weddell Sea water to flow into eastern Bransfield Strait promoting mixing between oceanic and coastal waters. As a result, Chl *a* concentrations were low, salps numerically dominated the zooplankton and krill recruitment was poor. In contrast, increased frequency of north-west winds and poleward movement of the SACCF allowed an increased influence of oceanic waters

and mixing with cold coastal waters. These periods are characterized by numerical dominance of copepods, elevated concentrations of oceanic zooplankton taxa and phytoplankton blooms that promote krill reproduction and recruitment. Similar responses were found from a number of other euphausiid species which were generally more abundant in the higher productivity La Niña phase (Loeb and Santora 2015).

From these studies it has become clear that Southern Ocean plankton abundance, composition and productivity can be linked to conditions brought about by ocean-atmosphere interactions such as SAM and ENSO at temporal scales that are presently decadal. The majority of such correlative studies have been carried out in a relatively small region of the Southern Ocean where frontal zones interact with shelf bathymetry causing upwelling and mixing of warmer nutrient rich Circumpolar Deep Waters (CDW) from the ACC with shelf waters where water masses abut. The studies are therefore somewhat constrained spatially, but located in a region that has been warming rapidly and where physical and biological changes are clearly apparent. The extent to which results are applicable to the wider Southern Ocean remains to be seen, although, with increasing circumpolar westerlies, temperature increases over the continent (average $0.34^{\circ}\text{C dec}^{-1}$) and a reduction in sea-ice of up to 33% ($\pm 9\%$) both predicted by 2100 (Bracegirdle et al. 2008), change will undoubtedly occur. There are however enormous difficulties in sampling at the frequency required over greater spatial scales. With the exception of the Southern Ocean CPR survey (Hosie et al. 2003) there are no other time-series samples that are comparable.

CHAPTER 8: ADAPTATION AND/OR CHANGE WITHIN THE SCOTIA SEA

Adaptation

Paper 7 (Tarling*, Ward* & Thorpe 2017 - * joint first authors) and **Paper 8** (Ward et al. 2018) both investigated the potential impacts of warming on the mesozooplankton populations within the Scotia Sea. Initially, the question of whether plankton had responded to ocean warming by following the thermal envelope that they occupied in the 1920-30s and moved polewards, as suggested by Mackey et al. (2012), was investigated. This is one of three possible options generally cited as a response to warming, the other two being adaptation or extinction (Clarke 1996). Samples taken with the N70V within the Scotia Sea were identified from the *Discovery Investigations* Station Lists (Anonymous 1929; 1931; 1932; 1941; 1942; 1943) and then located in the collections of the Natural History Museum (London), the current repository for the *Discovery* collections. Samples from a total of 155 stations occupied during the period 1926-1938 were analysed using standard protocols (Ward et al. 2012c **Paper 6**) and a comparison made with 451 contemporary samples taken during 1996-2013 with a variety of different nets. All stations were located south of the APF in water depths > 500 m, from the region defined by 65°-49°S, 80°-20°W and were taken between October and April.

Temperature data relating to the *Discovery* stations was also transcribed and compared with that from contemporary campaigns. Analysis was confined to the crustacean component of the sample data which comprised ~90% of the sample by abundance and specifically the 16 dominant (in both abundance and biomass) species of copepod. All data were normalised so that each taxon made an equal contribution to the community response. As the contemporary samples were taken with two different nets utilising three different modes of deployment, this process was undertaken separately for each mode, before concatenating the three matrices into one before further analysis.

It was determined that the median surface temperature had increased by 0.74°C and the temperature at which community abundance peaked had also increased, this time

by 0.98°C. Spatial projections suggested that little change had taken place in the geographical location of plankton in the intervening years. If plankton had followed the thermal envelope from the earlier era, then plankton would be expected to be up to 500 km further south in the contemporary era.

The ranked abundance of the 16 species between eras was also compared using the N70V nets and contemporary Bongo net catches that sampled the upper 200 m, as these were deemed closest in sampling method to the N70V. No major shift in rank of the dominant taxa was observed (Figure 10).

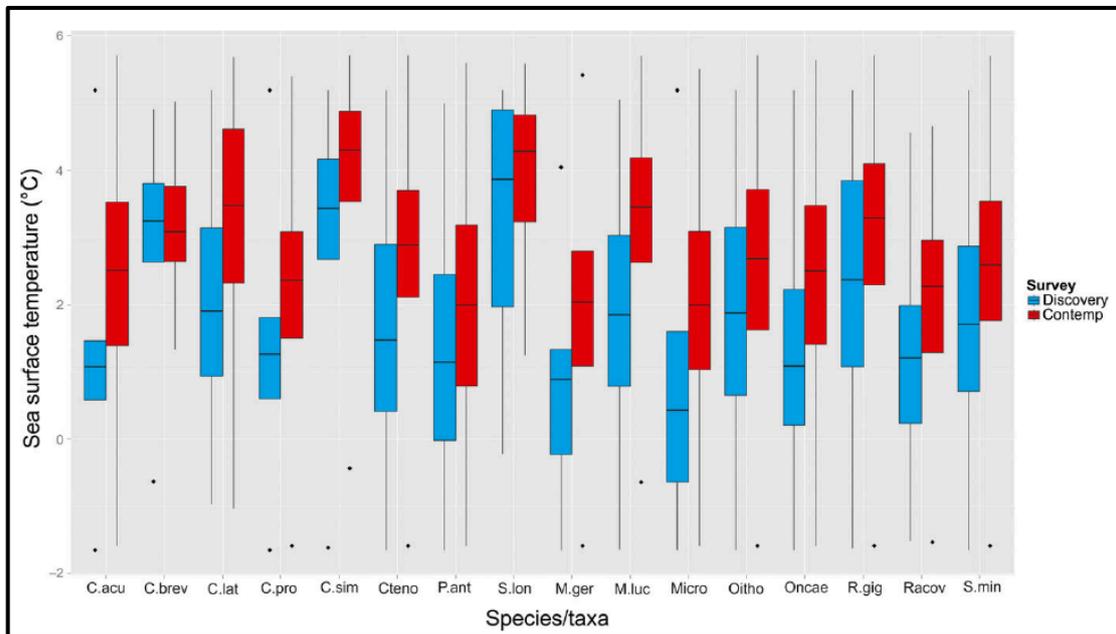


Figure 10: Sea surface temperature ranges of individual mesozooplankton taxa between eras. Sea surface temperature ranges of 16 dominant taxa (in terms of abundance and biomass) in the Southern Ocean Atlantic sector (65–49°S, 80–20°W) during the *Discovery Investigations* (October to April 1926–1938) and contemporary times (October to April 1996–2013). The horizontal line in each box represents the median temperature of occurrence (M_0). Upper and lower box limits denote the 25th and 75th percentiles, whiskers, 5th and 95th percentiles, and dots, maximum and minimum.

The names of taxa have been abbreviated, as follows: C.acu = *Calanoides acutus*, C.brev = *Clausocalanus brevipes*, C. lat = *Clausocalanus laticeps*, C. prop = *Calanus propinquus*, C.sim = *Calanus simillimus*, Cteno = *Ctenocalanus* spp., P.ant = *Pareuchaeta antarctica*, S. lon = *Subeucalanus longiceps*, M. ger = *Metridia gerlachei*, M. luc = *Metridia lucens*, Micro = *Microcalanus pygmaeus*, Oitho = *Oithona* spp., Oncae = *Oncae* spp. R. gig = *Rhincalanus gigas*, Racov = *Racovitzanus antarctica*, S. min = *Scolecithricella minor*

Factors determined as part of a series of comparative net trials (Ward et al 2012c **Paper 6**) were applied to the catch data to compensate for differences in size related catching ability. Figure 9 shows that there was a high degree of uniformity in the response to ocean warming with the median temperature of occurrence (M_0) of 15 of

the 16 taxa being higher in contemporary times than in the *Discovery* era. Data ranked according to M_o did alter between eras with some species moving towards colder rankings e.g. *Pareuchaeta antarctica* and *Clausocalanus brevipes*, whereas others such as *Calanoides acutus* moved towards a warmer ranking. However, no major shift in the rank of the dominant taxa was apparent between the two eras when ranked according to abundance.

These data are the first to emerge documenting the response of mesozooplankton to long-term temperature change in the Southern Ocean. The fact that the dominant taxa have been resilient to the poleward shift in surface isotherms is in contrast to species in the northern hemisphere that have tended to maintain their historical relationship with temperature (Beaugrand et al. 2002; Hinder et al 2014). Reasons for this may lie in the limited scope to move south in this sector of the Southern Ocean. The current flow in the ACC across the Scotia Sea is in a north-eastwards direction and is bounded to the south by the Weddell Gyre where, presently, sea-ice persists until well into the Antarctic summer. Food supply will also be a major factor in determining plankton distributions. There is strong evidence that iron availability controls the distribution and growth of phytoplankton in the south-west Atlantic sector (Martin et al. 1990, de Baar et al. 1990, Buma et al. 1991). High chlorophyll concentrations are associated with temperature and density profiles that indicate mixing of ACC waters and iron enriched waters from coastal regions or upwelling of deeper waters associated with bathymetric features (Wadley et al. 2014). Given the foregoing, it is unlikely that the distribution and periodicity of chlorophyll will have changed much in the last 60-70 years. The capacity of many of the plankton to avoid the worst of warming via, for example, seasonal migrations out of the surface waters and into the underlying Circumpolar Deep Water (CDW), where warming is an order of magnitude lower than at the surface, will also be important. Physiological conditioning by exposure to a varying temperature regime either seasonally or via, for example, the intrusion of mesoscale eddies from north of the APF (e.g. Boehme et al. 2008), is also likely to be a factor.

Change

Having established that mesozooplankton in this sector of the Southern Ocean appears to have adapted to a warming ocean, **Paper 8** investigated whether plankton abundance in the Scotia Sea has changed markedly in the last 60 years. Abundances of the large calanoids *Calanoides acutus*, *Rhincalanus gigas*, *Calanus simillimus* and *C. propinquus* which between them dominate copepod biomass in the Southern Ocean were considered.

Data from **Paper 6**, the N70: Bongo comparison (Ward et al. 2012c), were used to facilitate this and calibration factors based on normalised residual differences between the N70 and the Bongo catches were determined to produce a species-specific calibration for each of the four species. Analysis was confined to samples taken in the austral summer months of December-February and the dataset was further restricted to exclude geographical extremes and thus removed anything equatorwards of 52°S and polewards of 66°S. The sample set accordingly comprised 53 N70V stations supplemented with the addition of a further 10 stations sampled during December 1926 and January 1927, for which data were extracted from the *Discovery Report 11* (appendix of Hardy and Gunther 1935, see Ward et al. 2008 **Paper 5**).

These were compared with 147 contemporary Bongo net samples taken from 200-0m. Samples were spread unevenly across the months, particularly in January, where contemporary samples greatly outnumbered *Discovery* samples and so for both the *Discovery Investigations* and contemporary datasets 10 data points were selected at random (with replacement) from each of the three months and combined to make a new resampled dataset of 30 data points, for which an average was determined. The process was repeated 30 times for each species, to which statistical tests were then applied. Sensitivity analyses considered increasing the calibration factors by 25%, 50% and 100% or none at all. For seasonality, sensitivity runs were carried out to determine the effect of removing the resampling process. The 1.25 multiplication factor to the *Discovery Investigations* nets was also removed in a further test to determine its implications.

Having accounted for differences in seasonal coverage on abundance, absolute abundances were found to be significantly different between eras. Of the four species examined, 3 were significantly more abundant during contemporary times (~20-55%) with only *Calanus propinquus* being marginally more abundant in the *Discovery* era (Figure 11).

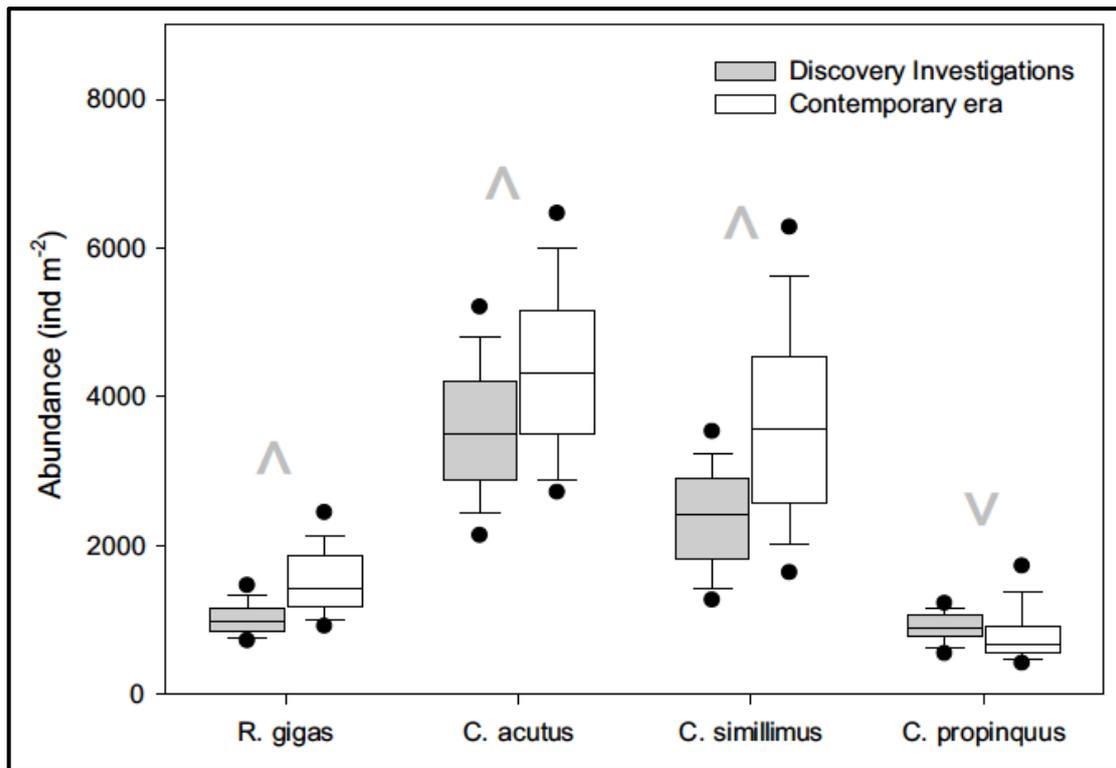


Figure 11: *Discovery Investigations* vs Contemporary abundance: Box plot of estimated abundance (ind m⁻²) of *R. gigas*, *C. acutus*, *C. simillimus* and *C. propinquus* during the *Discovery Investigations* and contemporary times. Horizontal line represents the median, limits of boxes, 25th and 75th percentiles, limits of whiskers, 10th and 90th percentiles, dots, 5th and 95th percentiles. ^ indicates abundances during contemporary era were significantly larger than those during the *Discovery Investigation* era, v, that *Discovery Investigation* era abundances were significantly larger than those in the contemporary era ($p < 0.05$).

Levels of significance were relatively insensitive to the net intercalibration factor and only when it was increased by 50% was there any change in the result with the difference in *C. simillimus* no longer being significant. Increasing the calibration factor by 100% made the difference in *C. acutus* no longer significant although that in *R. gigas* remained significant. Greater sensitivity was exhibited in relation to

seasonality in abundance levels, with the removal of resampling procedure to dampen the effect of different levels of sampling effort between months increasing the level of difference between eras, with even *C. propinquus* now exhibiting significantly greater abundances in contemporary times. Removal of the 1.25 multiplication factor to accommodate the different integrated depth intervals between the *Discovery* and contemporary nets made little difference to the levels of significance in abundance between eras.

Having established differences in copepod abundance between eras, these were considered in the context of how the Southern Ocean, or at least the Scotia Sea, may have changed in the intervening 70 years. Temperature was initially considered as the agent of change but the $<1^{\circ}\text{C}$ increase in Sea Surface Temperature (SST) in itself was insufficient to have had an impact on the biogeography of species and it is hard to see how this alone would impact on population demography and account for the differences observed.

Changes elsewhere in the food web were also considered, initially focussing on available Chl *a*, although there is no sure knowledge as to whether primary production was higher in the *Discovery* era. More recently, satellite data are ambiguous in this regard, with both significant increases (Smith and Comiso 2008) and decreases (Gregg et al. 2003) being reported. Increased abundance of large calanoids could have arisen due to an increase in available food, a relaxation of predation pressure, or both. It has been suggested that krill may have a central role in the foodweb where it influences trophic levels above and below itself in a so-called 'wasp-waist' ecosystem (Flores et al. 2012; Atkinson et al. 2014). Looking down the food chain, intense preferential grazing of diatoms by krill swarms can alter phytoplankton species composition, leading to a dominance of flagellates $<20\ \mu\text{m}$ (Jacques and Panouse 1991; Kopczyńska 1992; Granéli et al. 1993). Looking up the food-chain, fluctuations in krill biomass varies its availability to higher predators and can affect breeding success and population size (Reid and Croxall 2001; Trathan et al. 2007). It has been suggested that, historically, both whales and krill were able to act as 'ecosystem engineers' in the sense that by virtue of their great abundance they were, and are, important recyclers of nutrients essential for phytoplankton growth (Tovar-Sanchez et al. 2007; Willis 2007, 2014; Smetacek 2008; Nicol et al. 2010;

Schmidt et al. 2011; Lavery et al. 2014). In this way, increased phytoplankton production would have supported a greater krill population, ultimately benefiting whales and perhaps placing greater pressure on copepods, both as competitors and as potential prey. Krill may also act as predators of copepods (Atkinson and Snýder 1997; Atkinson et al. 1999) and, under conditions of low phytoplankton biomass and production, have the potential to impact copepod stocks.

Ecosystem impacts

The reported recent decline in abundance of krill in the South Atlantic sector of the Southern Ocean (Atkinson et al. 2004, Atkinson et al. in press) as a result of rapid regional warming will have changed the amount of carbon passing through direct diatom - krill - higher predator food-chains. Copepod and krill food-webs have different characteristics in terms of carbon demand and fate, depending on which is the dominant organism. Krill grazing can decrease phytoplankton standing stocks, particularly when swarms are present, although copepods rarely do unless standing stocks are low (Atkinson 1996; Dubischaar and Bathmann 1997). Within the Scotia Sea, krill and copepods are the dominant crustaceans, with krill tending to be more abundant in the southern part and copepods towards the north (Ward et al. 2012b **Paper 4**). At South Georgia, abundances of krill and copepods are negatively related across a range of scales suggesting direct interactions, either as competitor or predator (Atkinson et al. 1999). Priddle et al. (2003) modelled the biogeochemical consequences of grazing by krill and copepods and found they had different outcomes in terms of nutrient regeneration and resupply to primary producers. In a low krill-high copepod scenario, higher phytoplankton biomass and production, lower mixed layer (ML) ammonium, nitrate and silicate concentrations, and higher detrital carbon were predicted than for a high krill-low copepod scenario. Phytoplankton chlorophyll biomass was negatively related to krill biomass, and ML nutrients were positively correlated with krill biomass in these data. Both observations and model results suggest that variation in biogeochemical carbon and nitrogen cycles in the South Georgia pelagic ecosystem is determined largely by changes in zooplankton community composition and its impact on phytoplankton dynamics.

Contemporary estimates of krill and copepod biomass suggest that copepod standing stocks are at least equal to those of krill and may exceed them (Voronina 1998). Estimates of copepod versus krill production around South Georgia (where the biomass of both groups is generally high) indicated that the copepod community as a whole may be 4 times as productive as krill (Shreeve et al. 2005). Over the wider scale, Voronina (1998) estimated that 92% of annual zooplankton production in the Southern Ocean can be attributed to copepods whereas Conover and Huntley (1991) considered it to be three times higher based on estimates of ingestion and assimilation. Given that the biomass of baleen whales was so much higher in the past, it seems axiomatic that krill biomass must also have been higher than contemporary estimates to support it (Willis 2007, 2014; Smetacek 2008). The balance of production would also have changed, but even with large calanoids being 50% less abundant in the past, copepods would still have contributed significantly to secondary production.

Paper 7 showed that over the last 70 years, despite warming, the geographical distribution of the plankton community of the Scotia Sea has remained the same. **Paper 8** subsequently showed that, despite the rank order of species abundance staying broadly the same across time, there have been changes in absolute abundance of three of the four of biomass dominant copepod species. The factors we deem most likely to be responsible are linked through to changes occurring within the food chain brought about by decreasing krill abundance, both as a result of warming induced habitat loss and possibly also the commercial exploitation of whales.

CHAPTER 9: THE FUTURE

Predicted physical changes

Predicted physical changes in Antarctica are based on IPCC Fourth Assessment Report (AR4) models in which surface warming over Antarctica is predicted to increase by 0.34°C (0.14-0.5°C) per decade over land (Bracegirdle et al. 2008). Predicting changes in ocean temperature is harder due to the uncertainties of the mechanisms behind current warming trends linked to atmospheric circulation and sea-ice extent. Model iterations suggest warming of the ACC by 1-1.5°C over the 21st century as well as a significant loss of sea-ice, particularly in the Atlantic and Indian Ocean sectors (Liu and Curry 2010). The rise in SST recorded across much of the Scotia Sea to date is, in physiological terms, small (Clarke et al. 2007; Peck 2011), although continued warming may induce ecosystem effects that may have important consequences. Murphy et al. (2007b), for example, predicted that a further 1°C rise in temperature will reduce krill biomass at South Georgia by up to 95% in the next 100 years and Hill et al. (2013) suggested significant reductions in habitat suitable for krill growth over similar projected temperature increases. It has also been recently suggested that the impacts of a changing food environment are likely to be more important to copepods such as *Calanus* spp. than increases in temperature of the order currently predicted (Mayor et al. 2015).

Recent reviews by Constable et al. (2014) and Gutt et al. (2015) discussed in broad detail how projected changes in physical habitats may affect marine biota and also acknowledge the difficulties in doing so. They concluded that the output of coupled ocean-atmosphere models predict strengthening of westerly winds with potential southerly movement of the winds and frontal zones and an increase in eddy activity. The projected major physical changes in the upper water column will be an overall warming and freshening, hence increased density stratification and shallower surface mixed layers. Such stratification may reduce nutrient supply from the deep ocean (Boyd et al. 2008), although shallower mixed layers mean increased irradiance levels. However, Sallée et al. (2010) predicted asymmetric deepening of the mixed layer depth as a result of the above changes.

It can also be inferred that southerly movement of winds may lead to movement of plankton assemblages if fronts move south and there may also be a rebalancing of krill and salp populations as a result of sea-ice loss (Loeb et al. 1997; Atkinson et al. 2004; Bernard et al. 2012). Increased eddy transport across the ACC is also predicted to occur (Meredith and Hogg 2006; Hogg et al. 2008, Hogg et al. 2015) which may also be a causal factor in future warming

Southwards movement of ACC frontal zones have often been predicted as a result of changes associated with climate variability, in particular the strengthening of winds promoting the southwards flux of heat. Movements have been detected via changes in sea surface height (SSH) (Gille 2008; Solokov and Rintoul 2009a, 2009b), and Gille (2014) suggested that meridional shifts may be associated with large-scale changes in SSH rather than frontal displacements. Within the Scotia Sea, fronts are generally thought to be steered by bathymetry (Murphy et al. 2007a), and are relatively constrained, rather than being free to meander as they may otherwise do over flat abyssal regions.

Much of the potential for warming to affect Southern Ocean plankton is based on observation and modelling of how the ocean physics will respond. For example, Gregg et al. (2003) suggested that decreases in satellite-sensed chlorophyll from CZCS and SeaWiFS records in the Antarctic basin may be due to increased wind stress rather than increased temperature. Reductions in sea-ice, which is an important seasonal structuring factor in the Scotia Sea, has already been implicated in the loss of krill spawning and overwintering habitat (Atkinson et al. 2004). Melting of icebergs also has the potential to increase nutrient supply into surface waters and increase primary production (Smith et al. 2007), whereas increased stratification could potentially reduce the supply of nutrients from the deep ocean which will control rates of primary production (Boyd et al. 2008). It is anticipated that the impact of all of these factors will vary regionally.

Predicted Biological Changes

Although the present level of Southern Ocean warming is within the bounds of variability experienced by many pelagic organisms over the course of their lifetime ($\sim 1^{\circ}\text{C}$), there has been a great deal of speculation regarding how organisms will respond to prolonged long-term change (Clarke et al. 2007; Trathan and Agnew 2010; Constable et al. 2014; Gutt et al. 2015). Many species are adapted to life at low temperature and having a reduced ability to adapt to increasing temperatures. However, not all plankton are evenly spread across the ACC, and many have biogeographic ranges that extend beyond the ACC on one side or the other. Consequently they have different core temperatures and their ability to adjust will vary accordingly. Thus community composition is likely to change over time, favouring species better able to cope with increasing temperatures. At the moment it is assumed, somewhat simplistically, that this will in future mean warmer water species will be distributed further south whilst the range of cold-water species contracts (Mackey et al. 2012).

Data presented in **Paper 7** suggested that this has not yet happened in the Scotia Sea and that dominant mesozooplankton species have conserved their distributions. How long this will continue, or indeed whether it will be the case in other regions of the Southern Ocean, remains to be seen. The paper simply considered whether changes in SST over the last ~ 70 years are correlated with any changes in plankton distribution over the same period. It is not known whether temperature, directly acting on the physiology of the organisms, or in combination with other environmental changes, as a result of increasing temperature, would be the most important factor in any future scenario.

Increasing temperatures will also affect zooplankton in terms of their basal metabolism, with a greater proportion of energy being devoted to maintenance rather than growth and reproduction (Clarke 1990). This may ultimately affect individuals and populations, particularly if food is limiting. In terms of growth and development, Ward and Shreeve (1998) showed that copepod species had differing responses of egg development times to changing temperatures. Warming will decrease development

times and may eventually allow completion of life-cycles in a single year as opposed to areas where this currently takes two (Atkinson et al. 1997; Ward et al. 1997). Those species that have multi-generations within a year may well be favoured. Hill et al. (2013) have suggested that, for *E. superba*, food availability in regions like South Georgia, in the northern part of its range, can compensate for high temperatures which would otherwise reduce growth. However, reductions in primary production as a result of warming may compromise the amount of habitat currently available for growth.

Marine ecosystems are extremely complex in terms of feedbacks and interactions (Stenseth et al. 2002) and there are numerous ways populations can be influenced, either through physical and foodweb effects, competitive or predator prey interactions, or directly on the physiology of the organisms (Murphy et al. 2007a). In this respect, probably more is known about the response of Antarctic krill, a long-lived species of macroplankton, to warming than any other pelagic species. For example, decreasing sea-ice in certain sectors of the Southern Ocean appears to influence krill in a number of ways. Decreased over-wintering habitat, because of its importance for larval recruitment and survival, was recognised early on as affecting population size (Siegel and Loeb 1995; Loeb et al. 1997; Atkinson et al. 2004; Murphy et al. 2007a).

Sea-ice was also seen to be important in the dispersal of krill across the Scotia Sea. Larvae released from an ice-edge further south may not disperse across the Scotia Sea to the same extent as those released further north in a good ice year (Thorpe et al. 2007). Sea-ice also has a function in conditioning the water column. At the WAP, Saba et al. (2014) have shown that a negative mode of the SAM is commensurate with cold southerly winds in winter, increasing sea-ice extent and duration. This, coupled with reduced winds in spring/summer, leads to increased water column stratification and higher phytoplankton biomass fuelling successful krill recruitment. A recent view that challenges the central importance of climate variability on krill population dynamics has been put forward by Ryabov et al. (2017), identifying intraspecific competition for food as the main reason for cyclic changes in krill biomass. When krill biomass passes a critical level, such a factor is thought to operate on recruitment particularly in the autumn period when phytoplankton is generally

scarce. Increased competition for food leads to a longer period of starvation that has to be faced by larval krill which are less able to resist starvation. However when krill biomass is small, there is less grazing on phytoplankton stocks and larval survival is consequently greater.

Further up the food chain, from the perspective of higher predators, a warming environment has had measurable adverse impacts on fur seal pup production at South Georgia, almost certainly through cascading effects of krill scarcity in warm years (Forcada et al. 2005, 2008). It is also thought to contribute to declining population trends in albatrosses and penguins (Reid and Croxall 2001) and for similar trends in birds and seals in the Indian Ocean sector of the Southern Ocean (Weimerskirch et al. 2003). Declining numbers of adult krill at South Georgia has also been attributed to local mortality and the average size of krill consumed by predators in the 1990's was distinctly smaller (mode of 42 mm compared to 56 mm) when compared to the 1980s (Reid and Croxall 2001).

Because of the great inter-annual variability in timing of population processes within the Southern Ocean foodweb, phenological change is currently hard to detect although will be seen first where long data series exist, such as for many of the avian land-based predators (Chambers et al. 2013; Forcada and Trathan 2009).

Whaling and its possible consequences

Alongside warming effects, Southern Ocean food-webs have been greatly perturbed over the last century by commercial whaling which dramatically reduced stocks of top predators (Figure 12).

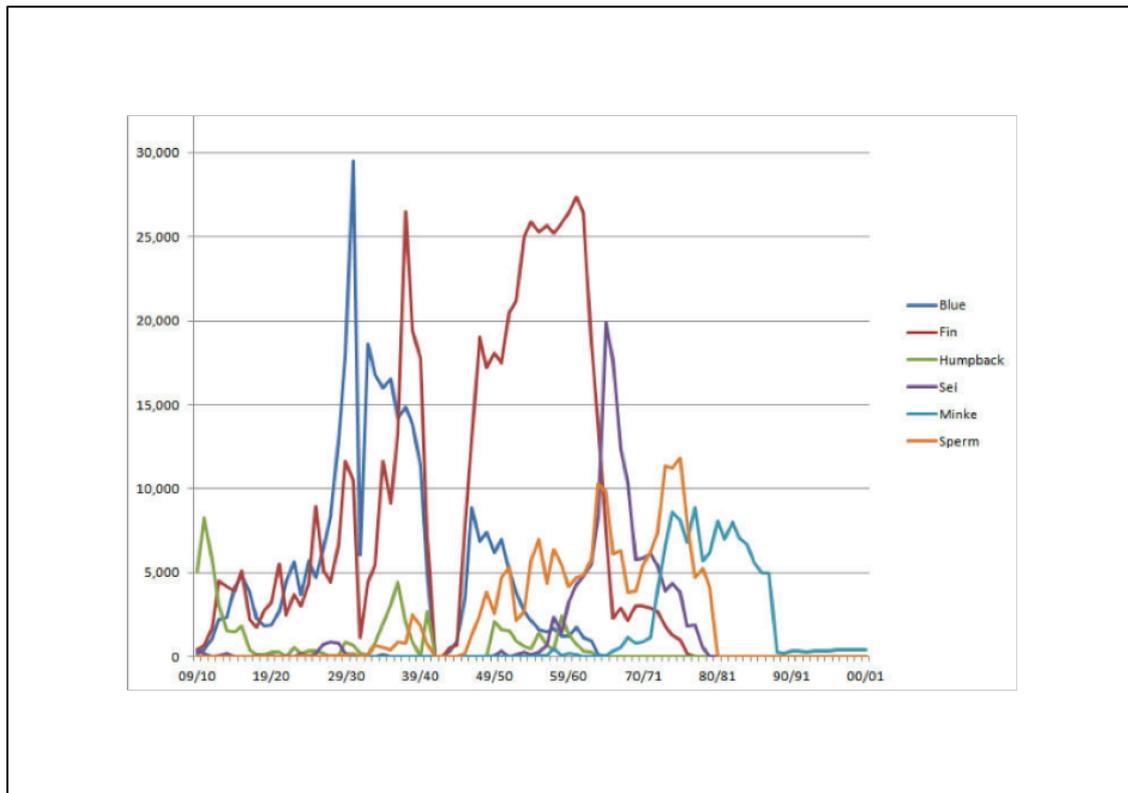


Figure 12: Whale catches by year from the 1909-1910 Antarctic whaling season to 2000-2001 by species.

https://www.coolantarctica.com/Antarctica%20fact%20file/science/threats_sealing_whaling.php

It is unclear whether the krill surplus proposed by Laws (1977, 1985) following the near extinction of whales in the Southern Ocean actually existed, although it is generally held that the increased biomass of krill predators such as seals and penguins falls far short of the biomass removed by whaling (e.g. Smetacek 2008). Laws (1977) initially attempted to understand the ecosystem consequences of harvesting whales by determining how much krill then became available and how this could explain population trends in other higher predators. He estimated that up to 150 million tons of krill per year taken by the pre-exploited whale populations might become available to other higher predators. Increases in fur seal and Adélie and Chinstrap penguin populations within the Scotia Sea have been apparent during the latter part of the 20th century and fur seals, a formerly exploited species, are now thought to be approaching pre-exploitation levels (Trathan et al. 2012).

The consequences for ecosystem function, following the removal of whales from the Southern Ocean, has been the subject of much recent speculation. The replacement of

whales by pinnipeds and penguins as dominant consumers of krill represents a large-scale reorganisation of the Southern Ocean food web (Surma et al. 2014). There is currently little evidence of a putative krill surplus, rather suggesting that a decline has happened that may be synonymous with that shown by satellite sensed chlorophyll in the marginal ice zone (Gregg et al. 2003).

Although acknowledging the possible role of sea-ice retreat on krill population size, Smetacek (2008) instead emphasised the role of whales and krill in recycling necessary trace elements such as iron, required for promoting phytoplankton growth. An increasing population of whales may ultimately further reduce the 'krill surplus' with unknown consequences for other predators. It seems unlikely, given the pressures of a changing environment that the Scotia Sea will revert to its previous pre-exploitation state. For example Mori and Butterworth (2006) estimated that in the absence of harvesting it would take blue whales 300-400 years to recover to their previous levels, given that, without overlaying the impacts of climate variability, they would have to outcompete other predators that respond more quickly

A number of authors have suggested that whales not only functioned as top predators but also as ecosystem engineers (Willis 2007, 2014; Smetacek 2008; Nicol et al 2010; Roman et al. 2014). Baleen whales consumed vast quantities of krill which themselves fed on iron rich diatoms. By defecating in the near-surface waters, whales (and a greater biomass of krill) recycled nutrients, particularly iron, and enhanced productivity in a positive feedback loop. As whales were hunted to near extinction less nutrient recycling occurred and production declined. Declining krill abundance from whatever cause has had measureable impacts on predator reproductive performance (e.g. Reid and Croxall 2001, Trathan et al. 2012). It is unclear where the balance will lie in the years ahead although changes are probably still on-going (Trathan and Reid 2009) and some whale populations are currently increasing (Nicol et al. 2010).

Surma et al. (2014) estimated that the standing stock of krill must have been close to 900 million tons to support the pre-exploitation levels of whales. They examined the plausibility of the krill surplus hypothesis of Laws (1977) and modelled four scenarios, examining the effect that the depletion of rorqual whales had on other

groups. In three of these scenarios, primary production was set at a level required to suit all consumers (including unexploited whale populations) and was allowed to decrease to an end point, some 60% of the starting value, consistent with an estimate by Arrigo et al. (2008). However, changes in slope of this decline were introduced into two of the simulations at various time points on the 108 year model run, consistent with observational data and projected changes in the bioavailability of iron as a result of the depletion of whales. A base run commencing in 1900 and finishing in 2008 simply looked at changes in other consumers in the absence of changing primary production. This was the only simulation that gave rise to a krill surplus and suggested that whales may have exerted some top-down pressure on krill. The remaining model scenarios suggested that declining primary production would have swiftly depleted the krill surplus. The output is consistent with the hypotheses advanced by Smetacek (2008) and Nicol et al. (2010), that whales may have promoted primary production through nutrient recycling, but Surma et al. (2014) failed to capture the increases in contemporary copepod biomass demonstrated by Ward et al. (2018). The only model run that showed a slight increase in copepod biomass was the basal model which ran independently of changes in phytoplankton. However the South Atlantic sector is not typical of the rest of the Southern Ocean, with 70% of the krill stock being found in the 0°-90°W quadrant (Atkinson et al. 2008). A high standing stock of krill may result in intense interspecific competition and predatory control of copepods, in contrast to regions such as East Antarctica where krill biomass is up to 10 times lower (Nicol 2006).

Contemporary estimates of krill and copepod biomass suggest that copepod standing stocks are at least equal to those of krill and may exceed them (Voronina 1998). Estimates of copepod production versus krill production around South Georgia (where the biomass of both groups is generally high) suggest that the copepod community as a whole may be four times as productive as krill (Shreeve et al. 2005). Over the wider scale, Voronina (1998) estimated that 92% of annual zooplankton production in the Southern Ocean can be attributed to copepods whereas Conover and Huntley (1991) estimated it to be three times higher based on estimates of ingestion and assimilation. Copepod production generally passes through longer food-chains linking fish, krill, and some avian predators compared to krill which are directly consumed by higher predators, both avian and mammalian. Given that the biomass of

baleen whales was so much higher in the past, it seems axiomatic that krill biomass must also have been higher than contemporary estimates to support them (Willis 2007, 2014; Smetacek 2008). The balance of production would also have changed, but even with large calanoids being 50% less abundant in the past, copepods would still have contributed significantly to secondary production.

Given that large calanoid copepods represent a significant proportion of plankton biomass in the Southern Ocean, a 50% increase in numbers, even if restricted to the Scotia Sea, represents an important shift in the food web dynamics. Flores et al. (2012) noted that copepod-dominated food chains tend to occur in less productive parts of the Southern Ocean and are responsible for most of metazoan secondary production (Voronina 1998; Shreeve et al. 2005). This may subsequently become more widespread as warming and ice-loss increasingly affect krill population dynamics and feedback through the food web.

There is little doubt that the Southern Ocean has changed profoundly over the last century, initially as a response to the commercial exploitation of whales and seals, latterly through regional warming (Moline et al. 2004; Steinberg et al. 2015) and, potentially, through ocean acidification as well (Orr et al. 2005; Bednaršek et al. 2012). Disentangling the effects of each will be a difficult task requiring well-structured, testable hypotheses (Nicol et al. 2007). Whilst the mechanisms of warming and the links between plankton and climate variability in the Southern Ocean are starting to be recognised, at least at the sub-decadal and inter-annual scale (Murphy et al. 2007a; Loeb et al. 2010; Saba et al. 2014; Steinberg et al. 2015), the consequences of past exploitation on the food-web are not yet well understood.

If warming of the Southern Ocean continues, we may be moving towards a system state where krill decline further in abundance and copepods increasingly dominate secondary production (Hill et al. 2012). This is especially the case in regions such as South Georgia where krill are already at the northern limits of their distribution (Murphy et al. 2007b). Understanding the consequences of this ecosystem shift will require ‘research efforts that provide quantification of food web processes and interactions at a range of scales and development of modelling procedures and techniques that can link processes across the key scales’ (Murphy et al. 2012).

Important in this context are the conclusions and recommendations for further research, made by Flores et al. (2012) in a report to the workshop ‘Antarctic krill in a changing ocean’ held in 2011. These included an improved understanding of the factors involved in successful krill recruitment, their resilience to environmental change and improved estimates of krill biomass. In particular a greater understanding of the role of krill in structuring food webs and the effects of changes in the habitat of krill on their life cycle and competitiveness is required. Obtaining greater insight into the effects of climate variability versus intraspecific competition (Ryabov et al. 2017) on krill population dynamics will also be crucial.

More information is also needed regarding copepod distributions, population dynamics and their interactions with krill. In this regard the relative paucity of time series measurements in the Southern Ocean is noteworthy, although a number now extend back ~25 years. In particular the Southern Ocean CPR survey, operated by Australian Antarctic Division since 1991, has extensive large-scale coverage in the Indian Ocean sector of the Southern Ocean (Hosie et al. 2003). Where possible this technology and standardised methods of analysis should be adopted by other national Antarctic operators. Finally renewed efforts to understand the consequences of the past exploitation of whales on ecosystem processes generally, not just in regard to higher predators, should be pursued.

Such research is relevant, topical and timely and should be pursued through current programmes such as Southern Ocean Observing System (SOOS) and future initiatives such as the newly instigated Marine Ecosystem Assessment for the Southern Ocean (MEASO) programme. Here four themes are visualised by the programme organisers in which assessments of status and trends of species and ecosystems to change as well as modelling and the implementation of observing systems will be undertaken. Outputs will contribute to the 6th Assessment Review of the Intergovernmental Panel on Climate Change which will report in 2022.

SUMMARY

1. A series of net samples undertaken during two recent ‘synoptic’ basin-scale cruises in the Scotia Sea (Southern Ocean) during austral summer were used to characterize the mesozooplankton and investigate community structure. Major groupings of stations that were geographically coherent were disclosed by cluster analysis in both surveys. Many species were common across the entire survey area, but abundance was an order of magnitude or greater in the more northerly station groups. Considerable variability in the production and development of mesozooplankton populations was observed across the groups with overwintering stages of dominant copepods apparent in the south, contrasting with a spring generation in the north. The differences in stage composition of the copepod *Calanoides acutus*, for example, suggested temporal differences in population age of up to 3 months across the 1000 km latitudinal extent of the Scotia Sea. While there is intense seasonal variability in many of the physical and biological properties of the Southern Ocean, it was concluded that quantifying the impact that sea-ice dynamics has on production cycles will be an extremely important part of understanding community structure and function.
2. Repeat sampling of a transect running from south to north within the Scotia Sea, during spring, summer and autumn, provided a seasonal context. Both physical and biological data from all three surveys suggested that the Scotia Sea could effectively be partitioned into two main bioregions either side of the Southern Antarctic Circumpolar Front (SACCF). However, there is little evidence that the SACCF either constrains the meridional movement of zooplankton or forms a significant faunal boundary. Similarities in distribution patterns of a range of taxa across surveys suggested that temperature which, despite seasonal warming, exhibits a persistent gradient across the Antarctic Circumpolar Current, and seasonal ice-cover are more important in structuring the biota of the Scotia Sea.

3. A comparison between historical zooplankton catch data collected by the *Discovery Investigations* from around South Georgia in the 1926/27 season and contemporary collections (1995-2005) from the same region suggested that, despite lower catch abundances, *Discovery* data fell within the overall range as found by contemporary nets, both in terms of abundance and species composition. However *Discovery* samples were collected using an N70 ring net comprised of 3 different mesh sizes (5mm, 440 and 193 μm) and contemporary samples with a superficially similar paired Bongo net equipped with a 200 μm mesh net.
4. Given the differences in net design, a N70 net was constructed and fished alongside the Bongo net to provide a catch comparison. Results indicated that Bongo net catch abundance was ~ 3 times greater than the N70 and ~ 4 times greater when only copepod instars ≤ 0.5 mm body length were considered. Calibration factors to take account of these differences were determined.
5. A large-scale study using 155 N70 samples collected by *Discovery Investigations* within the Scotia Sea was compared with a series of 451 contemporary samples to see if plankton had responded to ocean warming by following the thermal envelope that they occupied in the 1920-30s and moved polewards. Despite median warming of 0.74°C , the temperature at which median community abundance peaked increased by 0.98°C . Ranked abundance of 16 dominant copepod species was compared between eras. The calibration factors determined from the previous study were applied to the N70 data. There was a near uniform response to ocean warming with the median temperature of occurrence of 15 of the 16 taxa being higher in contemporary times than in the *Discovery* era. Although some species moved towards colder rankings, others moved towards a warmer ranking. However no major shift in the ranked abundance of the dominant taxa was apparent between the two eras. Species did not appear to retain their thermal niche and their spatial distribution was very similar between eras suggesting that other factors such as prevailing current flow and food availability were more important in determining distributions.

6. To further investigate the question of whether zooplankton abundance has changed in the last ~70 years, net samples taken between December and February were selected from both eras. Following the application of reworked calibration factors to account for population stage structure and adjusting for seasonal differences in sampling effort, abundances of four biomass dominant copepod species, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus simillimus* and *C. propinquus* were compared. The first three species were found to be ~20-55% more abundant today than they were during the *Discovery* era, considered to be the result of greater food availability and potentially less predation pressure as a consequence of a reported decrease in Antarctic krill. *Calanus propinquus*, a more southerly distributed species, was marginally less abundant in contemporary samples and may not have benefitted from increases in available food, particularly in the Southern Scotia Sea. Its dependence upon ice-algae over part of its range is also discussed in relation to the distribution of ice-algae biomarkers in the wake of a receding ice-edge.

7. The future structure and function of the Scotia Sea are discussed in light of these findings and those of other authors. Projected ocean temperature increases over the remainder of the present century are of the order of 1-1.5°C. Despite this and substantial other physical changes predicted, it is thought likely that changes within the food web of the Southern Ocean will be at least as important in determining the future balance and distribution of the biota.

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APPENDIX - ORIGINAL PAPERS

Paper 1

Ward , P., Grant, S., Brandon , M., Siegel, V., Sushin, V., Loeb, V., and Griffiths, H. (2004). Mesozooplankton community structure in the Scotia Sea during the CCAMLR 2000 Survey: January-February 2000. *Deep Sea Research II*, 51: 1351 - 1367.



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Mesozooplankton community structure in the Scotia Sea during the CCAMLR 2000 survey: January–February 2000

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Abstract

An analysis of mesozooplankton community structure in the Scotia Sea was carried out, based on 123 RMT1 double oblique hauls (0–200 m) taken during the CCAMLR 2000 Survey. Standardized sample data (log abundance per 1000 m³) were grouped into taxonomic categories and subjected to cluster analysis and multi-dimensional scaling. Two ordinations were performed, the first based on a reduced taxonomic dataset (31 categories out of a full 120) obtained by pooling ontogenetic stages within species and by including only those taxa that contributed at least 4% to total abundance at any one station. This disclosed two major station groups, which separated north and south, forming ‘warm’ and ‘cold’ water communities respectively, whereas four minor groups were mainly associated with stations around the Antarctic Peninsula and within the Weddell Scotia Confluence. Mean zooplankton abundance (238 000 individuals per 1000 m³) within the northerly group G1 was up to 12 times higher than in other groups. The second ordination using all taxonomic categories disclosed an additional intermediate group (G1a), which was geographically consistent with the southern part of the northern group 1 from the previous ordination. However, because of taxonomic similarities between all the major station groups it was concluded that they represented a single community, which differed only in its phenological development and the mass occurrence of patchily distributed organisms such as krill larvae. Testing the relationships of station groups with the position of water masses and frontal boundaries indicated that the Weddell Front was broadly coincident with the boundary of the northern and southern communities over much of its length. However, the presence of stations belonging to group G2, to the north of the Weddell Front, to the west of the Antarctic Peninsula, and around the South Sandwich Islands, was consistent with the distribution of ice-influenced

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surface water. Low zooplankton abundance and species developmental composition suggested that this 'community' was largely in an over-wintered state. Copepods and euphausiids dominated the mesozooplankton throughout the study area with small copepods (*Oithona* spp., *Ctenocalanus* spp. and *Metridia* spp.) particularly abundant.

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1. Introduction

The Atlantic sector is arguably one of the best studied regions of the Southern Ocean. It was the focus for the extensive Discovery Investigations undertaken during the 1920s–1930s, and again in the early 1950s, and for many other national and international programs including BIOMASS (Biological Investigations of Antarctic Marine Systems and Stocks), which generated the First and Second International Biological Experiments (FIBEX and SIBEX). The major focus of these programs was to extend knowledge of the living resources of the Southern Ocean, particularly for Antarctic krill (*Euphausia superba*); however, parallel research greatly increased ecological understanding of other polar zooplankton and some of the factors governing their distribution. Various approaches to the large-scale characterization of plankton distributions in the Southern Ocean and their relationship to the physical environment have been advanced in recent years. Mackintosh's (1936) initial view of the region south of the Antarctic Polar Front (APF), based on 600 samples collected between 1927 and 1931 in the top 100 m of the water column emphasized the distribution of cold- and warm-water plankton and spatio-temporal variability in its richness. Communities were distinguished that were broadly associated with different water masses; a northern zone populated by typically warm water species, a zone of permanently scarce plankton in the region of the Antarctic Peninsula, and a zone enclosing the line separating Bellingshausen and Weddell Sea faunas. Hempel (1985) reviewed the geographical distribution of plankton in the Southern Ocean and described the occurrence of latitudinal zones that were mainly determined by seasonal variations in ice cover. There are obvious parallels between this view of ecological zonation and the patterns described by Mackintosh (1936) in that the latter connected the distribution of cold-water

species and pack-ice movement. The regional oceanography developed by Longhurst (1998) based on algal ecology emphasized the importance of frontal zones within the Southern Ocean as separating ecological provinces. The annular ring between the APF and the Antarctic Divergence is synonymous with the southern branch of the Antarctic Circumpolar Current (ACC) and was viewed as a single province with its ecology driven by the presence of krill, salps and copepods. Most recently Pakhomov and McQuaid (1996) and Pakhomov et al. (2000) have described the distribution of zooplankton communities along transects running from the region of the Sub-tropical Convergence across the Southern Ocean to the Antarctic Continent in which the major fronts variously serve to delimit and define community structure. However, some frontal features such as the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) have only recently been described (Orsi et al., 1995), and their importance in terms of zooplankton dynamics and distribution has not been assessed. The ACC in the Atlantic sector is a very dynamic region and downstream of Drake Passage meandering of frontal zones and eddy shedding can geographically alter the distribution of plankton (e.g., Atkinson et al., 1990). Additionally, large-scale movements of water masses due to atmospheric forcing have been reported which can also fundamentally alter plankton distributions (e.g. Priddle et al., 1988) and more recently there has been speculation about the affect ENSO (El Niño Southern Oscillation) events might have on large-scale distribution (Quetin et al., 1996).

Unlike the Indian Ocean sector where a number of large-scale oceanographic surveys have recently taken place (see Chiba et al., 2001; Hosie, 1994; Hosie et al., 2000), there have been few opportunities to assemble a comparably large-scale view of

the Atlantic sector. The survey sponsored by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR)—the CCAMLR 2000 Survey—covered an extensive area (approximately 15 degrees of latitude and 50 degrees of longitude) and under normal circumstances a synoptic view of the plankton over such a large area would have been difficult to achieve without temporal aliasing of the data. However, the four-ship survey enabled all the observations to be obtained in only 29 days. Analysis of the resulting 123 RMT1 samples collected over an area stretching from the South Sandwich Islands through the Scotia Sea and down the western side of the Antarctic Peninsula—an area of just over 2 million km²—has provided a synoptic basin-scale view of plankton distribution and made it possible to investigate community structure and to assess the importance of frontal regions as community boundaries.

2. Methods

Double oblique rectangular mid-water trawl (RMT8+1) samples (0–200–0 m) were taken as part of a suite of standard netting protocols carried out at each station (Watkins et al., 2004). Nets were towed for an average of 32 min (quartile ranges 27–39 min), and the resulting samples, or in some cases subsamples, were preserved in 10% v:v formalin in seawater and shipped to the UK for subsequent analysis. This paper presents results based on an analysis of samples taken with the smaller of the two nets; the RMT1 (1 m² mouth area, 330 µm mesh). Once in the UK, large species such as krill, salps, and other gelatinous forms were removed. Samples were then split using a folsom plankton splitter into a series of aliquots. Two fractions of between $\frac{1}{2}$ to $\frac{1}{64}$ of the preserved amount were usually counted to ascertain the numbers of larger mesozooplankton (copepods, chaetognaths, euphausiid larvae etc.) and two fractions usually between $\frac{1}{256}$ and $\frac{1}{512}$ were counted for the smaller end of the spectrum (Oithiniids, *Ctenocalanus* spp., copepod nauplii, etc.). Data were standardized to abundance per 1000 m³ based on flow rates determined from flow meters

placed in the RMT8 nets. It is known that the RMT1 can fish independently of the RMT8 and presents a mouth area to the water, which is dependent on ship speed (Pommeranz et al., 1983). During this survey the average speed of the net through the water for all deployments was 2.25 kn (quartile range 2.04–2.53 kn) at which speeds the mouth area ranges from around 0.5 to 0.65 m² (mean ~0.6 m²). Data were standardized accordingly.

A total of 120 taxonomic categories were enumerated including species, species stages, genera, or in some cases higher taxa. Copepods were the dominant organism (67 taxonomic categories) along with euphausiids (22 taxonomic categories). Data were analyzed using the statistical package Plymouth Routines in Multivariate Ecological Research, PRIMER 5 (PRIMER-E Ltd 2000) see Clarke and Warwick (1994). Copepod species stages and larval euphausiids were initially pooled within species to give overall totals, thus reducing the dataset to 77 taxonomic categories. Standardized data were log-transformed and a similarity matrix created containing those zooplankton that contributed $\geq 4\%$ of the total abundance at any one station which further reduced the list to 31 taxa (Field et al., 1982). Data were then subjected to nearest neighbor clustering using the Bray-Curtis dissimilarity index and non-metric multi-dimensional scaling and station groups arbitrarily identified. These groupings were then subjected to the ANOSIM (analysis of similarity, analogous to one-way ANOVA) and SIMPER (similarity percentages) routines to determine the significance of differences between groups and to identify the species contributing to similarity within, and differences between, groups. The routine BIOENV (see Clarke and Ainsworth, 1993) was used to test the extent to which measured environmental variables (mean temperature in the top 50 m, salinity, density, latitude, and surface chlorophyll) accounted for pattern in the species data, and BVSTEP (see Clarke and Warwick, 1998) was used to test for redundancy in the taxonomic dataset by seeing if a limited subset of species could produce the same pattern.

The same procedure was then performed on the full (unpooled) dataset to investigate whether the

inclusion of ontogenetic species stages altered the basic patterns which resulted from the initial analysis.

3. Results

3.1. Community structure

Results of clustering analysis and multi-dimensional scaling on the reduced dataset are shown in Fig. 1.

Two main groups (G1 and G2) were identified as a result of clustering the data, containing 60 and 44 stations, respectively, and a further four groups (G3 to G6) with 7, 7, 3 and 2 stations, respectively.

When overlaid on the survey area the two largest station groups (G1 and G2) showed strong geographic integrity, with G1 occupying the northernmost part of the survey area and forming a boundary with G2 to the south, broadly along the line of the Weddell Front (WF) (Fig. 2). However stations belonging to G2 also were found on the western side of the Antarctic Peninsula and around the South Sandwich Islands suggesting that this was a cold-water community and was influenced by the extent of ice-influenced surface waters (see Brandon et al., 2004). The four minor groups (G3–G6) were geographically consistent with neritic waters around the South Shetland Islands and also water influenced by the Weddell Scotia Confluence. Mean zooplankton abundance within G1 was up to 12 times higher than in the additional groups (Table 1 and Fig. 3).

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

Analysis of similarity (SIMPER) was carried out to establish which species were responsible for similarities within and dissimilarities between groups. Data from the first ordination are

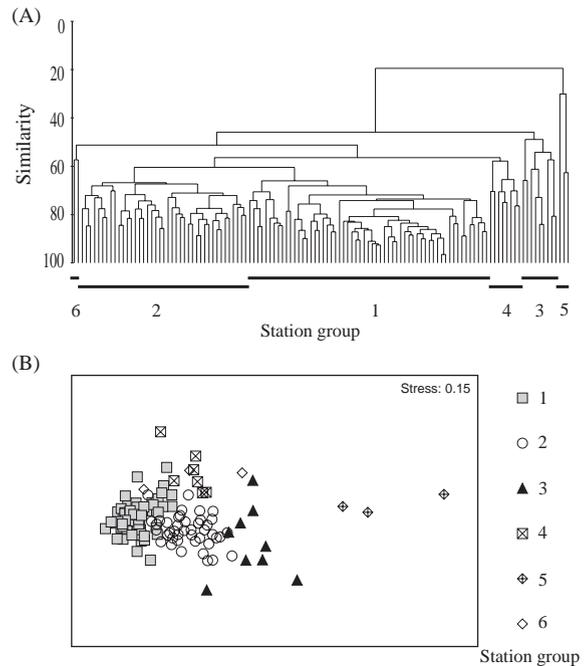


Fig. 1. Identification of station groups based on the results of (A) Bray–Curtis Clustering of the reduced species by station data matrix. Station labels have been omitted for clarity; and (B) non-metric multi-dimensional scaling ordination of the reduced species by station matrix.

summarized in Table 2 where mean abundance (individuals per 1000 m³) of the 23 taxa which contributed $\geq 4\%$ to within-group similarity or between-group dissimilarity are presented. The listed taxa accounted for $>90\%$ of within-group similarity across all groups. The two largest groups (G1 and G2) were more similar in taxonomic composition than any other of the group comparisons (average dissimilarity = 39.52) and differences were primarily accounted for by species that were more abundant in G1, reflecting the increased zooplankton abundance in this group and the more northerly distributions of many of its component taxa e.g. *Limacina helicina*, *Calanus simillimus*, *Rhincalanus gigas* and *Clausocalanus laticeps*. G3 and G5 were both characterized by relatively low abundance and although G5 contained many of the species serving to characterize G1 and G2, it was dominated by the swarm-forming zooplankton *Thysanoessa macrura*, *Euphausia superba*, and *Salpa thompsoni*

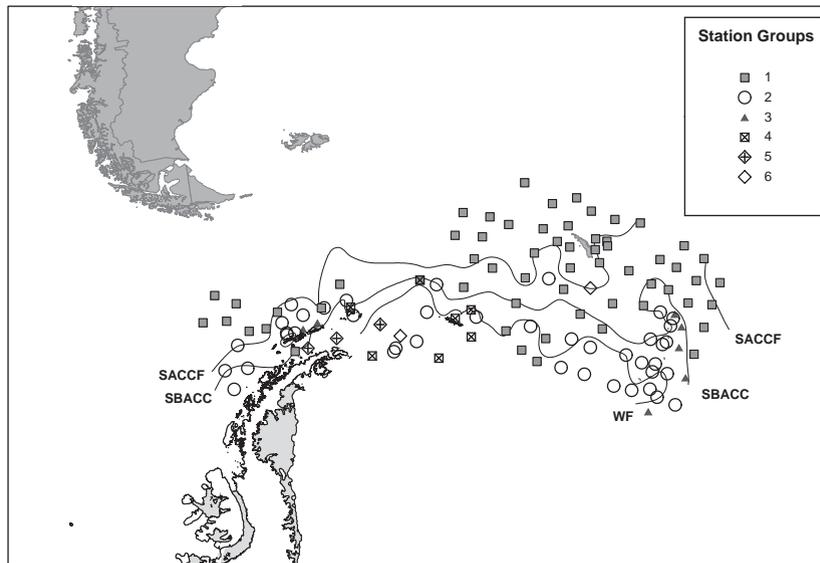


Fig. 2. Distribution of station groups derived from the reduced species by station ordination. Positions of fronts from north to south are: the Southern Antarctic Circumpolar Current Front (SACCF), the Southern Boundary of the Antarctic Circumpolar Current (SBACC), and the Weddell Front (WF).

Table 1
Zooplankton abundance (individuals per 1000 m³) by station grouping for the reduced ordination

Station group (no. sites)	Mean abundance	Median abundance	Upper quartile	Lower quartile
G1 (60)	238 578	107 256	39 571	359 891
G2 (44)	61 698	16 761	3822	76 276
G3 (7)	33 653	7433	1837	59 610
G4 (7)	99 104	33 407	14 328	268 857
G5 (3)	20 442	9940	323	51 002
G6 (2)	28 061	28 061	—	—

blastozooids. G4 encompassed a number of stations occurring between the tip of the Antarctic Peninsula and the South Orkney Islands and was distinguished from all others by the high abundances of *Euphausia superba* larvae.

An ordination of stations based on the full selection of species stages was also performed, i.e., without pooling stages within species, or selecting those that contributed a certain percentage of the abundance. This time five groups were identified in the log-transformed data, with three containing in

excess of 30 stations and two with seven and four stations, respectively. The northern G1 was smaller than previously, and its boundary was now approximately coincident with the SACCF. G2 was also smaller and mainly restricted to the area around the South Sandwich Islands. An intermediate group (G1a) was present to the south of the SACCF, which now incorporated a number of stations from the southern part of G1 in the first ordination and others that were previously found along the southern perimeter of the survey area (Fig. 4). Stations within this group were characterized by many of the small copepod species such as *Ctenocalanus* spp., *Oithona* spp., and all stages of *Metridia* spp., which were also common in G1, as well as the younger and intermediate stages of some of the biomass dominant copepods such as *Calanus propinquus* CII and CIII and *Calanoides acutus* CIII. It was distinguished from G1 by the presence of *Euphausia superba* calytopis stage 1 and reduced numbers of the more northerly distributed *Thysanoessa vicina*, *Scolecithricella minor*, and *Calanoides acutus* CV (Table 3). With minor changes, the remaining groups were largely as identified in the first ordination.

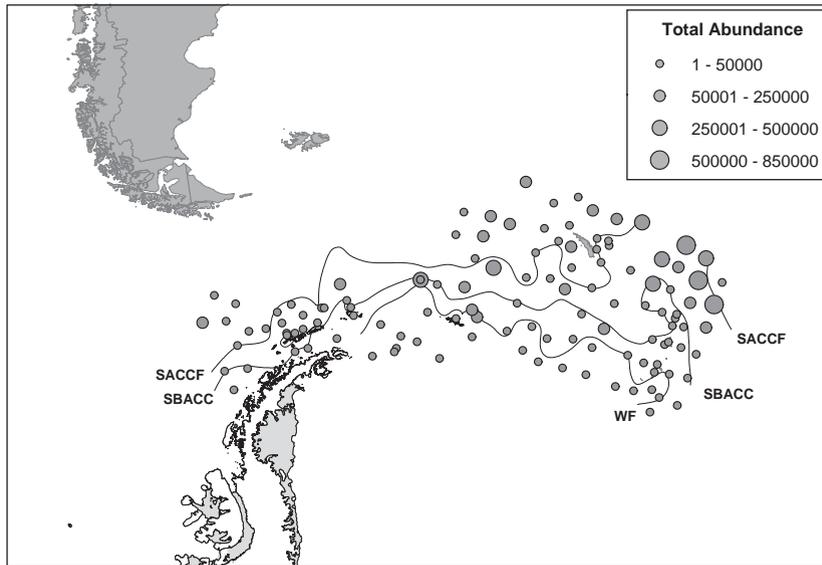


Fig. 3. RMT1 total abundance (individuals per 1000 m³) by station.

Table 2
Reduced dataset

Species	G1	G2	G3	G4	G5	G6
<i>Oithona</i> spp.	87 316	7752	78	243	<1	40
<i>Euphausia superba</i> larvae	8287	10,462	4550	42 947	<1	69
<i>Metridia</i> spp.	40 384	4629	565	3465	2	2366
<i>Calanoides acutus</i>	16989	4143	56	22 518	7	5796
<i>Ctenocalanus</i> spp.	35 926	2327	38	2040	1	111
<i>Limacina helicina</i>	16 669	130	<1	16	0	432
<i>Thysanoessa</i> spp. Calyptopes	2375	920	9	675	0	560
<i>Thysanoessa vicina</i>	6322	652	7	1536	3	2684
<i>Calanus simillimus</i>	11 036	11	<1	0	0	187
<i>Calanus propinquus</i>	3025	1162	85	2450	4	4221
Copepod nauplii	10 546	36	0	0	0	0
<i>Oncaea</i> spp.	8965	728	12	0	0	0
<i>Rhincalanus gigas</i>	6018	196	14	73	1	1351
<i>Pelagobia longicirrata</i>	4030	231	4	774	0	0
Chaetognaths	2215	998	35	419	3	133
<i>Rhincalanus gigas</i> nauplii	3394	19	<1	42	1	0
<i>Scolecithricella minor</i>	1233	248	74	108	0	138
<i>Euchaeta antarctica</i>	602	346	49	315	0	129
<i>Thysanoessa macrura</i>	452	197	348	95	73	7
<i>Clausocalanus laticeps</i>	934	7	<1	13	0	67
<i>Salpa thompsoni</i>	37	119	224	318	73	0
<i>Euphausia superba</i>	17	39	41	56	38	3
<i>Limacina</i> spp.	<1	9	<1	12	22	0

Mean abundance (individuals per 1000 m³) by station grouping of those species that contributed $\geq 4\%$ to within-group similarity or between-group dissimilarity. Highest values emboldened. Species/taxa ranked according to mean abundance summed across all groups.

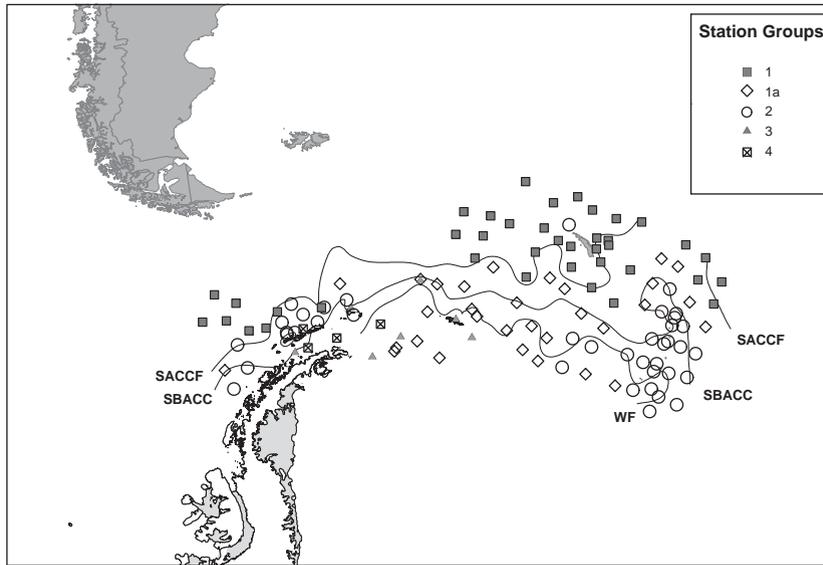


Fig. 4. Distribution of station groups derived from the full species by station ordination. Fronts as defined in Fig. 2.

Table 3
Full dataset

Species	G1	G1a	G2	G3	G4
<i>Oithona</i> spp.	47 054	40945	3974	73	2
<i>Ctenocalanus</i> spp.	22 281	13601	839	741	7
<i>Metridia</i> spp. CIV-CVI	13 372	11781	537	1381	10
<i>Metridia</i> spp. CI-CIII	8269	9717	533	38	1
<i>Euphausia superba</i> Calytopis 1	36	9120	577	1671	<1
<i>Calanoides acutus</i> CV	5368	2540	290	155	2
<i>Calanoides acutus</i> CIV	2645	2452	34	2867	1
<i>Thysanoessa vicina</i>	4549	2049	130	530	2
<i>Calanoides acutus</i> CIII	1050	3140	14	2976	0
<i>Thysanoessa</i> spp. Calytopes	1370	1678	112	175	<1
Chaetognaths	1050	1741	233	198	2
<i>Calanus propinquus</i> CIII	604	1086	43	398	1
<i>Scolecithricella minor</i>	813	451	102	94	0
<i>Calanus propinquus</i> CII	149	840	39	79	0
<i>Calanus propinquus</i> CIV	369	418	15	102	1
<i>Thysanoessa macrura</i>	263	115	205	75	33
<i>Salpa thompsoni</i>	29	32	74	263	35
<i>Euchaeta antarctica</i> CII	66	226	81	<1	0
<i>Euphausia superba</i>	13	1	27	40	29
<i>Limacina</i> spp.	<1	3	5	2	10

Mean abundance (individuals per 1000 m³) by station grouping of those species that contributed ≥4% to within-group similarity or between-group dissimilarity. Highest values emboldened. Species/taxa ranked according to mean abundance summed across all groups.

The PRIMER routine BVSTEP was used to identify the smallest subset of taxa in the reduced species by station matrix, which could explain most of the pattern in the data. This identified a subset of 19 of the original 31 species/stages in the

matrix ($\rho = 0.953$). Seventeen of these taxa (along with Ostracoda and *Euphausia frigida*) were previously identified as contributing strongly to within-group similarity and between-group dissimilarity (Table 2). With the exception of *Salpa*

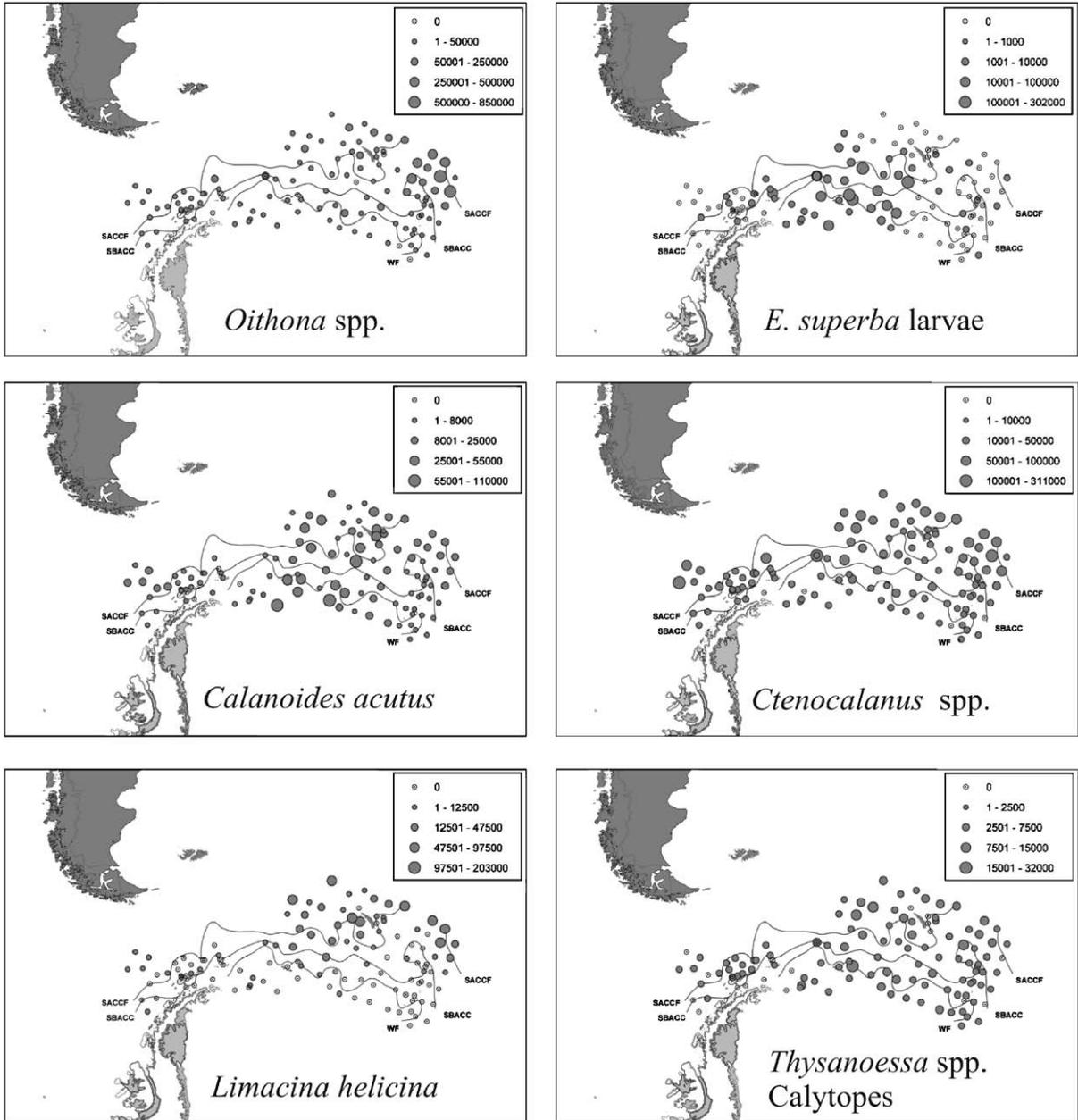


Fig. 5. Species by station abundance. The twelve species that were common to the SIMPER and BIOENV analyses (see text for further details). Fronts as defined in Fig. 2.

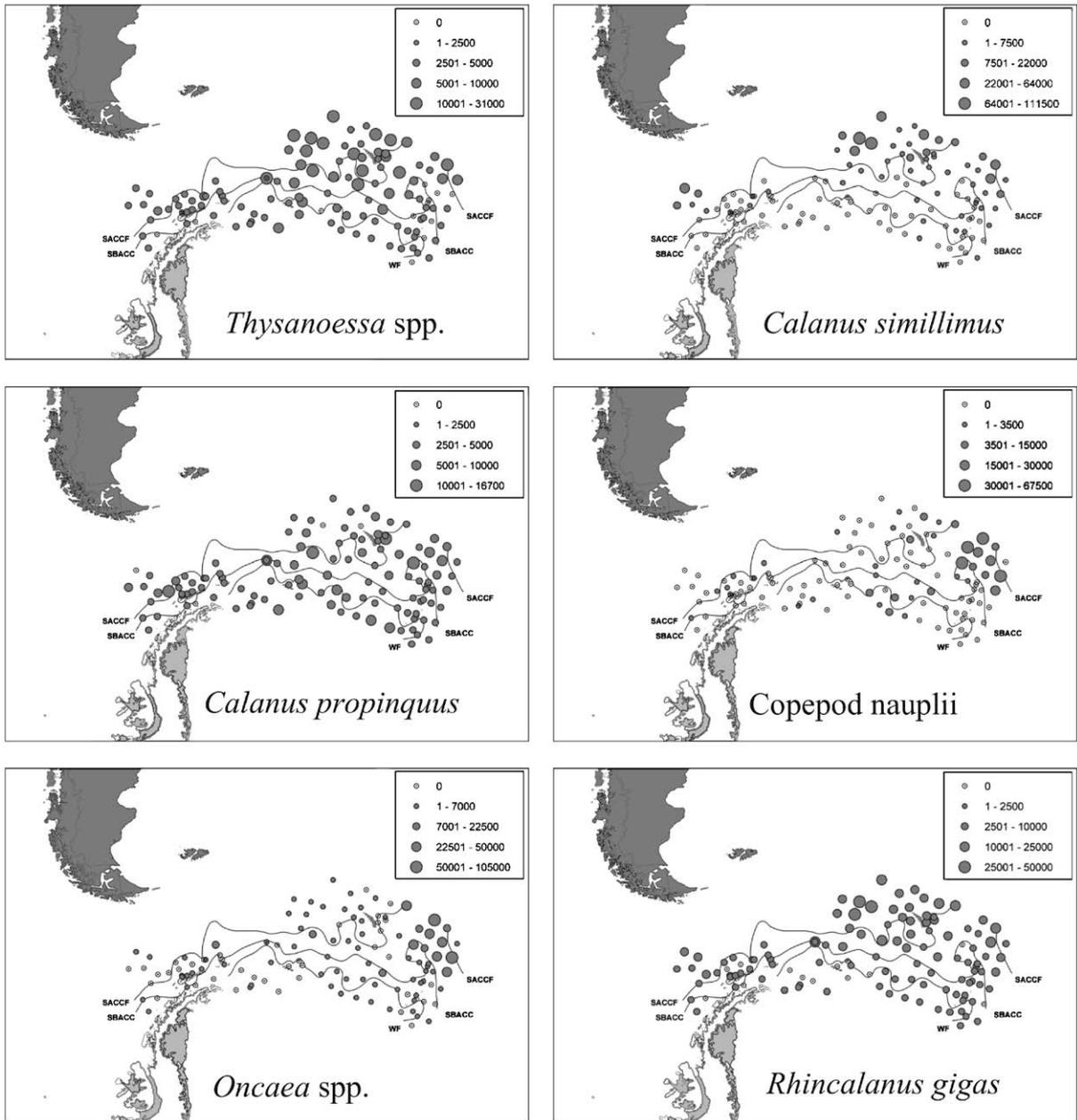


Fig. 5. (Continued)

thompsoni (distribution described by Kawaguchi et al., 2004) their distributions are presented in Fig. 5, as they describe much of the variation between station groups. Distribution patterns of these taxa fell into three basic types; those that were abundant in the north of the survey area, e.g.,

Limacina helicina, *Rhincalanus gigas*, and *Calanus simillimus*; those abundant to the south, e.g., *Euphausia superba* larvae and *Calanus propinquus*, and a number of other taxa, which despite varying enormously in abundance, were nonetheless widespread.

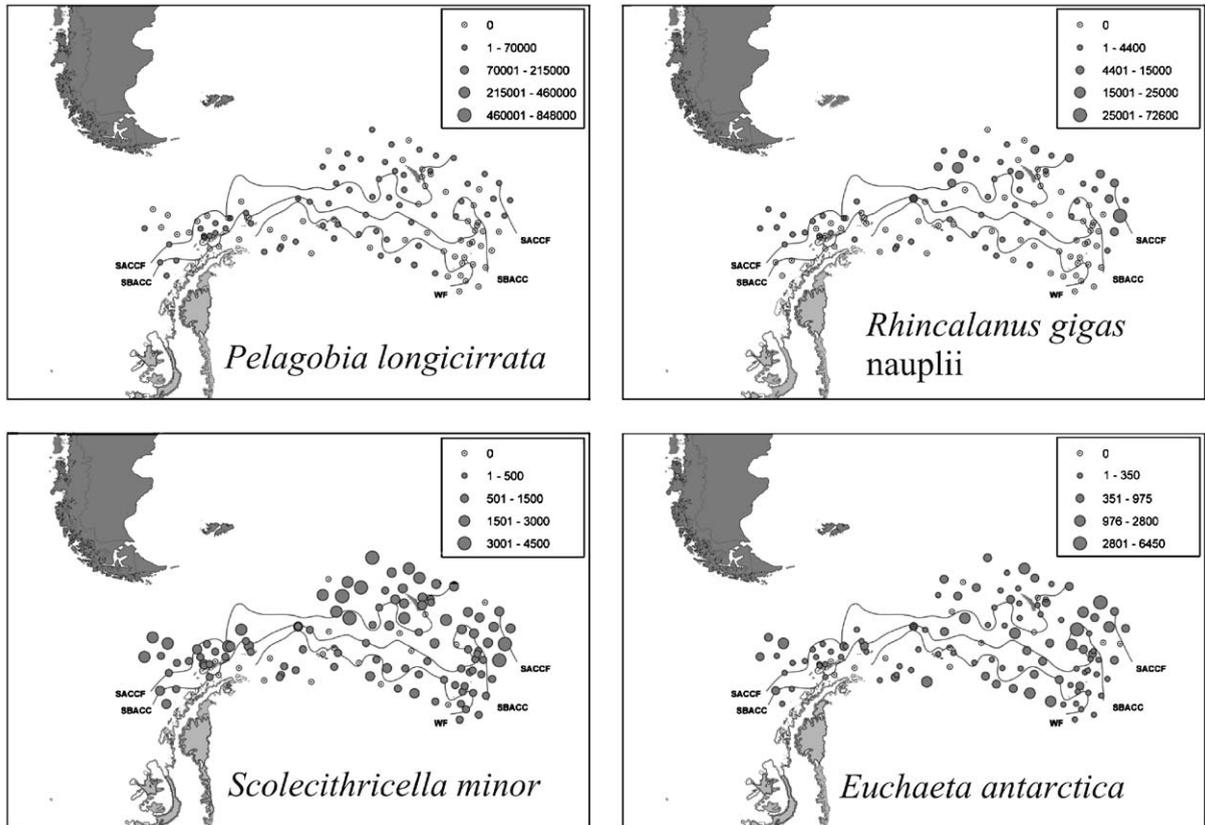


Fig. 5. (Continued)

3.2. Relationships with water mass distributions and environmental factors

To test the robustness of grouping the stations on the basis of the water mass in which they occurred, each station was characterized according to where it lay in relation to the main frontal positions (Brandon et al., 2004). Global R for both ordinations was considerably lower than for the original station groupings ($R = 0.175$) and significant differences only existed between the grouping of stations corresponding to the northern part of the ACC (mainly G1) and those to the south of the SBACC ($R = 0.323$) and the WF, which comprised mainly stations from G2 ($R = 0.303$). On this basis it can be concluded that the original grouping of stations (Fig. 2) was most robust and that the SACCF in particular had little overall effect on community structure.

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

4. Discussion

4.1. Species occurrence and distribution

Major differences in zooplankton abundance were apparent between station groups and also in

the proportions of the dominant taxa; copepods and euphausiids (see Tables 1 and 2). Within the two largest groups defined in the first ordination (G1 and G2), they accounted for ~90% of total abundance and between 53% and 75% for remaining groups.

4.1.1. Copepods

The dominance of small copepod species was confirmed throughout the study area, with *Oithona* spp. and *Ctenocalanus* spp. contributing greatly to the increased abundance in G1 (Table 1). Similar findings have been made by Sushin et al. (1985), Errhif et al. (1997), Atkinson and Sinclair (2000), Pakhomov et al. (2000), and Chiba et al. (2001). The highest overall abundances of many of the important species, *Oithona* spp., *Oncaea* spp., and *Metridia* spp., were located in the northern part of the region and to the east of South Georgia and the lowest overall abundances occurred in the vicinity of the Antarctic Peninsula (Fig. 3). Without exception all of the copepods (and many of the non-copepod taxa) that comprised $\geq 4\%$ of the total sample abundance (see Section 2) were more abundant in the northern G1 (Table 1). Presumably, here the combination of lower latitude, warmer water, and enhanced production (see Holm-Hansen et al., 2004) has promoted the recruitment of species which in Weddell Sea waters have yet, or are only just beginning to reproduce. Temporal delays of the order of three months or so have previously been found between commencement of recruitment of copepod species in the Scotia and Weddell Seas (Atkinson et al., 1997; Ward et al., 1997). In this survey the presence of copepodite stage V *Calanoides acutus* from the summer generation in the northern part of the survey area and of early copepodite stages or adult females from the over-wintered generation to the south also indicates a lag in the timing of recruitment of the order of two to three months. Such differences are often seen in this sector of the Southern Ocean, particularly where the meridional extent of the ACC is wide. Marin (1987) also found pronounced age differences for *Calanoides acutus* and *Calanus propinquus* during the Melville study (Brinton, 1985) with a younger population present in waters south of the WF.

4.1.2. Euphausiids

Euphausiids had their highest proportionate share of abundance in G3 to G5 (19–32%) with 7–9% in G1 and G2. Highest mean abundances of euphausiids were found in G4, largely as a result of *E. superba* larvae which occurred at all seven stations and contributed 12% to within-group similarity. *E. superba* larvae were also present in both of the main station groups, but were concentrated along both sides of the WF and occurred in somewhat lower abundance up to the approximate position of the SACCF (Fig. 5; see also Siegel et al., 2004). Previous work on euphausiid larvae from the Melville expedition (Brinton, 1985) has also highlighted the importance of this frontal region for reproduction in *E. superba* and Spirodonov (1995) has characterized the region as one in which krill reproduction starts early and has a variable but normally long duration. *Euphausia frigida* occurred throughout the region but were more abundant to the north of the position of the SACCF as were older calyptopes and furcilia stages. Calytopis stage 1 was widespread but had a more southerly distribution. This is somewhat similar to *E. superba* larvae and suggests that larvae are moved north and east in surface waters. Makarov (1977) in a survey of the central Scotia Sea in December/January also highlighted the widespread distribution of larval forms but concluded that the most intense reproduction took place in the WF zone.

Thysanoessa spp. calyptopes were generally widespread, although once again furcilia and post larvae generally occurred in greater numbers further north. Previous work around South Georgia has established that the majority of these are likely to belong to *T. vicina*, whereas a separate category of large *Thysanoessa* spp. (> 16 mm total length are probably *T. macrura*; see Mauchline, 1980) were concentrated at the eastern end of the survey area distributed in the region of the outflow of Weddell Sea water.

4.1.3. Other species

Chaetognaths were not separated into species or genera because in many cases they were too badly damaged to identify consistently. Nonetheless they were generally abundant throughout the survey

area, the exception being the region of the South Sandwich Islands in the cold outflow of Weddell Sea water. Mackintosh (1936) characterized them as being a warm water group that may sometimes occur in colder water.

Salp blastozooids (*Salpa thompsoni*) were one of the very few taxa that were more abundant in the cold-water community G2. They were largely absent north of the latitude of South Georgia and were concentrated in a zone straddling the WF and up to the approximate position of the SACCF. Salps are heterogeneously distributed within the Southern Ocean although Mackintosh (1936) indicated that along with *Euphausia superba* they had a tendency to occur in colder waters, although Siegel et al. (1992) and Park and Wormuth (1993) indicate a preference for warmer water masses (see also Kawaguchi et al., 2004).

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

4.2. Community structure

Overall the mean abundance of zooplankton within G1 was much greater than for G2 and higher than determined in many other studies within the ACC (see Pakhomov et al., 2000; Sushin et al., 1985). Regional studies by Foxton (1956) and Hopkins (1971) demonstrated a latitudinal decrease in mesozooplankton biomass and low zooplankton biomass seems typical of the Antarctic Coastal Current and Weddell Sea areas. Hopkins and Torres (1988) commented on the low zooplankton biomass in a study in the western Weddell Sea compared to the stations in the ACC although in a study by Boysen-Ennen et al. (1991) no difference in mesoplankton biomass was found between the Weddell Sea oceanic community and other data reported for the Southern Ocean. The remaining station groups were largely associated with the Weddell Scotia Confluence and Antarctic Peninsula regions. They were characterized by low

numbers of stations, lower within-group similarity, and with the exception of G4, much lower abundance. Previous work has indicated that this is a hydrodynamically complex area where many of the frontal zones lie close together and that consequently there is the potential for zooplankton from different sources to be present in the region (Jazdzewski et al., 1982; Piatkowski, 1989; Siegel and Piatkowski, 1990). Most however are in agreement with Mackintosh (1936) in that compared to other areas, the plankton in Bransfield Strait is impoverished (Jazdzewski et al., 1982; Mujica and Asencio, 1985; Mujica and Torres, 1982). Reasons for this have been variously ascribed to the influence of upwelling water masses (Mackintosh, 1936) or variations in ice cover (Foster, 1981). Schnack-Schiel and Mujica (1994) have reviewed the zooplankton found in this region and conclude that an oceanic community influenced by the ACC and a neritic community influenced by the Weddell Sea in Bransfield Strait and by Bellingshausen water off the Palmer Archipelago are present. Jazdzewski et al. (1982) also conclude that oceanic and continental zone communities are present in the region separated by the continental water boundary. They also found that the mean volume and abundance of plankton were much less in Bransfield Strait and inshore of the 500 m isobath compared to offshore, where it was three to four times greater. This is somewhat similar to the findings of Siegel and Piatkowski (1990), although as the latter make clear, separation of communities based simply on abundance or biomass, which can change over time, is inappropriate. Evidence for the existence of a neritic community in the Weddell Sea and around the Antarctic Peninsula has been provided by Boysen-Ennen and Piatkowski (1988) and Siegel and Piatkowski (1990), respectively. In addition to describing changes in abundance of species which also occur in the oceanic community they describe the presence of different dominant species such as *Euphausia crystallorophias* and *Pleuragramma antarcticum*.

Data obtained during this study although not as finely resolved as many of the surveys in this region show the presence offshore of Antarctic Zone and Weddell Sea influenced station groups,

although within the Bransfield Strait G3 and G5 predominate with stations from G3 extending along the Weddell Scotia Confluence to the South Orkney Islands.

4.3. Frontal regions as faunal boundaries

Deacon (1982) drew attention to the fact that the rise in surface temperature from the Antarctic continent northward is not uniform. A number of sharp transition zones exist in addition to the break between the continental shelf and deep water, and these frontal regions often appear as discontinuities in the distribution of phytoplankton and zooplankton (Errhif et al., 1997; Pakhomov and McQuaid, 1996; Pakhomov et al., 2000). This analysis initially suggested that two main zooplankton groups were present, broadly separated along the line of the WF. This broad boundary zone is the product of the mixing of waters of three different origins (ACC, Bellingshausen Sea, and Bransfield Strait) interacting with water from the Weddell Sea. It is a mobile feature and is characterized by meanders and eddy-like structures, particularly to the east of the South Orkney Islands, where it becomes very diffuse (Foster and Middleton, 1984). For some taxa it is reported as the southernmost limit of distribution e.g. the copepods *Calanus simillimus* (Kanaeva, 1968; Marin, 1987; Vladimirskaia, 1978) and *Clausocalanus laticeps* (Jazdzewski et al., 1982; Marin, 1987), and is an important spawning area for at least two species of euphausiid: *E. superba* (Brinton, 1985; Marr, 1962; Siegel et al., 2004; Spirodonov, 1995) and *E. frigida* (Brinton, 1985; Makarov, 1977). Marin (1987) viewed the WF as an important boundary in terms of the abundance and age structure of zooplankton populations, but concluded that it did not separate two distinct communities as the order of abundance of species did not differ significantly. A similar conclusion was reached by Siegel et al. (1992).

Within the Scotia Sea a number of full depth frontal features have been observed (Orsi et al., 1995) all lying close together in the region immediately downstream of Drake Passage, before diverging further eastward (Brandon et al., 2004).

A number of studies have emphasized that the APF marks an important transition between subantarctic and Antarctic fauna and that the WF (continuing as the Antarctic Divergence in other sectors of the Southern Ocean) between the oceanic and continental shelf communities (Boysen-Ennen and Piatkowski, 1988; Deacon, 1982; Hosie et al., 2000; Longhurst, 1998). However while fronts may reflect distinct changes in some species distributions, for many others, they do not represent a boundary (Atkinson and Sinclair, 2000; Mackintosh, 1960). In an analysis of copepod distribution taken from the surface to 1000 m, in waters ranging from the subantarctic to the Weddell Scotia Confluence, Atkinson and Sinclair (2000) discounted Deacon's suggestion of the APF as a biogeographic boundary. They found some species to be more abundant within the front itself, rather than it representing either the northern or southern limits to distributional ranges. They concluded that there was no indication of species clustering into warm- or cold-water types and that a continuum existed between the two extremes. In the Indian Ocean sector of the Southern Ocean Errhif et al. (1997) investigated copepod composition and community structure on a transect running past Kerguelen and Heard Islands towards the Continent. They found highest densities in the region between the APF and the Antarctic Divergence with peak abundance in the region of the Antarctic Divergence. Increased abundance within fronts is commonly seen as they are often productive (see Fransz and Gonzalez, 1997; Lutjeharms et al., 1985; Pakhomov et al., 2000) or may act to physically concentrate plankton (Franks, 1992; Voronina, 1970). A transect of closely spaced stations run from Cape Town to Sanae in the Atlantic sector resolved four major station groupings separated by three major frontal systems: the Subantarctic Front, APF, and Sub-Tropical Convergence (Pakhomov et al., 2000). Within the group south of the APF a further three subgroups were apparent, the first associated with the Marginal Ice Zone and a further two in the Polar Open Ocean Zone, roughly separated by the Northern Extension of the Cold Water layer which coincides with the northernmost extent of the 0 °C isotherm and

approximates to the northernmost limit of winter sea ice. The latter feature appears synonymous with the SACCF, and according to Pakhomov et al. (2000) approximates the northern limit of Antarctic krill distribution and the southern limit of *Salpa thompsoni*, although in the Atlantic sector there is considerable overlap in the distribution of both species (see Kawaguchi et al., 2004; Mackintosh, 1936). Nonetheless their analysis, like that of Marin (1987) suggested the existence of a single oceanic community south of the APF. Data from the present survey lend only limited support to the idea of frontal regions defining the limits to oceanic zooplankton communities in this sector of the Southern Ocean. In this case, samples were all obtained poleward of the APF and although both ordinations suggested the WF as being a feature separating the two main groups, similarities in species composition between G1 and G2 lead to the conclusion that they essentially belong to the same biological community, differing only in their degree of development, probably because of differences in the timing of seasonal productivity. Although the division between the two groups broadly followed the line of the WF, particularly west of 40° W, there was a pronounced northward extension of G2 across the front to the east. This follows the path of the outflow of Weddell Sea water (Maslennikov and Solyankin, 1980), and consequently stations north of the WF around the South Sandwich Islands also belong to G2. The second ordination also shows this as being a strong structuring feature. The presence of stations belonging to this group over the shelf and shelf break area of the Antarctic Peninsula also suggests that this is more likely to be a 'cold-water community' rather than be derived exclusively from the Weddell Sea, although Weddell Sea water is known to intrude into Bransfield Strait (Stein and Heywood, 1994). The secondary frontal features such as the SACCF and the SBACC did not appear to be important in terms of defining community structure. Ordination 2 using the full species stages dataset introduced an additional group in the Scotia Sea which lay broadly between the positions of the SBACC and the SACCF. However, the composition of

this group had distinct similarities with adjacent groups and as such was only separable in terms of differing proportions of some species stages.

The distribution of the cold, ice-affected Antarctic Surface Water (Brandon et al., 2004) fairly closely follows the boundary between G1 and G2 (Fig. 2) and may be largely responsible for differences between the two. Thus the existence of a single community modified by the presence of seasonal ice cover is indicated.

5. Conclusions

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

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Paper 2

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Plankton community structure and variability in the Scotia Sea: austral summer 2003

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ABSTRACT: Plankton community structure in the Scotia Sea was investigated during January/early February 2003 based on phytoplankton cell counts from 20 m depth and mesozooplankton counts from 0 to 400 m net hauls. Cluster analysis and multi-dimensional scaling revealed 4 major groups of stations within each ordination that broadly corresponded geographically. A grouping of stations to the east of the Antarctic Peninsula was characterised by low phytoplankton cell counts. The corresponding grouping of stations in the mesozooplankton data were characterised by low abundance, overwintered state of many species, low egg production rates, and low carbon mass of copepod instars. In contrast, groupings of stations in the northern part of the Scotia Sea were characterised as chlorophyll and mesozooplankton rich, and the summer generation was well advanced. Latitude was most strongly correlated with mesozooplankton community pattern (rank correlation $\rho = 0.608$), whereas surface chlorophyll *a* was a weaker correlate ($\rho = 0.344$) but along with measures of size-fractionated chlorophyll contributed towards explaining variation in species stages carbon mass and egg production rates. Additional hauls to 1000 m with an LHPR indicated copepod populations were broadly in an overwintered state in the south of the region, whereas to the north of South Georgia recruitment had been completed and some species were undergoing a seasonal descent. A comparison with January/February 2000 revealed higher abundances of krill larvae throughout the Scotia Sea in 2000 as well as a more advanced generation of the copepod *Calanoides acutus*. Ice cover during the 2 years differed considerably; in 2000 the position of the summer ice edge broadly accorded with the 25 yr average, whereas in 2003 the ice edge lay much further north than usual. We suggest that the timing of ice retreat influenced the timing of reproduction with the late retreat in 2003 causing delayed reproduction and reduced population sizes.

KEY WORDS: Southern Ocean · Phytoplankton · Zooplankton · Community structure · Production · Sea ice

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INTRODUCTION

Concern over the consequences of climate change makes it increasingly necessary to understand how ocean ecosystem structure and dynamics are related to environmental variability. Trends in long-term data from the Northeast Atlantic and European shelf seas increasingly point to large-scale, climate-mediated changes of plankton populations, albeit with considerable regional variability (Planque & Taylor 1998, Edwards et al. 2002). In the Southern Ocean extensive

time-series data are presently lacking, although recent findings by Atkinson et al. (2004) suggest a dramatic decline in krill abundance has taken place in recent decades, particularly in the Atlantic sector, which may be related to changes in sea-ice distribution. Whilst satellite technologies have dramatically improved our ability to view the Southern Ocean in terms of sea-ice cover, sea-surface temperature, sea-surface height and phytoplankton distribution over large spatial and temporal scales, our present view of zooplankton distribution and dynamics is largely a composite derived from

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shipboard surveys carried out at sub-basin scales in different years and places (e.g. Mackintosh 1934, Marr 1962, Andrews 1966, Atkinson 1991). Nonetheless one characteristic feature of the larger-scale environment that has been clear for some time is that a latitudinal gradient in production cycles exists within the Southern Ocean, with community development commencing earlier in the northern part of the Antarctic Circumpolar Current (ACC) during spring and summer, compared to further south (Hart 1942, Voronina 1970).

Repeated observations at smaller spatial scales have also established variability in the timing and extent of production processes within different regions (e.g. Whitehouse et al. 1996) and within various taxonomic groups (e.g. Brinton et al. 1986, 1987, Siegel & Loeb 1995, Shreeve et al. 2002). Despite the formidable logistical difficulties in surveying such a large and complex area, a number of surveys undertaken in various parts of the Southern Ocean in the last 20 or so years have provided quasi-synoptic views of community structure. Many of these surveys have used the macroplankton catch composition to provide a view of community structure (e.g. Piatkowski 1989, Hosie 1994, Hosie et al. 2000), whereas others have used the more ubiquitous mesozooplankton provided by finer mesh nets (e.g. Errhif et al. 1997, Pakhomov et al. 2000, Ward et al. 2004). Both approaches provide differing views of community structure, although there is general agreement about many of the factors that structure such communities. Thus the positions of frontal zones such as the Antarctic Polar Front (APF) and the Antarctic Divergence are in many studies consistent with discontinuities in zooplankton distribution (Boysen-Ennen et al. 1991, Longhurst 1998, Hosie et al. 2000, Pakhomov et al. 2000, Ward et al. 2002); zooplankton abundance is often elevated within frontal zones either through physical concentration (Voronina 1970, Franks 1992) or because fronts are productive (Fransz & Gonzalez 1997, Pakhomov et al. 2000). Ice cover can also influence community development through its impact on food availability (Mackintosh 1934, Atkinson & Shreeve 1995, Burghat et al. 1999, Quetin & Ross 2003, Ward et al. 2004). The development of blooms of large diatoms is often crucial for enabling many species of calanoid copepods and Antarctic krill to maximise growth and reproductive rates (Ross et al. 2000, Shreeve et al. 2002), and changes in phytoplankton properties, expressed either as biomass, size or measures of phytoplankton quality, are also often associated with such faunal discontinuities (Shreeve et al. 2002, Ward et al. 2005).

Understanding the nature of the constraints on Southern Ocean plankton community development and allied seasonal and interannual variability will become increasingly important if we are to identify secular change against background variability. As well as a requirement to document structure over large spatial and temporal

scales there is also a need to assess the impacts of physical features such as frontal zones and variable ice cover on production processes. The data presented in this paper were collected during a survey that formed part of the UK's Southern Ocean GLOBEC initiative, which was to examine the large-scale population processes among krill and copepods within the Scotia Sea. Our objectives were to characterise spatial and temporal variability in community structure and development across the area and assess how this variation reflected that of other environmental properties. We compare our present results with those of a 4-ship survey centred on the Scotia Sea and undertaken in early 2000 when ice conditions were dramatically different.

MATERIALS AND METHODS

Between 8 January and 9 February 2003 as part of cruise JR82 on board RRS 'James Clark Ross', 8 zig-zag transects were run across the Scotia Sea commencing at a position north of Elephant Island and traversing eastwards (Fig. 1). Fifty-five stations were located along the transects at 60 nm intervals, and at each a full depth CTD cast was carried out followed by vertical Bongo net deployments to 400 m. A further 6 stations located within a mesoscale box straddling the shelf break to the northwest of South Georgia were also sampled. Here CTDs were deployed to 1000 m in the deeper parts of the box or near bottom over the shelf. Bongo net deployments were to a depth of 200 m at these 6 stations.

Phytoplankton. Water for analysis of chlorophyll *a* (chl *a*) and phaeopigments, size-fractionated chl *a* and nutrients was obtained from standard depths (ca. 20, 40, 60, 80, 100, 125, 150 and 200 m, and a further 4 evenly spaced depths sampled between 200 m and the bottom of the cast) at each of the 61 stations using a Seabird 911+ CTD and carousel sampler equipped with twelve 101 Niskin bottles (see Korb & Whitehouse 2004 for details). Additional samples were obtained from the ship's non-toxic seawater supply located 6 to 7 m below the sea surface as the CTD was surfacing. Size-fractionated chl *a* was measured on water samples from a depth of 20 m by passage through a series of 47 mm polycarbonate filters (12, 2 and 0.2 μm). Thus pico-, nano- and microphytoplankton were represented by the 0.2 to 2 μm , 2 to 12 μm and >12 μm size fractions. Macro-nutrient concentrations were determined using a Technicon segmented flow analyser (Whitehouse 1997).

Species composition representative of the upper mixed layer was determined at each station from water samples collected at 20 m and preserved in 1% acid Lugols solution. Microplankton were enumerated by use of the Utermöhl (1958) technique. Sample solutions

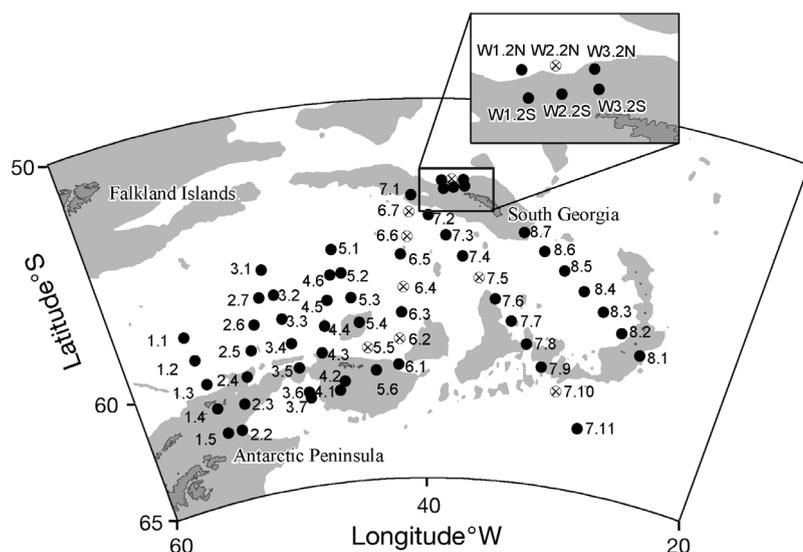


Fig. 1. Scotia Sea study area showing 61 station positions worked during cruise JR82. Bongo nets were worked at all stations and Longhurst-Hardy Plankton Recorder (LHPR) hauls were additionally made at stations shown with cross-hairs. Transects were run from west to east. Station identifiers shown relate to transect number first followed by station number. Transect 2 commenced at Stn 2.2 and not 2.1, which lay further south in ice-covered waters and was not sampled. Grey tones represent the 2500 m isobath in this and subsequent figs

were left to settle in 50 ml chambers for at least 24 h before analysis of selected microplankton taxa by inverted microscopy. Sixteen selected categories were examined on either 2 or 3 perpendicular transects across the whole slide on 100× magnification. The categories were chosen on the basis of the dominance of the >12 µm microplankton and their ease of identification. Species counted ranged in size from ~5 to 200 µm.

Mesozooplankton. At each station a motion-compensated Bongo net (mouth diameter opening 61 cm, net mesh 200 µm) with 2 solid cod-ends was deployed from the surface to 400 m and then hauled vertically back onboard the stationary vessel. Upon recovery the contents of one cod-end were immediately diluted with surface seawater at ambient temperature for sorting of live material. To investigate production processes and understand how they varied spatially, we required species and stages that we were confident would be present over much of the survey area. Therefore, *Calanoides acutus* and *Rhincalanus gigas* females were chosen for egg production experiments and carbon (C) mass determinations and additionally stages CIV and CV of *C. acutus* for C mass determination. Female copepods were sorted and incubated in groups of 10 for 24 h to determine egg production rates (EPR see Ward & Shreeve 1995 for further details). Females were then removed, rinsed briefly in ammonium formate and placed in pre-weighed ultra lightweight tin foil capsules. Additionally, ~30 CIV and CV *C. acutus* from each station

were frozen for C mass determination. Samples were frozen at -80°C and subsequently dried at 60°C onboard ship within 1 wk of collection. They were then transferred in a sealed container to the UK where they were again dried at 60°C to constant weight. Dry mass was measured on a Mettler MT5 balance to an accuracy of ±1 µg. Whole samples were then analysed for C and N using a Fisons EA 1108 elemental analyser using acetanilide as a standard.

The contents of the second cod-end were preserved in 10% (v:v) formalin in seawater for community analysis in the UK, where they were divided into appropriate aliquots with a Folsom plankton splitter and examined under a binocular microscope. Zooplankton were identified to species and stage or higher taxonomic categories and enumerated. An average number of between 1000 and 1500 individuals were counted in each sample.

Fatty acid and POC analyses. Seawater samples (between 1.2 and 3.6 l)

collected at 20 m for particulate organic carbon (POC) and total fatty acid (TFA) analysis were filtered onto pre-ashed GF/F filters. Those for TFA analysis were placed in chloroform:methanol (2:1 v/v) and both were then stored at -80°C until analysis. After the addition of an internal fatty acid standard (21:0) lipids were extracted according to Folch et al. (1957). Fatty acid methyl esters were prepared in methanol containing 1% sulphuric acid and transmethylated at 50°C for 16 h (Christie 1982). After purification by thin-layer chromatography, fatty acid methyl esters were dissolved in hexane at a concentration of 1 mg ml⁻¹ and analysed on a Carlo Erba Trace 2000 gas chromatograph equipped with a ZBWAX fused silica capillary column (30 m × 0.32 µm). Hydrogen was used as the carrier gas, and fatty acids were identified by comparison with a well-characterized marine fish oil.

Similar quantities of seawater for POC analysis were also filtered onto pre-ashed filters and stored at -80°C. In the UK samples were acidified under an atmosphere of fuming hydrochloric acid for 24 h and then dried in a vacuum desiccator for 24 h. Elemental C and N were determined in 3 replicate subsamples as for the above copepod samples.

LHPR sampling. At 8 stations (Fig. 1) a Longhurst-Hardy Plankton Recorder (LHPR) equipped with a 200 µm mesh net and 38 cm diameter nose cone was rapidly deployed to 1000 m. The net was allowed to stabilise at depth and was then fished to the surface,

hauling at a rate of $\sim 30 \text{ m min}^{-1}$. The LHPR was programmed with a gauze advance time of 90 s and fished at a ship's speed of 3.5 to 4 knots. In this way the ascent profile contained 45 to 60 patches with an average depth resolution of $\sim 20 \text{ m}$, representing approx. 18 m^3 filtered per patch. Upon recovery the gauzes were cut into individual patches and frozen at -20°C . In the UK gauzes were thawed and fixed in formalin and the copepodite stages of 2 of the biomass dominant species (*Calanoides acutus*, *Rhincalanus gigas*) were enumerated. Data were standardised to ind. m^{-2} .

The mean stage of the population (S) was estimated according to the equation where CI, CII...C VI represent successive copepodite stages, n is the number of individuals within each stage and N is the overall abundance of all stages combined.

$$S = \frac{n\text{CI} + 2n\text{CII} + \dots + 6\text{C VI}}{N}$$

Data analysis. Phytoplankton cell counts and mesozooplankton data were initially analysed with the statistical package PRIMER 5 (Primer-E). Standardised data in the form of phytoplankton cell counts ($\text{ind. } 50 \text{ ml}^{-1}$) and mesozooplankton abundance (ind. m^{-2}) were double-root-transformed and subjected to q -type cluster analysis to group stations based on the Bray-Curtis similarity and group average linkage classification (Field et al. 1982). The treatment of the mesozooplankton data prior to running PRIMER analyses differed from that of the phytoplankton cell count dataset in that rare species and stages were not removed from the data matrix, and species stages were not aggregated into higher groupings, although data were standardised to ind. m^{-2} (0 to 400 m) and double-root-transformed to normalise abundance. This approach was dictated largely by the fact that previous research (Pakhomov et al. 2000, Ward et al. 2004) indicated that differences between zooplankton communities are very often the result of changes in species abundance rather than species composition and that variable abundance, as well as being attributable to changing distribution across a species range, can often result from differences in rates and timing of recruitment across that range. By distinguishing between ontogenetic stages rather than aggregating them under species headings we wished to see how station groupings differed in terms of community development.

Non-metric multi-dimensional scaling (MDS) was also performed to allow relationships between groups to be assessed. Its purpose is to represent the samples as points in low-dimensional space (2D) such that the relative distances from all the points are in the same rank order as the relative dissimilarities of the samples (as calculated by Bray-Curtis coefficients). The starting configuration in this instance is a random

set of points. There is no guaranteed method of ensuring that a global minimum stress has been reached; therefore the algorithm dictates that the analysis is repeated several times (in this instance 25 times) starting with different random positions of samples. The stress levels indicates how faithfully the high-dimensional relationships among the samples are represented in the 2D plot with a value of ~ 0.1 indicating a good representation of the data.

The SIMPER (similarity percentages) routine was also performed on both datasets. SIMPER examines how much each species/taxon contributes to the average sample similarity within and dissimilarity between groups (Clarke & Warwick 2001). We also used the RELATE procedure (non-parametric Mantel-type coefficients) to compare the 2 multi-variate representations and BIO-ENV, a routine that calculates a measure of agreement between 2 (dis)similarity matrices, on the mesozooplankton data matrix and another containing information on environmental variables measured at each station (see Table 7 and Results section for details of variables included). Within the analysis, rank correlation (ρ) of the matching elements was carried out with combinations of the environmental variables being considered at steadily increasing levels of complexity. In this way an optimal subset of environmental variables that 'best explains' the biotic structure is identified. A value of $\rho = 0$ would imply an absence of any match between the 2 patterns, but typically values of ρ will be positive with a value of +1 being a perfect match (Clarke & Ainsworth 1993).

The relationship between C mass, abundance and EPR data collected at each station and a suite of 9 potential predictor variables (see Table 9 and 'Results' for full details) was examined using best subsets regression. Response and predictor variables were log-transformed where necessary to linearise the relationship, stabilise variability, and reduce skewness. The Akaike Information Criterion with small-sample adjustment (AIC_c) was used for model selection (Burnham & Anderson 2002). Low values of AIC_c indicate parsimonious models with good fit and few parameters. For presentation, values of AIC_c for different models are expressed relative to the smallest value as a difference $\Delta = \text{AIC}_c - \min(\text{AIC}_c)$. Models within about 2 units of the minimum are considered as competing models in a statistical sense (Burnham & Anderson 2002). Spatial autocorrelation was examined using the variogram of the standardised residuals from the fitted model (Cressie 1993). The residuals at locations i and j along a particular transect were denoted by r_i and r_j , respectively, with the corresponding distance between locations denoted by d_{ij} . The variogram was formed by plotting the square of the difference between the residuals $v_{ij} = (r_i - r_j)^2$ against d_{ij} over all

pairs of residuals. An increase of v_{ij} with d_{ij} indicates a pattern of autocorrelation that decreases with distance between locations. Analyses were implemented using the statistical software package MINITAB v.13 (Pennsylvania State University).

Sea-ice cover. Sea-ice-concentration data were calculated from the U.S. Defense Meteorological Satellite Program's Special Sensor Microwave Imager passive microwave data by the National Oceanic and Atmospheric Agency/National Centers for Environmental Prediction (NOAA/NCEP). These data were first previewed as the northern extent of the 15% ice concentration. Spurious values (for example from icebergs) were removed before plotting the monthly positions of the northern extent of 15% sea-ice concentration in the geographical information system package ArcGIS8.2 (ESRI).

RESULTS

Physical characteristics and position of fronts

CTD potential temperature-salinity data were used to characterise the different water masses occurring within the Scotia Sea (Fig. 2). While there was a clear distinction between waters to the south of the Southern Boundary of the Antarctic Circumpolar Current (SB) and waters to the north of the Southern Antarctic Circumpolar Current Front (SACCF) compared with the rest of the survey stations, there was a degree of overlap in the TS characteristics at the SACCF. Here, nutrient and oxygen data were used to further discern the position of the SACCF (Sievers & Nowlin 1984). The major frontal jets were generally orientated in a southwest-to-northeast direction through the study site, with meandering and eddy-shedding particularly evident within the mid-survey area (Fig. 2). The Polar Front (PF) was not traversed, although water in the extreme northwest of the survey area may have originated from north of the front. At the southern extremities of the survey, Weddell Front and Weddell Scotia Confluence characteristics were evident only intermittently. Within the Scotia Sea typical Antarctic surface-

water profiles were found at 25 of the 27 stations occupied between the northernmost stations (excluding casts downstream of South Georgia) and the SB (median T min 70 m).

Microplankton community structure

Cluster and MDS analysis identified 4 groups of stations and 1 outlier (Table 1, Fig. 3). Median values of chl a and other chemical indices relating to the phytoplankton characterising each station group are presented in Table 2 and size-fractionated percentages in Table 3.

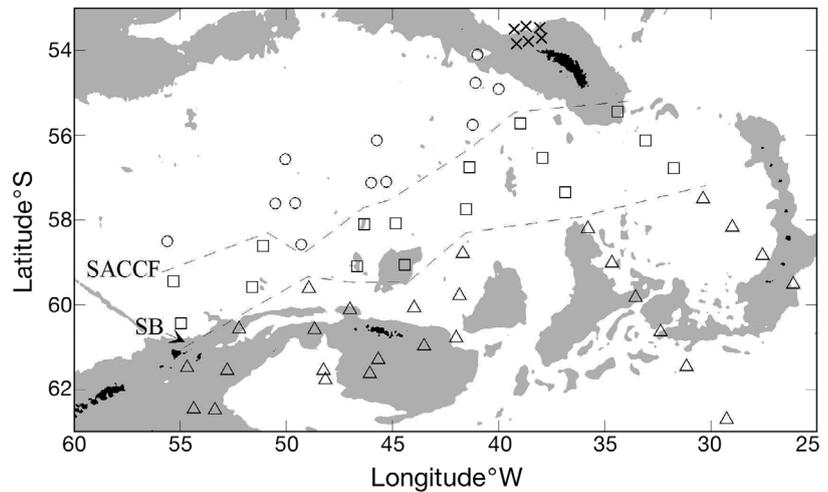


Fig. 2. Water mass distribution within Scotia Sea during cruise JR82. x = South Georgia Modified Shelf water, O = water lying to north of the southern Antarctic Circumpolar Current Front (SACCF), □ = water lying between SACCF and the Southern Boundary of the Antarctic Circumpolar Current Front (SB), Δ = water lying to south of SB. Approximate frontal positions indicated by dashed lines

Table 1. Average cell count abundance (no. ind. 50 ml⁻¹) within phytoplankton station groupings of species and taxa that SIMPER analysis indicated contributed most to within-group similarity and between-group dissimilarity. Highest value for each species/taxa in bold. Species have been arranged in order of total abundance across all groups with respect to major taxonomic groupings. Species taxonomy in accordance with Scott & Marchant (2005). Highest value for each species/taxon in bold

Species/taxon	Abundance no. ind 50 ml ⁻¹			
	Group 1 (n = 6)	Group 2 (n = 17)	Group 3 (n = 24)	Group 4 (n = 14)
<i>Eucampia antarctica</i>	16143	0	0.4	148
<i>Nitzschia/Pseudonitzschia</i> spp.	735	96	657	8096
<i>Fragilariopsis Kerguelensis</i>	544	52	785	6257
<i>Chaetoceros</i> spp.	748	24	252	6379
<i>Thalassiosira</i> sp.	3619	19	165	1336
<i>Thalassionema/Fragilariopsis</i> spp.	1986	291	744	1438
<i>Rhizosolenia</i> sp.	27	0.6	120	125
Small dinoflagellates	2462	610	787	2749
Small ciliates	172	50	57	47

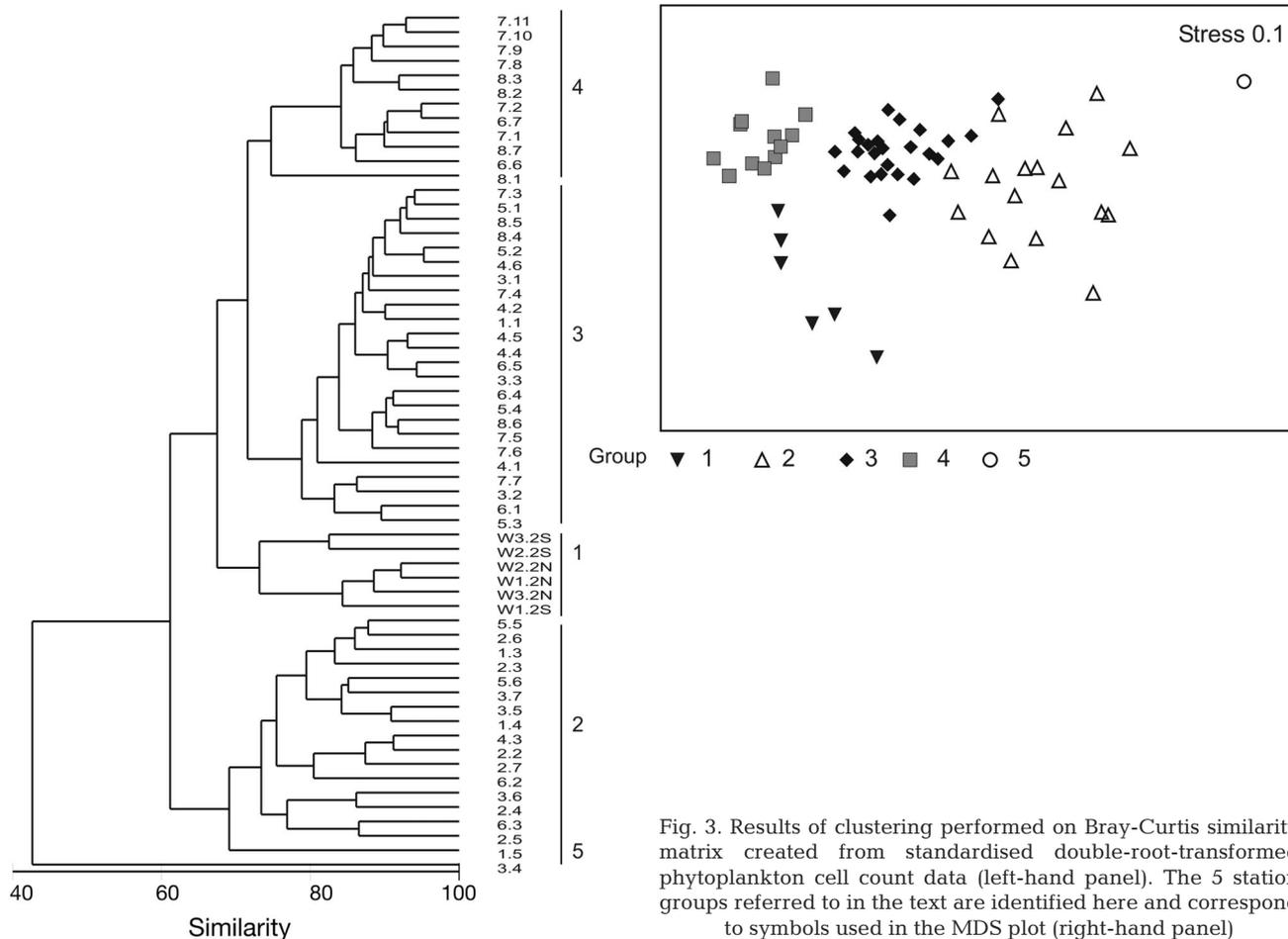


Fig. 3. Results of clustering performed on Bray-Curtis similarity matrix created from standardised double-root-transformed phytoplankton cell count data (left-hand panel). The 5 station groups referred to in the text are identified here and correspond to symbols used in the MDS plot (right-hand panel)

Table 2. Median values (upper and lower quartile values) for chl *a*, POC, particulate C:N and total fatty acids with respect to phytoplankton station groups

	Group 1 (n = 6)	Group 2 (n = 17)	Group 3 (n = 24)	Group 4 (n = 14)
Chl <i>a</i> (mg m ⁻² , 0–100 m)	5.72 (2.91–8.63)	0.21 (0.14–0.53)	0.29 (0.16–0.49)	1.12 (0.17–2.34)
POC (µg l ⁻¹ , 20 m)	146 (115–229)	52 (42–69)	57 (41–116)	91 (67–136)
C:N (particulates, 20 m)	6.00 (5.62–6.43)	5.44 (5.06–5.70)	5.44 (5.26–5.73)	5.60 (5.35–5.89)
Total fatty acids (µg l ⁻¹ , 20 m)	153 (119–165)	28 (22–34)	33 (22–41)	96 (68–118)

Group 1 comprised 6 stations north of South Georgia where cell counts were high as were surface chl *a* values (1.9 to 11.4 mg m⁻³). Here *Eucampia antarctica* was characteristic and almost exclusive to this group. Group 2 (17 stations) was located mainly along the southern portions of the first 6 transects and were characterised by surface chl *a* values of ≤1 mg m⁻³ and by low overall cell counts. Small dinoflagellates characterised these stations with remaining taxa occurring in low abundance. Group 3 (24 stations) generally occurred at the northern por-

tions of transects 3 to 5 and thereafter in the middle portions of transects 6 to 8. Surface chl *a* was slightly higher (≤1.9 mg m⁻³), although cell counts were modest and no one particular taxon dominated. Whereas the stations in the above groups had clear geographic integrity (Fig. 4), those in Group 4 (14 stations) were distributed along the tops of transects 1, 6, 7 and 8 and additionally comprised the southerly portions of transects 7 and 8. Here surface chl *a* was higher (≤9 mg m⁻³) and highest values of *Nitzschia/Pseudonitzschia* spp., *Fragilariopsis kerguelensis* and *Chaetoceros* spp. were found.

SeaWiFS composites for January indicated that the southerly bloom stations may have been influenced by the retreating ice edge (Korb et al. 2005).

Mesozooplankton

Four main station groupings were disclosed by the cluster and MDS analysis with a single outlier (Fig. 5).

Table 3. Mean values of percentage size-fractionated chl a biomass from 20 m water bottle with respect to phytoplankton station groups (upper and lower quartile values)

Size fraction	Group 1	Group 2	Group 3	Group 4
% Microphytoplankton (>12 µm)	80 (70–89)	11 (2–16)	40 (15–65)	68 (49–87)
% Nanophytoplankton (2–12 µm)	12 (7–16)	42 (31–52)	32 (21–43)	1 (8–27)
% Picophytoplankton (<2 µm)	8 (4–14)	47 (39–55)	28 (12–41)	13 (4–21)

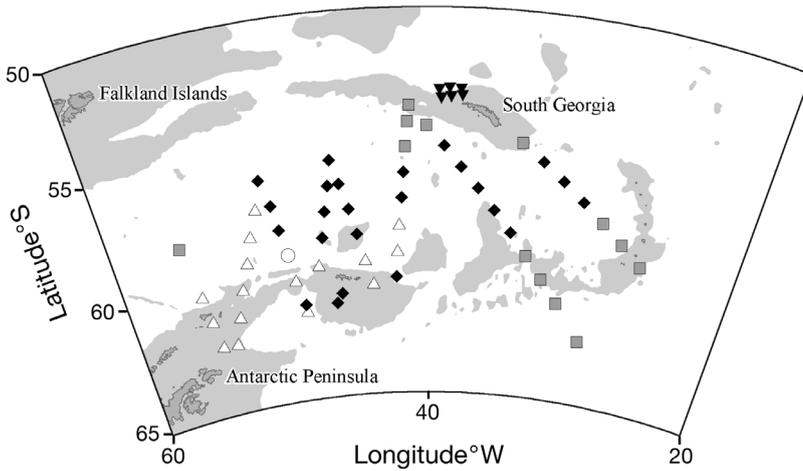


Fig. 4. Geographical distribution of station groups identified in phytoplankton cell count ordination. Symbols correspond to those used in Fig. 3

The station groupings were in modest agreement with those of the microplankton ordination (RELATE analysis $\rho = 0.438$, $p = 0.1\%$). Geographical positions of station groups are presented in Fig. 6. Once again Group 1 comprised stations to the north of South Georgia but additionally included stations at the northern end of transects 6 to 8. The average abundance of the 28 taxa, in this case with stages aggregated within species, which collectively contributed $\geq 2\%$ of similarity within groups or dissimilarity between groups, as indicated by SIMPER analysis, are presented in Table 4.

Most taxa were present across the entire Scotia Sea, but generally their abundance was highest within station Group 1. Groups 2 and 3 largely paralleled the geographic distribution of the microplankton station groupings and their respective qualities in terms of relative abundance of taxa across groups (Table 1). Group 4 in this case occupied the greater part of transects 6 to 8 rather than being restricted to their extreme ends. One other station comprised an outlier from the main station groupings indicated in Fig. 6. It was located near the ice edge just east of the South Orkneys (Fig. 7) and was characterised by an overall reduction of taxa. The

median abundance of mesozooplankton across groups was >3 times greater in Group 1 than in the remaining 3 groups or the outlying single station (Group 5). Overall, copepods accounted for between 77% and 97% of total mesozooplankton abundance with large copepods (prosoma length > ~1.5 mm) proportionately accounting for <4% of total abundance (Table 5).

There were also clear differences in the development of large calanoid copepod populations in the top 400 m over the Scotia Sea. Over-wintered populations of *Calanoides acutus* (low overall abundance and relatively high number of females) in a pre-recruitment phase characterised almost all of the stations in Group 2, whereas further north and east the spring generation had evidently developed and north of South Georgia was already undergoing a seasonal descent. Such an interpretation is consistent with the findings of Atkinson (1991) and Atkinson et al. (1997) and the life-cycle model developed by Tarling et al. (2004). Details of population vertical distribution are given below in the LHPR section (see below and Fig. 8b). The distribution of *Calanus propinquus* reflected that of *C. acutus* with older stages dominating

the majority of stations in Group 2, whereas a latitudinal cline was broadly discernible among the remaining stations. For *Rhincalanus gigas*, which generally spawns later than the other species, the population displayed a clear latitudinal cline with younger stages dominating Group 1 and older stages generally present further south. The mean stage of each species with respect to station group is presented in Table 6.

Although we were unable to distinguish ontogenetic stages for many of the other copepod species present, the ‘catch-all’ taxonomic groupings calanoid nauplii and cyclopoid nauplii also showed distribution patterns that reflected those described above with respect to station groupings (Table 4). Krill larvae were present, albeit in relatively low concentrations, in the northern part of the Scotia Sea and along transects 7 and 8. Highest larval densities (7000 ind. m⁻²) were unusually found in oceanic waters to the northwest of South Georgia (Fig. 9b).

Of the environmental variables used in the BIO-ENV analysis, latitude was the strongest of the correlates with mesozooplankton community pattern ($\rho = 0.608$). Inclusion of phosphate, which was inversely

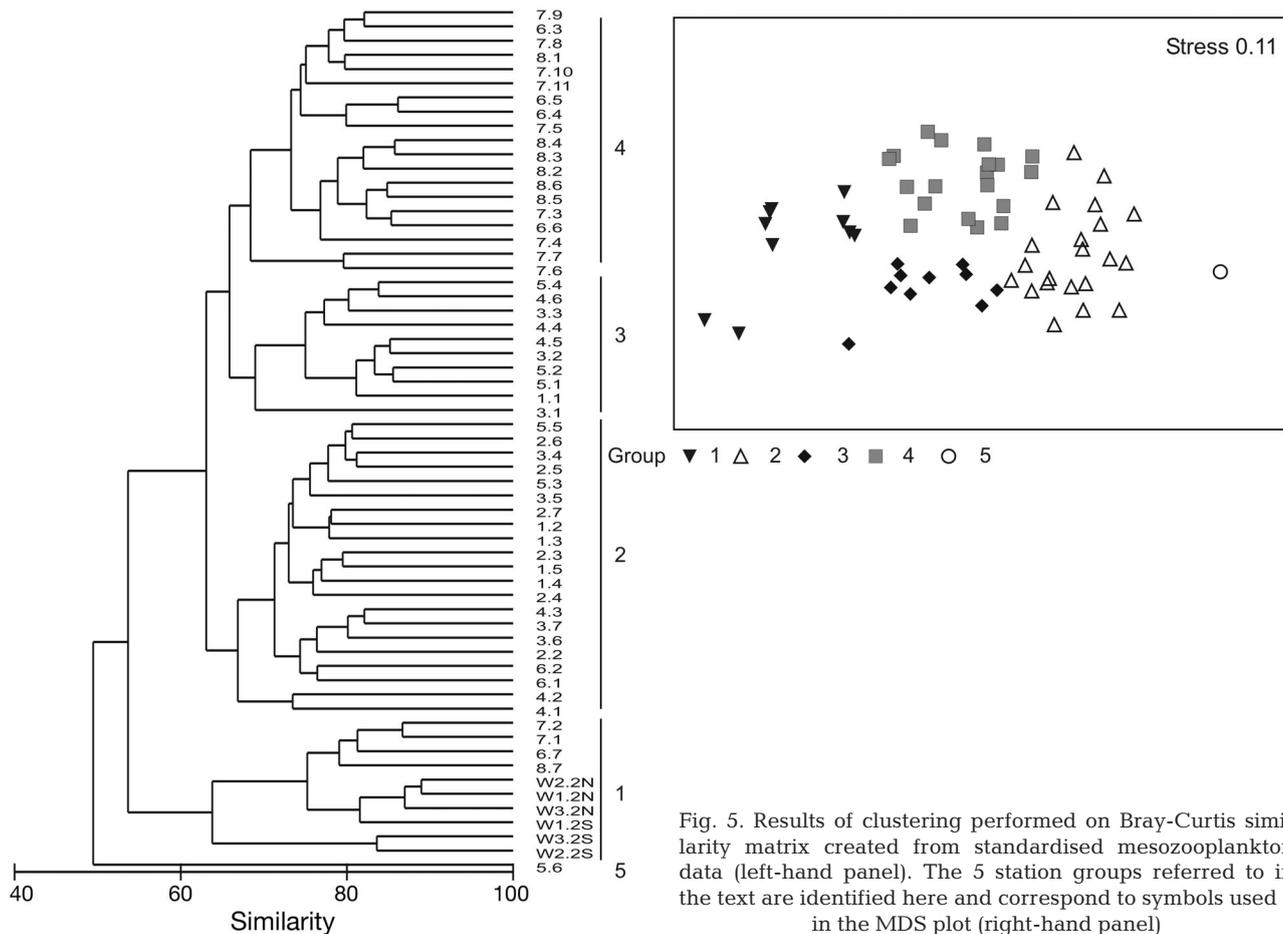


Fig. 5. Results of clustering performed on Bray-Curtis similarity matrix created from standardised mesozooplankton data (left-hand panel). The 5 station groups referred to in the text are identified here and correspond to symbols used in the MDS plot (right-hand panel)

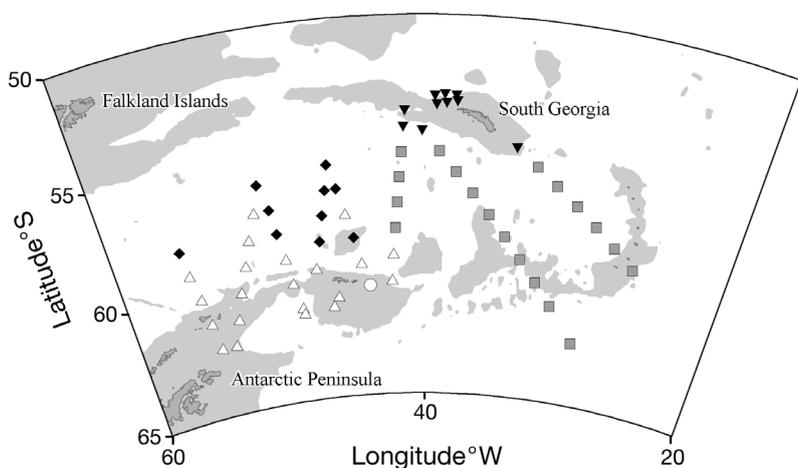


Fig. 6. Geographical distribution of station groups identified in mesozooplankton ordination. Symbols correspond to those used in Fig. 5

related to chl *a* biomass, increased the rank correlation coefficient ($\rho = 0.642$), whilst other variables did nothing to significantly improve the fit (Table 7). Although latitude might be considered a proxy for temperature (they were significantly correlated; $R^2 =$

0.85, $F = 345.95$, $p < 0.0001$), substitution of temperature for latitude in the analysis gave a lower rank correlation ($\rho = 0.44$). In contrast with stepwise regression analysis (see below), surface chl *a* was also a weaker correlate with overall community pattern ($\rho = 0.344$).

Carbon mass and egg production

For *Calanoides acutus* only stations where stages CIV and CV could be attributed with confidence as belonging to the new summer generation were included in the analysis of carbon mass. Stations where low abundance was coupled with a dominance of later stages were excluded because here copepod condition was thought likely to reflect their recent overwintered state rather than the influence of any of the measured environmental variables. Such populations were predominantly found at stations within Group 2.

Table 4. Average mesozooplankton abundance (ind. m⁻², 0–400 m*) within station groupings of species and taxa that SIMPER analysis indicated contributed most to within-group similarity and between-group dissimilarity. Species have been arranged in order of total abundance across all groups. Highest value for each species/taxon in bold. *Abundance at South Georgia stations sampled in water column of 200 m (see 'Materials & methods')

Species/Taxon	Group 1 n = 10	Group 2 n = 21	Group 3 n = 10	Group 4 n = 19
<i>Oithona</i> spp.	348267	34060	63479	82854
Cyclopoid nauplii	49408	97	268	12622
<i>Metridia</i> spp. CI–III	25536	2663	7742	12259
<i>Oncaea</i> spp.	17258	5310	6362	13313
Appendicularians	19492	2146	9647	8835
<i>Microcalanus pygmaeus</i>	5300	10495	6502	12716
<i>Drepanopus forcipatus</i>	34691	0	0	0
<i>Ctenocalanus</i> spp.	26675	1542	1533	1352
<i>Rhincalanus gigas</i> nauplii	17696	27	657	501
<i>Metridia</i> spp. CIV–VI	8968	607	1602	3054
Calanoid nauplii	6467	320	864	4620
<i>Calanus simillimus</i>	5590	54	1920	22
<i>Calanoides acutus</i>	3017	488	1556	1654
<i>Limacina</i> spp.	3811	21	712	911
Chaetognatha	808	585	1422	927
<i>Rhincalanus gigas</i>	2144	96	1010	216
<i>Pelagobia longicirrata</i>	2584	107	0	575
<i>Calanus propinquus</i>	1621	29	140	1333
Ostracoda	506	688	368	1013
<i>Euchaeta antarctica</i>	285	360	380	187
<i>Thysanoessa</i> spp. Calyptopes	394	101	340	122
<i>Clausocalanus brevipes</i>	294	0	281	0
<i>Heterorhabdus</i> spp.	197	106	123	115
<i>Thysanoessa</i> spp.	252	11	189	41
<i>Scolecithricella</i> spp.	96	51	79	249
<i>Scolecithricella minor</i>	128	33	99	153
<i>Gaidius</i> spp.	33	23	49	123
<i>Spinocalanus</i> spp.	29	20	70	90

Carbon masses of stages CIV and CV *Calanoides acutus* and female *Rhincalanus gigas* were highest in zooplankton Group 1 and lowest in Groups 2 and 3 (Table 8). In contrast female *C. acutus* were absent from Group 1 stations and their C mass was some 4 to 5 times greater in Group 4 than in others. Egg production rates for *R. gigas* were also highest in Group 1 and lowest in Group 2, whereas the highest EPRs for *C. acutus* were recorded at Group 4 stations, particularly those lying towards the southern end of transect 7. The low C mass values observed for all stages of *C. acutus* within Stn Group 2 reflects the fact that at the majority of stations in this grouping the population was in an overwintered state and had not commenced recruitment. Of the remaining station groups the new generation dominated all stations in Groups 1, 8 of 9 in Stn Group 3 and at 14 of 19 in Stn Group 4.

For *Calanoides acutus* CIV, the most parsimonious fit was a single-variable model comprising % Chlorophyll (2 to 12 µm). Two-variable models that in addition included either log TFA or latitude were also considered plausible models (Table 9). For stage CV,

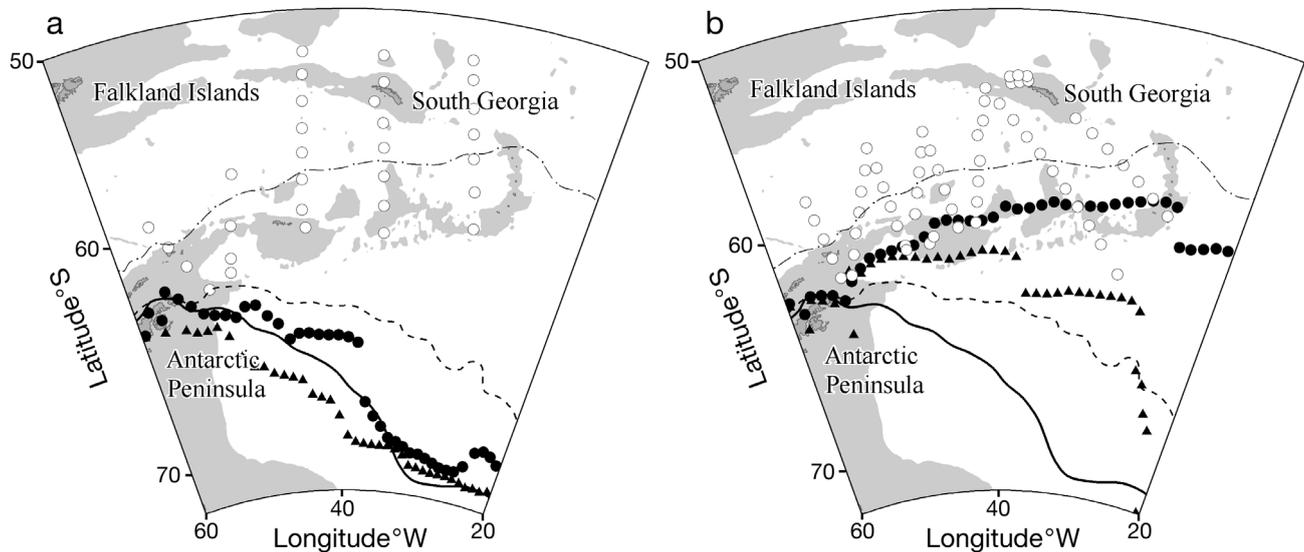


Fig. 7. Mean positions of 15% ice edge during January and February (a) 2000 and (b) 2003 in relation to 25 yr monthly mean position. The dashed line represents the 25 yr average position during January and the solid line February. Actual positions during January (●) and February (▲) are shown. (a,b) 25 yr average for August is shown as the most northerly broken line. Details on calculation of ice edge are given in 'Materials and methods'

Table 5. Median abundance (ind. m⁻², 0–400 m plus upper and lower quartile values) of mesozooplankton, large (adult of species > 1.5 mm) and small copepods (adult of species < 1.5 mm) with respect to mesozooplankton station group. Copepod abundance as a percentage of total zooplankton numbers is also shown

	Group 1 ^a (n = 10)	Group 2 (n = 21)	Group 3 (n = 10)	Group 4 (n = 19)	Group 5 (n = 1)
Mesozooplankton	5.1 × 10 ⁵ (3.5 × 10 ⁵ –8.4 × 10 ⁵)	6.3 × 10 ⁴ (4.1 × 10 ⁴ –7.9 × 10 ⁴)	1.06 × 10 ⁵ (7.3 × 10 ⁴ –1.66 × 10 ⁵)	1.5 × 10 ⁵ (1.01 × 10 ⁵ –2.4 × 10 ⁵)	3.7 × 10 ⁴
Large copepods	1.7 × 10 ⁴ (1.08 × 10 ⁴ –5.7 × 10 ⁴)	1.2 × 10 ³ (791–1,547)	4.3 × 10 ³ (1.9 × 10 ³ –7.6 × 10 ³)	2.9 × 10 ³ (22.3 × 10 ³ –6.7 × 10 ³)	0
Small copepods	3.9 × 10 ⁵ (2.8 × 10 ⁵ –6.9 × 10 ⁵)	5.7 × 10 ⁴ (3.7 × 10 ⁴ –7 × 10 ⁴)	9.1 × 10 ⁴ (6.5 × 10 ⁴ –1.33 × 10 ⁵)	1.4 × 10 ⁵ (7.78 × 10 ⁴ –1.8 × 10 ⁵)	3.6 × 10 ⁴
Copepods as % of total zooplankton	84	92	87	77	97

^aThe 6 stations north of South Georgia were only sampled to 200 m

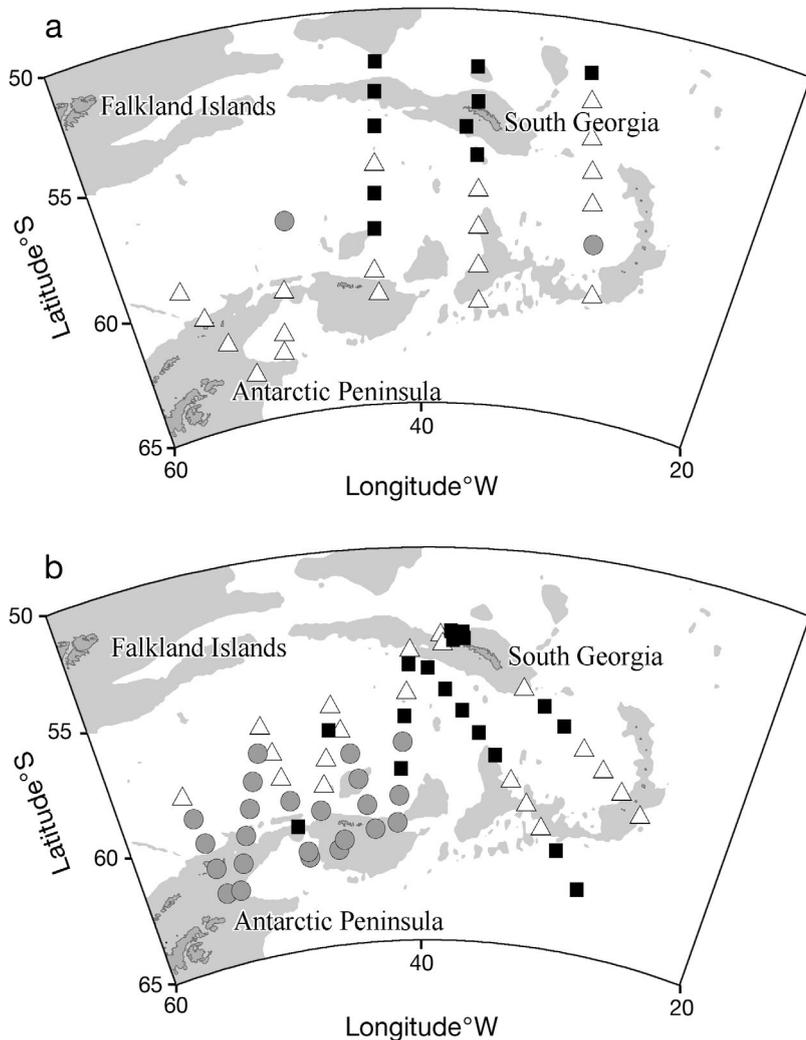


Fig. 8. *Calanoides acutus*. Relative ages of population at each station during (a) 2000 and (b) 2003. Δ = mean age CI–CIII, \blacksquare = mean age CIV, \bullet = mean age CV–VI

log surface chl *a* and latitude was considered most appropriate, whereas carbon mass of *Rhincalanus gigas* females was found to be strongly associated with log TFA and NO₃, which are indirectly measures of food quantity, quality and past production levels. The predictors for mesozooplankton abundance indicate positive relationships with % chl >12 μ m and log POC and negative relationships with PO₄ and latitude, the latter 2 reflecting the pool of unused PO₄ as one moves further south. EPR of *C. acutus* was also complexly related to measures of food abundance (% chl > 12 μ m and log TFA) as well as nutrients (NO₃ in this instance) and latitude. In contrast, EPRs of *R. gigas* were weakly related only to log POC.

LHPR hauls

The profiles, mostly taken to the east of the South Orkneys towards the end of January, included stations that a month earlier would have been covered in ice. All were taken in ice-free areas, although at varying distances from the ice edge, and all but one were sampled within a 13 d period (Table 10). Populations of both *Calanoides acutus* and *Rhincalanus gigas* lay deeper in the water column with increasing latitude, and younger copepodite stages were generally pre-

Table 6. Mean stage of 4 main biomass dominant species of calanoid copepod with respect to zooplankton station group. See 'Materials and methods' for details of calculation

Species	Group 1	Group 2	Group 3	Group 4
<i>Calanoides acutus</i>	4.13	5.34	3.68	3.73
<i>Rhincalanus gigas</i>	2.80	4.99	4.64	5.06
<i>Calanus simillimus</i>	3.08	2.68	2.55	2.26
<i>Calanus propinquus</i>	3.66	4.62	3.50	2.19

sent in increasingly significant numbers in the more northerly parts of the survey region, reflecting the Bongo net analyses. An exception to these trends was apparent at the next to most southerly station on transect 7, which had a population of *C. acutus* that, although low in abundance and largely comprised of later stages, was present in near surface waters, and also at stations to the north of South Georgia where CV *C. acutus* extended down to, and presumably in excess of, 1000 m, undergoing autumnal descent.

Sea-ice cover

Ice-edge positions during cruise JR82 (January and February) in relation to the mean monthly position determined over the period 1979 to 2004 are presented in Fig. 7 along with comparable data for the CCAMLR 2000 cruise undertaken in January/February 2000 (see 'Discussion').

During the 2 mo of maximum seasonal sea-ice extent (August and September) approx. half of the station positions lying within the main body of the Scotia Sea are generally ice-covered. By December the whole survey area are generally ice-covered. During periods of maximum extent, ice-affected stations belonged mainly to zooplankton Stn Groups 2 and 4 with remaining station groups either unaffected (Stn Group 1) or only marginally so (Stn Group 3). From September 2002 onwards the ice edge retreated at rates broadly in line with the monthly mean positions (1979 to 2004) until November, when the retreat slowed, and continued to do so throughout the remaining summer months into 2003. Thus by December the ice edge lay many kilometres north of its mean December position, with the gap widening throughout January and into February 2003, during which month the area eventually became ice-free. During CCAMLR 2000, the ice edge retreated slightly faster than the seasonal mean, and the same area was free of ice at least 1 mo earlier.

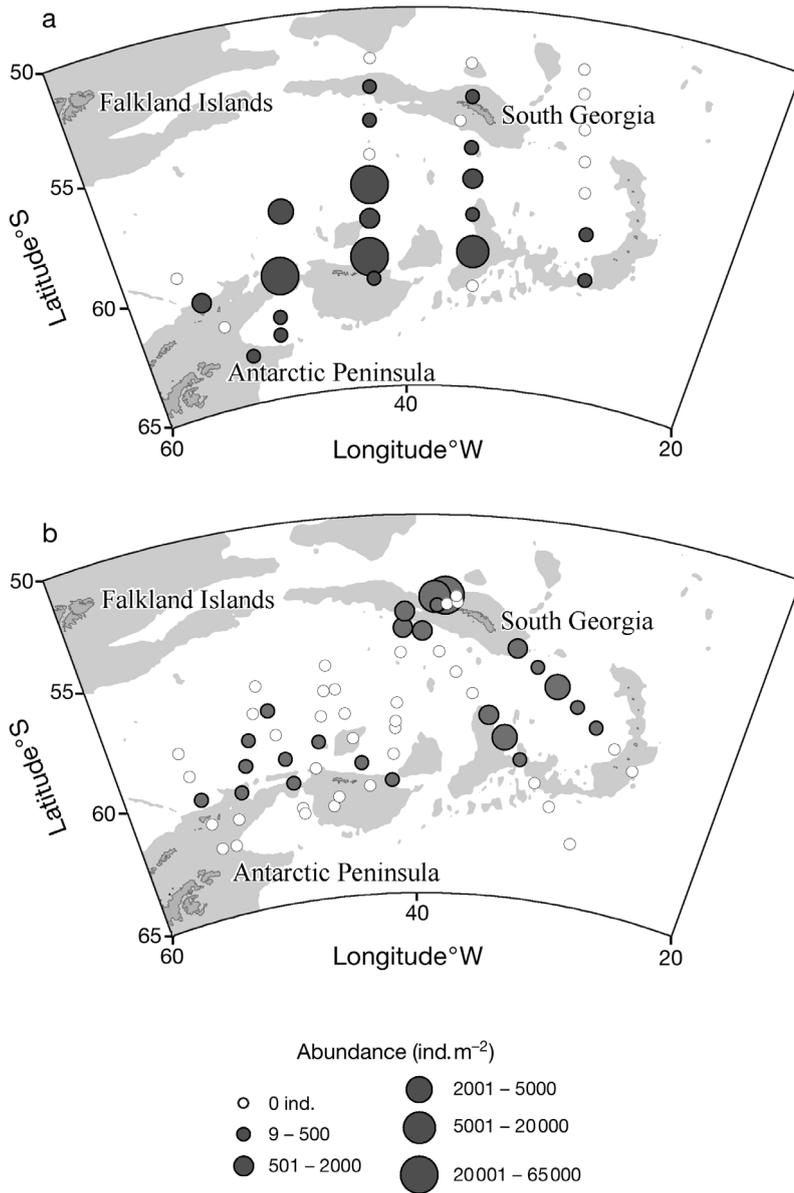


Fig. 9. Relative abundance and distribution of *Euphausia superba* larvae sampled during January and February (a) 2000 and (b) 2003. Abundance standardised to (a) ind. m⁻² (0–200 m) and (b) ind. m⁻² (0–400 m), except stations to north of South Georgia where data represent ind. m⁻² (0–200 m)

DISCUSSION

Zooplankton community structure

In line with previous studies in this and other sectors of the Southern Ocean, the various zooplankton groups identified here should be viewed as representing a single zooplankton community, albeit one with distinct regional differences in its phenological development (Marin 1987, Siegel et al. 1992, Pakhomov et al. 2000, Ward et al. 2004). Most species were present across the entire survey area, and changes in abundance were greater than those in species composition. Latitude emerged as the strongest single correlate with community pattern in the BIO-ENV analysis applied to the mesozooplankton data (Table 7). This is consistent with the latitudinal gradient in production cycles that exists within the Southern Ocean, with community development tending to commence earlier in the northern part of the ACC during spring and summer (Hart 1942, Voronina 1970). Previous surveys carried out in the Southern Ocean highlighted the importance of pack ice and temperature in influencing the distribution and composition of zooplankton communities (Mackintosh 1934, Marin 1987, Hosie et al. 2000, Ward et al. 2004). Hosie et al. (2000) found that temperature accounted for ~50% of the variability in community patterns during a survey carried out in East Antarctica, whereas chl *a* accounted for ~21% and was also slightly negatively correlated with total zooplankton abundance. They concluded that chl *a* per se was therefore relatively unimportant in the large-scale separation of zooplankton communities. The temperature association was however strongly related to latitude and did not explain east-west differences also apparent during their survey. Surface chl *a* was also a weaker correlate of overall community pattern in this study ($\rho = 0.344$). However, various food-related indices such as phytoplankton size, TFA and POC amounts and water column nutrient properties (a proxy for past production levels) figured prominently in explaining carbon mass and total abundance in the stepwise regression analysis (Table 9). Thus we have an apparent paradox in that, whilst C mass of some species and overall zooplankton abundance relate positively and strongly to measures of food biomass and quality, community pattern relates more strongly to latitude. Whilst most species are present across

the entire survey area, regional differences, exemplified by the station groups, are not wholly attributable to differences in the timing of production across a uniform community. Many species, for example, have inherently differing distributions across the ACC, which reflect species ranges, different relationships with temperature (e.g. Mackintosh 1934) and different behaviours, all of which will tend to promote regional differences in community structure (Hosie et al. 2000). On the other hand species stages attributes such as C mass will tend to reflect the influence of proximate factors, e.g. available food, irrespective of patterns of distribution.

Table 7. Results of BIO-ENV analysis. Combinations of *K* variables giving largest Spearman rank correlations (ρ_w) between mesozooplankton and environmental similarity matrices. First 3 models listed, best overall fit in bold. Environmental variables included were latitude, sea-surface temperature, chl *a* biomass (mg m^{-2} , 0–100 m), nitrate (NO_3 average 0–50 m, mmol m^{-3}), phosphate (PO_4 average 0–50 m, mmol m^{-3})

<i>K</i>	ρ_w	Environmental variables
1	0.608	Lat
2	0.642	Lat + PO₄
3	0.599	Lat + PO ₄ + Chl <i>a</i>

Table 8. Median C mass (μg) of *Calanoides acutus* copepodite stages CIV, CV and females, *Rhincalanus gigas* females and median *C. acutus* and *R. gigas* egg production rates (EPR) with respect to mesozooplankton station groups (lower and upper quartile ranges). *n* = no. of stations within station groups for which data are available out of possible total (second row)

	Group 1 (<i>n</i> = 10)	Group 2 (<i>n</i> = 21)	Group 3 (<i>n</i> = 10)	Group 4 (<i>n</i> = 19)
<i>C. acutus</i> CIV	46 (37–64) (<i>n</i> = 9)	21 (20–21) (<i>n</i> = 3)	24 (20–30) (<i>n</i> = 8)	3 (26–36) (<i>n</i> = 9)
<i>C. acutus</i> CV	238 (174–360) (<i>n</i> = 8)	59 (29–80) (<i>n</i> = 14)	48 (44–53) (<i>n</i> = 8)	129 (41–187) (<i>n</i> = 15)
<i>C. acutus</i> females	– (<i>n</i> = 0)	75 (44–174) (<i>n</i> = 16)	65 (62–78) (<i>n</i> = 7)	311 (110–421) (<i>n</i> = 12)
<i>R. gigas</i> females	1601 (1086–2085) (<i>n</i> = 7)	455 (–) (<i>n</i> = 1)	279 (233–337) (<i>n</i> = 9)	570 (349–804) (<i>n</i> = 14)
EPR <i>C. acutus</i> (eggs female ⁻¹ d ⁻¹)	–	0 (0–0) (<i>n</i> = 17)	3.3 (0–10) (<i>n</i> = 7)	12 (7–35) (<i>n</i> = 13)
<i>R. gigas</i> (eggs female ⁻¹ d ⁻¹)	7.60 3.7 (2.3–14) (<i>n</i> = 10)	0 (0) (<i>n</i> = 2)	1.4 (0–4) (<i>n</i> = 8)	(0–7) (<i>n</i> = 16)

Table 9. Selected models from best subsets regression analysis. Response variables tested against various predictor variables. Predictor variables included were latitude (Lat), sea-surface temperature (°C), % Chlor >12 µm, (20 m) % Chlor 2–12 µm (20 m), surface chl *a* (Chl *a*, mg m⁻³), POC (µg l⁻¹, 20 m), nitrate (NO₃ average 0–50 m, mmol m⁻³), phosphate (PO₄ average 0–50 m, mmol m⁻³), total fatty acids (TFA, µg l⁻¹). Models shown selected by calculation of Akaike Information Criterion (see 'Materials and methods' for explanation). Regression equations include (SE coefficient)

Regression equations	R ² (%)	p
Log C mass CIV <i>C. acutus</i> = 1.72 (0.009) – 0.009 (0.001) % Chl 2–12 µm	47.9	<0.001
Log C mass CV <i>C. acutus</i> = –1.99 (1.08) + 0.636 (0.081) Log Chl <i>a</i> + 0.072 (0.019) Lat	68.8	<0.001
Log C mass female <i>R. gigas</i> = 2.62 (0.40) + 0.452 (0.129) Log TFA – 0.028 (0.008) NO ₃	76.3	<0.001
√√Mesozooplankton Abundance = 40.3 (7.3) + 0.018 (0.009) % Chl >12 µm + 3.22 (1.11) Log POC – 1.77 (0.69) PO ₄ – 0.052 (0.101) Lat 79.7, <0.001 <i>C. acutus</i> EPR = –197 (59.0) + 0.311 (0.059) % Chl >12 µm + 13.5 (5.7) Log TFA + 1.88 (0.64) NO ₃ + 2.03 (0.836) Lat	55.6	<0.001
<i>R. gigas</i> EPR = –25.9 (12.6) + 13.3 (5.4) Log POC	17.1	0.018
Test of autocorrelation in residuals from fitted model based on trend in variogram (see text): Log C mass <i>C. acutus</i> CIV (R ² = 1.9%, p = 0.51); Log C mass <i>C. acutus</i> CV (R ² = 4.4%, p = 0.14); Log C mass female <i>R. gigas</i> (R ² = 6.0%, p = 0.07); √√Mesozooplankton Abund. (R ² = 0.7%, p = 0.34) <i>C. acutus</i> EPR (R ² = 0.1%, p = 0.83); <i>R. gigas</i> EPR (R ² = 1.9%, p = 0.28)		

Table 10. Median population depth (m), population abundance (ind. m⁻², 0–1000 m) and mean stage (see text) for *Calanoides acutus* and *Rhincalanus gigas* sampled by LHPR with respect to station. For details of mean stage calculation see 'Materials and methods'. Stations arranged in order of decreasing latitude (Fig. 1)

Stn	Sampling day (from 1 Jan)	<i>Calanoides acutus</i>			<i>Rhincalanus gigas</i>		
		Pop. depth	Abund.	Stage	Pop. depth	Abund.	Stage
7.10	35	85	1484	5.05	435	113	5.80
5.5	23	328	766	5.42	317	176	5.37
6.2	27	348	1068	5.39	320	71	5.51
6.4	28	60	709	3.77	273	468	5.10
7.5	32	271	1641	4.55	320	537	5.42
6.6	29	96	1143	3.85	102	637	4.92
6.7	30	5	7151	4.76	5	3026	4.58
W2.2N	49	177	3662	4.65	38	2294	3.21

Phytoplankton and zooplankton station ordinations were similar insofar as patterns of abundance and groupings of stations were, in the main, geographically consistent with one another (Figs. 4 & 6). In both ordinations the extremes were represented by the northerly South Georgia group of stations where diatoms dominated, in particular *Eucampia* sp., and zooplankton abundance and 'condition' were high, and low cell counts and low zooplankton abundance and 'condition' were found within the station groupings in the southern and western parts of the Scotia Sea (Tables 1, 5 & 8). Independent observations made around South Georgia further highlighted the positive relationships between copepod population recruitment processes (as assayed by abundance, C mass of species stages

and egg production indices) and the proportion of large diatoms present in water samples taken at these stations (Shreeve et al. 2002, Ward et al. 2005) and in the diet of many of the species present (Atkinson 1994). These findings strongly suggest the importance of bottom-up factors on Southern Ocean mesozooplankton communities, and food limitation has been identified as a major control, particularly in iron-limited regions (Smetacek et al. 2004).

Population development

Given the extent to which the zooplankton station groupings identified in this study represent a single 'community' at different stages in its phenological development, it is possible to provide an estimate of the extent to which some of its elements are chronologically separated. Differences in species and community development have been reported across the 600 nautical mile (1000 km) extent of the Scotia Sea during summer, as production cycles tend to proceed earlier in the ice-free northern parts. For example, Ward et al. (2004) reported differences in stage composition equivalent to a 3 mo advance in population development of *Calanoides acutus* from the northern part of the Scotia Sea compared to that south of the Weddell Front. Marin (1987) also found pronounced latitudinal age differences for *C. acutus* and *Calanus propinquus* during the Melville study of 1981.

Data from the LHPR profiles carried out on JR82 clearly exemplified such differences in terms of depth distribution, stage composition and abundance. In the southern part of the survey area within zooplankton Group 2, median population depths for *C. acutus* were ~330 to 350 m (Table 10). The low abundance, high proportion of females and deep median population depth at this time of year are indicative of an ongoing 'spring ascent' rather than a seasonal descent as might be expected in the more northern parts of the Scotia Sea (Atkinson et al. 1997).

Given that the stations were sampled at the end of January, it is remarkably late in the year for a population to be at the pre-recruitment stage in its development. It is presently unclear as to what cues cause plankton populations to ascend from overwintering depths back to surface waters or whether sea-ice cover is implicated in this process. Sea-ice cover can reduce primary production due to decreased light penetration, and therefore the ability of zooplankton populations to reproduce and develop at optimal rates in the surface layers; alternatively, a retreating ice edge may provide stabilisation of the water column and allow bloom conditions to develop. In an earlier study in the Bellingshausen Sea, Atkinson & Shreeve (1995) described the spring differences in population processes and depth distribution, stage development and chlorophyll in the water column in relation to ice cover. The *Calanoides acutus* population lay considerably deeper in the water column under pack ice compared to the ice edge and open water. Likewise the population was overwintered under the ice and reproduction was only apparent at the ice edge and in open water where chl *a* levels were higher. A similar situation was reported by Burghart et al. (1999) in a study of the marginal ice zone in the Weddell Sea during spring.

At the northern end of transect 6 both *Calanoides acutus* and *Rhincalanus gigas* were present in near surface waters and undergoing recruitment, whereas to the north of South Georgia, in early February, *C. acutus* was undergoing its seasonal descent. Thus based on development times determined by Shreeve (2002), population development of *C. acutus* at its spatial extremes within the Scotia Sea varied temporally by at least 3 mo and possibly more (Fig. 8).

Comparison of JR82 and CCAMLR 2000

Both cruises took place during January and February during 2 summers that differed greatly in terms of the rate of ice retreat and the distribution of phytoplankton biomass. During CCAMLR 2000, a 4-ship survey, 123 plankton samples were collected with RMT1 nets (0 to 250 m) across an area extending from

~20 to 70°W. Subsequent analysis indicated the existence of 2 main groups of stations which essentially formed a northern 'warm' and a southern 'cold' water community (Ward et al. 2004). Because of taxonomic similarities it was concluded that the two communities represented a single community differing only in phenological development and the mass occurrence of patchily distributed organisms such as krill larvae. The area surveyed during the present cruise was not as extensive, nor the sample size as large, but the same basic trends were detected in the data. A set of Bongo net samples (0 to 200 m) collected during CCAMLR 2000 ($n = 31$) also reflected this pattern and additionally served to confirm the delayed development of *Calanoides acutus* and to a lesser extent *Rhincalanus gigas* populations during JR82. During CCAMLR 2000 the new generation of *C. acutus* was present throughout the Scotia Sea, but during JR82 an overwintered generation dominated by pre-recruitment females and CVs was extensively found throughout the central and southern regions (Fig. 8).

Also of note was the differing distribution of krill larvae during the 2 cruises (Fig. 9). During CCAMLR 2000 early calyptopes were locally abundant throughout the southern central part of the Scotia Sea but were concentrated along both sides of the Weddell Front (Siegel et al. 2004). In this area spawning generally commences in late November or early December and has a variable but normally long duration of 3 to 3.5 mo (Spirodonov 1995). This variability in timing has also been documented by Brinton et al. (1986), and conditions for successful spawning in the Long-Term Ecosystem Research region of the Antarctic Peninsula have been positively linked to average sea-ice extent (Quetin & Ross 2003). In contrast, in the Antarctic Marine Living Resources region, 450 km further north, where krill have recently been hypothesised to be at the edge of their reproductive range (Quetin & Ross 2003), extensive sea ice (> average extent during summer) appears to enhance successful spawning (Siegel & Loeb 1995). Although complex, both hypotheses make explicit links to available food and the balance of under-ice and open-ocean food concentrations. As a general rule, bloom conditions within the Scotia Sea are often transient, chlorophyll rarely exceeds 1.5 mg m⁻³ (Trégeur & Jacques 1992), and as a consequence zooplankton populations may suffer severe food limitation (see also Huntley & Brinton 1991).

During JR82, krill larvae were abnormally distributed, being found in oceanic waters to the northwest of South Georgia, although T/S profiles indicated that the water here may have originated to the south of the SACCF. Chl *a* levels in the western part of the Scotia Sea were low during JR82, and the presence of unmated female krill with developing ovaries in the

normal spawning areas alongside sub-adult males (Shreeve pers. comm.) suggests that any shortfalls in food for the energetically expensive process of sexual maturation were felt more by males. In contrast, during CCAMLR 2000 when krill larvae were abundant, relatively high chl *a* levels were widespread and associated with water column profiles where temperature and density indicated mixing of ACC waters with waters originating either from coastal regions or by upwelling of deeper waters associated with bathymetric features (Holm-Hansen et al. 2004, their Fig. 2).

The presence of abundant krill larvae and the new generation of *Calanoides acutus* across the southern part of the Scotia Sea during January 1981 has also been reported by Brinton (1985) and Marin (1987) respectively. During 1981 monthly ice-edge positions were close to the long-term average as the ice retreated across the Scotia Sea from an extreme northerly position in September 1980 to a minimum in February 1981. The rates of ice retreat during JR82 and CCAMLR 2000 were largely indistinguishable from the mean value until, in the case of JR82, December, when the retreat of the ice edge slowed. During January it moved very little, particularly in the eastern part of the survey region (Fig. 7). The slow retreat continued throughout February when the survey area finally became ice-free a month later than during CCAMLR 2000.

It was noticeable that during JR82, in addition to the bloom conditions seen to the north of South Georgia, SeaWiFS images also showed blooms to be patchily present along transects 7 and 8 (see Korb et al. 2005, their Fig. 5). Blooms may at times be associated with the retreating ice edge, particularly where the freshening effect imparts stratification and stability (Nelson et al. 1987, Lancelot et al. 1993). Density sections taken along both of these transects showed a far greater degree of upper water column stratification and hence stability than elsewhere (Korb et al. 2005). Low chlorophyll levels pervaded much of the rest of the Scotia Sea, particularly in the regions of zooplankton Groups 2 and 3. Taken together these observations suggest that the presence of sea ice can strongly influence secondary producers and the timing of production cycles in contrasting ways. The 2 years (1981 and 2000) in which ice retreat occurred broadly in line with the 25 yr mean were characterised by an abundance of krill larvae and the presence of a spring generation of copepods throughout the southern Scotia Sea. The later retreat experienced during 2003 was characterised by overwintered populations of copepods being present well into the summer months and a dearth of krill larvae in areas where spawning generally takes place. However, to the east the presence of a bloom that appeared to be initiated along the retreating ice

edge was coincident with higher EPRs of *Calanoides acutus* and a shallower median population depth than at comparable latitudes further west.

CONCLUSIONS

The relationships disclosed in this and other studies between attributes of chl *a* (size, amount, quality, etc.) and zooplankton abundance and C mass supports the idea that for much of the time Southern Ocean zooplankton are food limited and are sensitive to changes in production (Ross et al. 2000, Shreeve et al. 2002, Quetin & Ross 2003, Ward et al. 2005, this study). Marine communities in the North Atlantic appear to be regulated by climatic phenomena that exert their influence either through temperature-mediated responses or through changes in wind fields and oceanic circulation (Fromentin & Planque 1996, Planque & Taylor 1998). The coupling of atmospheric and oceanic processes in the Southern Ocean is not yet well enough understood to enable predictions as to how future climate change may influence production patterns. The likelihood is that change will be complex as reflected in recent work by Edwards & Richardson (2004), who have shown that in the temperate North Atlantic the marine pelagic community is responding to climate change, although the level of response differs within communities and between different trophic groups, which is leading to mismatches between successive trophic levels. Quantifying the impacts sea-ice dynamics have on production cycles will be an important part of understanding community structure and function in the Southern Ocean.

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Paper 3

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Mesozooplankton community structure and variability in the Scotia Sea: A seasonal comparison

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ABSTRACT

Mesozooplankton distribution and community structure was investigated during 3 cruises to the Scotia Sea in austral spring, summer and autumn. Three mesh sizes of Bongo nets were used during each cruise with a 53 μm mesh net yielding on average 1.76 times higher densities (median 923,000 ind. m^{-2} , 0–400 m) than a 100 μm net and 7.42 times more than a 200 μm net across all cruises. Small copepods dominated numerically across all nets with *Oithona* spp., *Oncaea* spp., *Ctenocalanus citer* and *Microcalanus pygmaeus* being particularly abundant, with sample densities of up to 3.5×10^6 ind. m^{-2} recorded within the top 400 m. A more even distribution of biomass among net sizes was apparent, with median net ratios (1.15–1.25) smaller and more even than for abundance. To the south of the Scotia Sea plankton maxima occurred in autumn, consistent with a later spawning in many species, whereas further north, abundance in 53 and 100 μm nets varied little across seasons, although in the 200 μm net there was a clear summer maximum. Median biomass increased through summer and by autumn was twice than found during spring in all parts of the Scotia Sea. Cluster analysis indicated two main station groups in all 3 seasons. To the south of the Southern boundary of the ACC (SB-ACC), Group 1 contained stations, that lay within the seasonal sea-ice zone and where zooplankton abundance and biomass was persistently low. In contrast at Group 2 stations, north of the Southern Antarctic Circumpolar Current Front (SACCF) abundance and biomass was consistently higher. Differences between the two groups were largely apparent at the population rather than at the taxonomic level. LHPR hauls to 1000 m indicated that the large seasonal migrant copepods *Calanoides acutus* and *Rhincalanus gigas* were at a more advanced stage of development in the north in spring and summer where they were generally present in the upper water column. In autumn, at all stations, *C. acutus* was dominated by later stages and was dispersed throughout the water column. *Calanus simillimus* was only abundant at Group 2 stations with older stages dominant in spring and autumn and younger stages in summer. The influence of environmental factors such as sea-ice, temperature and chlorophyll *a* biomass (Chl *a*) which may have influenced the development and seasonal succession of zooplankton populations, is briefly discussed.

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1. Introduction

The Scotia Sea lies in the Atlantic sector of the Southern Ocean downstream of Drake Passage, extending some 2000 km towards its eastern boundary, the Scotia Arc, and ~ 750 km from North to South. It is bounded on three sides by the Scotia Ridge, is mostly > 2000 m deep and to the south is bordered by the sub-Polar gyre of the Weddell Sea. Its waters comprise the predominantly eastwards flowing Antarctic Circumpolar Current (ACC) within which is embedded two full depth frontal jets, the SACCF and the SB-ACC (Brandon et al., 2004; Orsi et al., 1995) (Fig. 1). The region is physically dynamic, is influenced by eddy shedding, particularly from the Antarctic Polar Front (APF) (Fach et al., 2002; Foster and

Middleton, 1984; Hofmann and Whitworth, 1985) and by seasonal sea ice, which covers the southern part during the winter months.

The Scotia Sea has been studied more intensively than many other regions of the Southern Ocean and was the focus of much of the “Discovery Investigations” work during the 1920s–1930s. Other programmes such as the multinational BIOMASS Investigations (Biological Investigations of Marine Antarctic Systems and Stocks) also operated in this region (El-Sayed, 1994) and during 2000 it was the locus of the CCAMLR multi-ship oceanographic survey which provided a synoptic view of the oceanography, zooplankton, krill and higher predator biomass and distribution (Brandon et al., 2004; Reilly et al., 2004; Siegel et al., 2004; Ward et al., 2004).

These surveys have suggested that despite spatial and temporal heterogeneity there is essentially a single ‘zooplankton community’ present throughout the region (Marin, 1987; Ward et al., 2004, 2006). Seasonal changes in the proportion of ‘warm-’ and ‘cold-water’ species have been observed (Mackintosh, 1936), and the strong

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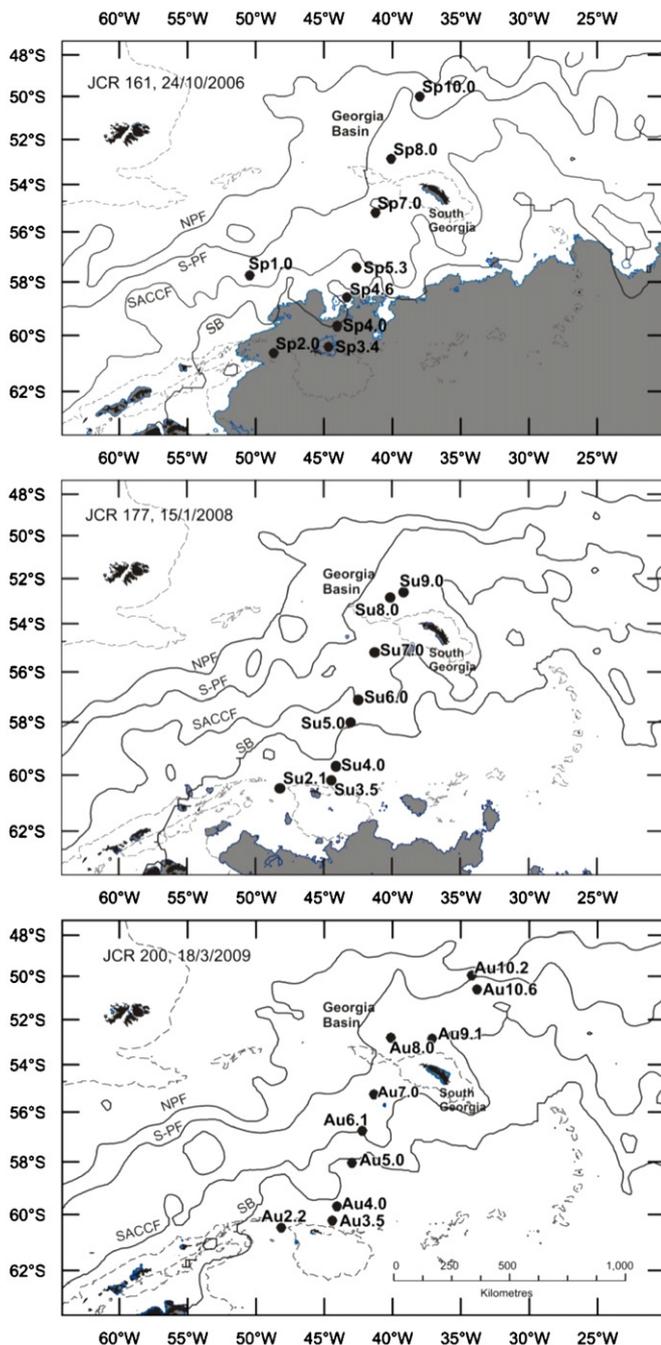


Fig. 1. The Scotia Sea and stations sampled during spring (cruise JR161), summer (cruise JR177) and autumn (cruise JR200). Mean frontal positions determined during the course of the cruise from dynamic height data (Venables et al., 2012). N-PF (northern Polar Front), S-PF (southern Polar Front), SACC (Southern Antarctic Circumpolar Current Front), SB-ACC (Southern Boundary of the ACC). Half-tone shading shows the position of the 15% ice-edge cover indicated for 24/10/2006 at the start of the spring cruise and for 15/1/2008, two weeks into the summer cruise. The ice edge in autumn lay well south of the transect.

influences of water temperature and the presence of pack-ice on community development have been emphasised (Mackey et al., 2012; Mackintosh, 1936; Marin, 1987; Ward et al., 2004, 2006). Spring development of plankton populations is not uniform across the Scotia Sea and at a given time populations in the north are generally in a more advanced state of development than further south (Atkinson, 1991; Marin, 1987; Voronina, 1970; Ward et al., 2006).

Murphy et al. (2007) have recently reviewed the spatial and temporal operation of the Scotia Sea ecosystem, although largely

from a krill centred perspective. Whilst the ecological significance of krill as food for predators and as potential mediators of carbon flux is beyond any doubts (see Atkinson et al., 2012), the role of mesozooplankton, which are estimated to constitute at least 50% of the total plankton standing stock and which are dominated by copepods, is less clear. Estimated annual production of Southern Ocean copepods has been variously estimated as 3–12 times that of postlarval krill (Conover and Huntley, 1991; Shreeve et al., 2005; Voronina, 1998). This may indeed be an underestimate as the $\geq 200 \mu\text{m}$ mesh nets normally used in most plankton surveys have seriously undersampled the small species and stages (Gallienne and Robins, 2001). The role of smaller copepods as producers, grazers and recyclers is being re-assessed as more is discovered about their contribution to this community (Atkinson, 1996; Dubischar et al., 2002; Metz, 1995; Pollard et al., 2002; Schnack et al., 1985; Swadling et al., 1997; Thompson et al., 2011). With the smaller copepod fractions generally assumed to have production rates at least equal to or higher than the larger fractions (Bamstedt et al., 2000; Hirst and Bunker, 2003), it has become clear that we need better and more realistic abundance and biomass estimates before we can assess their importance to grazing, recycling and vertical flux.

A majority of large-scale surveys in the Scotia Sea have taken place in summer, so we therefore wished to obtain a seasonal perspective on the spatial distribution, development and composition of plankton populations in the Scotia Sea in relation to environmental conditions and to assess the relative abundance and biomass of different size fractions.

2. Methods

The samples used in this study were collected during 3 cruises to the Scotia Sea during spring (Cruise JR161, October–December 2006), summer (Cruise JR177, January–February 2008) and autumn (Cruise JR200, March–April 2009). The main sampling effort was focussed on a series of stations spaced along a transect ~ 1000 km long, running north-eastwards from close to the South Orkneys to the north of South Georgia. Additional sampling at the Polar Front also took place at various locations during spring and autumn cruises (Fig. 1).

During each of the 3 cruises mesozooplankton samples were obtained from each station using a paired motion-compensating Bongo net (61 cm mouth dia., 2.8 m long) equipped with solid cod-ends and 100 and 200 μm mesh nets. A smaller (18 cm mouth dia., 2.3 m long), paired Bongo net equipped with 53 μm mesh nets was also used at each station. Nets were deployed to 400 m and hauled vertically to the surface at $\sim 0.22 \text{ m s}^{-1}$ during hours of daylight. Flow-meters were not used to record volume swept by the nets as the slow hauling speeds are at the bottom end of the calibration range for most flow-meters. Based on a calculation of mouth area multiplied by vertical sampling interval (400 m), we estimated that the 53 μm mesh net sampled just over 10 m^{-3} and the 100 and 200 μm nets $\sim 120 \text{ m}^{-3}$, assuming 100% catch efficiency as no obvious clogging was observed during sampling. This assumption is examined below in the results section. Samples were preserved in 4% formalin (w:v) in seawater and subsequently aliquots were analysed under a binocular microscope (see Ward et al., 2005). Abundances were standardised to ind. m^{-2} (0–400 m). Published body size to weight algorithms were used to convert from abundance to biomass. Estimates of body size were either extracted from the literature or measured directly (Appendix A). Krill were occasionally caught by the Bongo nets, which had a marked effect on biomass estimates. They were therefore not considered in subsequent calculations so that biomass more accurately reflected mesozooplankton.

Longhurst Hardy Plankton Recorder (LHPR) profiles were obtained at 4 stations during spring (Stations Sp 1, 2, 7 and 8), at every major zooplankton station ($n=8$) during summer and at each station, except station Au 10.2, during autumn ($n=9$). A 200 μm mesh net was used with a nose cone opening of 38 cm dia. during all cruises. Gauze advance was set to 90 s during spring and 120 s during summer and autumn. The equipment was deployed to 1000 m, allowed to stabilise at depth and then the gauze advance mechanism activated as the net was hauled to the surface at a ship's speed of 2–2.5 kts. In this way ~ 40 – 50 samples were obtained from each haul with a depth resolution of ~ 20 – 25 m per sample, each representing ~ 25 – 30 m^{-3} of water filtered. Due to the large number of samples, patches were analysed for four species only, the seasonal migrants, *Calanoides acutus*, *Rhincalanus gigas*, *Calanus simillimus* and *C. propinquus*. These species are both widely distributed and abundant within the Southern Ocean with a depth distribution that changes throughout the year, giving a clear seasonal signal that can be used in part to reference conditions throughout the Scotia Sea. Counts were standardised to ind. m^{-2} (0–1000 m).

Mesozooplankton data were initially analysed using the PRIMER 6 statistical package (Primer-E-Ltd.) (Clarke and Gorley, 2006). Bongo net data were used to determine community structure by inputting standardised counts into a species by station matrix and applying a double root transformation. A matrix was created and subjected to q type cluster analysis based on the Bray–Curtis similarity and group average linkage classification (Field et al., 1982). The similarity profiles routine (SIMPROF) was used to look for statistically significant evidence of genuine clusters in samples. Mesozooplankton abundance and biomass data were also analysed in Minitab V14.

3. Results

3.1. Environment

The oceanographic conditions encountered during the three cruises have been described in detail by Venables et al. (2012) and Whitehouse et al. (2012). Briefly, during spring the southernmost 3 stations sampled for zooplankton (Sp 2, 3.4 and 4) lay south of the SB-ACC within waters where surface temperatures were < -1.5 $^{\circ}\text{C}$ and influenced by ice-melt, although there was no freshwater layer apparent. At the time of sampling, these stations lay within the receding ice-edge, which extended to $\sim 58.6^{\circ}\text{S}$ in September/October and was still at $\sim 60^{\circ}\text{S}$ in December although retreated rapidly from January onwards. Further north, station Sp 5.3 lay between the SB-ACC and the SACCF. Station Sp 7, to the southwest and upstream of South Georgia, was close to the APF, Sp 8 to the northwest, south of the APF and Sp 10 on the edge of the APF where surface temperatures were ~ 5 $^{\circ}\text{C}$. Phytoplankton

blooms (up to 8 mg m^{-3} Chl *a*) were apparent between the SACCF and the SB-ACC, elsewhere levels were ~ 0.5 mg m^{-3} on the South Georgia shelf and within the Georgia Basin and < 0.2 mg m^{-3} elsewhere (Whitehouse et al., 2012).

During summer (January) the southernmost stations (Su 2.1, 3.5, 4 and 5) again lay south of the SB-ACC. Temperatures in the mixed layer at these stations ranged from -0.9 to 1.8 $^{\circ}\text{C}$. The SACCF lay between Su 5 and 6 and further north temperatures ranged up to ~ 4 $^{\circ}\text{C}$ at Su 9. During the preceding September, winter sea-ice extended along the transect as far north as 57°S and was slow to clear the region, still being present at $\sim 60.5^{\circ}\text{S}$ during the period when the southernmost stations were being sampled. Chl *a* levels of > 5 mg m^{-3} were observed in the Georgia Basin, 1 – 2 mg m^{-3} north of the SACCF and considerably lower further south.

In autumn all stations were clear of ice, which had extended as far north as $\sim 59^{\circ}\text{S}$ during the preceding September and had retreated rapidly at the end of that month. During the cruise the SB-ACC lay between Au3 and Au5. The SACCF was located between stations Au5 and Au6 and the APF at Au 10.2. Surface temperatures ranged from ~ 1 $^{\circ}\text{C}$ at the southernmost stations up to almost 8 $^{\circ}\text{C}$ at the APF. Peak Chl *a* levels were found north of South Georgia over the Northwest Georgia Rise (8 mg m^{-3}), and elsewhere were between < 0.5 and 1.5 mg m^{-3} (Whitehouse et al. 2012).

3.2. Mesozooplankton abundance and biomass

To test our assumption regarding net catch efficiencies we compared the standardised abundance (no. m^{-2} 0–400 m) of two large calanoids, *R. gigas* (pooling stages CVI female–CIV) and *C. acutus* (pooling stages CVI female and CV). These were present at most stations during all 3 cruises and we considered them to be unequivocally retained by all 3 nets. We compared the median abundances of the pooled species stages by net and with respect to the two major station groups determined by cluster analysis within each cruise (see below). Barring one exception (*R. gigas* JR200), no significant differences in median abundance (ind. m^{-2} 0–400 m) were found between nets within station groups during all three cruises (Table 1). We therefore believe that our catch data are comparable within and between cruises.

Plankton abundance was highly variable within and between cruises, although basic patterns in relation to latitude were consistent across cruises. An assessment of seasonal pattern in the data was made by comparing median abundance values within two groups of stations identified by PRIMER (basically south of the SB-ACC (Group 1) and north of the SACCF (Group 2)—see below). At Group 2 stations, abundances found within all nets across all 3 cruises were between ~ 2 and 9 times higher than in Group 1 (Fig. 2). Highest abundances within Group 1 were found in autumn across all nets, whereas within Group 2, broadly similar values across all cruises for the 53 μm nets contrasted with the 100 μm nets which had high and similar values

Table 1
Results of Kruskal–Wallis median tests performed on combined abundances (ind. m^{-2} , 0–400 m) of *Calanoides acutus* copepodid stages CV and CVI female and *Rhincalanus gigas* CIV–CVI female within the 53, 100 and 200 μm nets with respect to station group and season. $\text{df}=2$ in all cases. Significant values of *p* emboldened.

	<i>R. gigas</i>				<i>C. acutus</i>			
	53 μm	100 μm	200 μm		53 μm	100 μm	200 μm	
Spring Gp1	10	13	39	$H=0.05$, $p=0.973$	537	583	511	$H=0.19$, $p=0.908$
Gp2	1431	1981	1572	$H=0.470$, $p=0.791$	583	835	511	$H=1.09$, $p=0.580$
Summer GP1	82	92	79	$H=0.52$, $p=0.773$	332	376	432	$H=0.24$, $p=0.889$
Gp2	931	972	629	$H=0.40$, $p=0.818$	1314	1505	1218	$H=0.42$, $p=0.811$
Autumn Gp1	48	123	0	$H=0.06$, $p=0.027^a$	246	274	295	$H=0.06$, $p=0.969$
Gp2	1369	1150	1493	$H=2.62$, $p=0.27$	274	739	413	$H=0.02$, $p=0.989$

^a Only two 53 μm nets available.

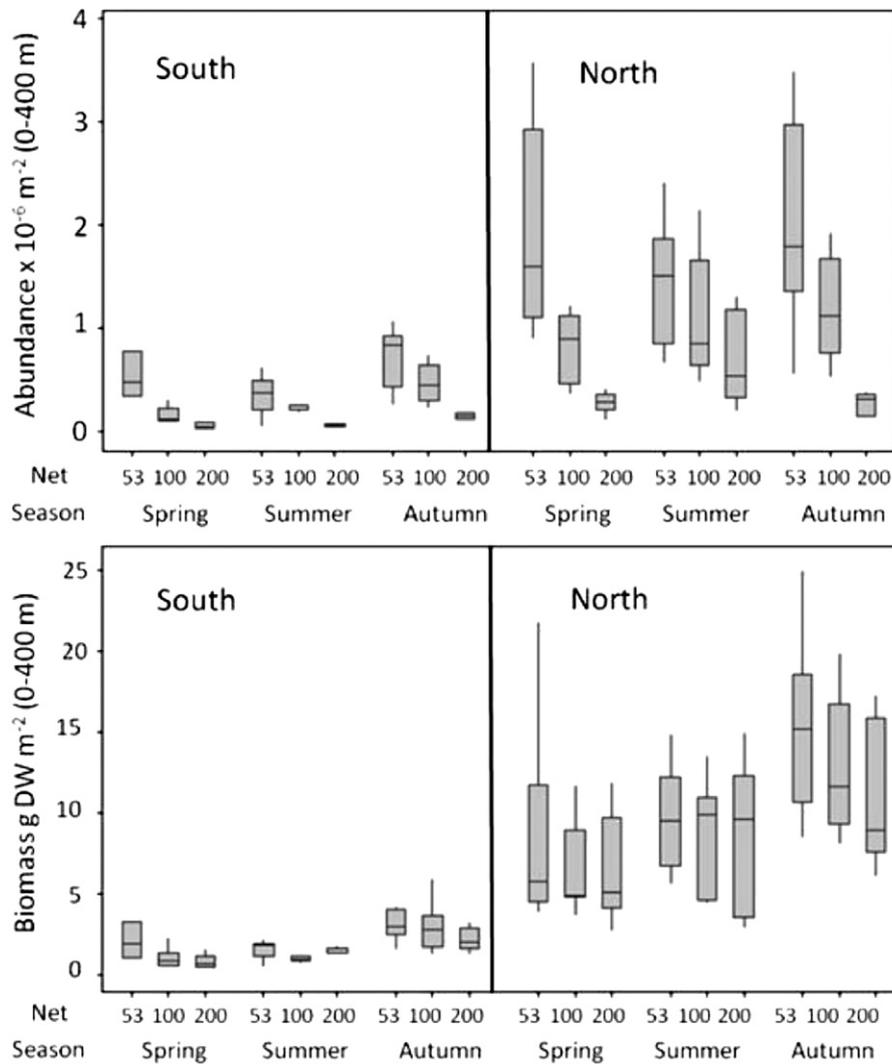


Fig. 2. Boxplots of mesozooplankton abundance and biomass captured by 53, 100 and 200 µm mesh Bongo nets. Data shown on plot are median (line within box), Q1–Q3 (box ranges) and whiskers representing upper limit=Q3 + 1.5 (Q3–Q1) and lower limit=Q3 – 1.5 (Q3–Q1). Data are presented in relation to net mesh, season and station group as determined by cluster analysis (see Fig. 3).

in summer and autumn and the 200 µm nets which had a clear summer maxima (Fig. 2).

Biomass patterns contrasted with those of abundance insofar as there were no consistent differences between nets within Group 1 stations (Fig. 2 and Table 2), with median values ranging from 0.73 to 2.99 g dw m⁻² across nets. Overall, autumn values were about twice those of spring and summer and significantly different (Kruskal–Wallis $H=29.02$, $df=2$, $p < 0.001$). Substantial differences between Groups 1 and 2 were however evident. Median values within Group 2 showed little difference between nets within spring and summer sample sets (Fig. 2 and Table 2), although overall median values increased from spring (5.79 g dw m⁻²) through summer (9.96 g dw m⁻²) and into autumn (15.22 g dw m⁻²) (Kruskal–Wallis $H=23.6$, $df=2$, $p=0.000$).

3.3. Mesh selection

With few exceptions, comparisons of net hauls made within station groups indicated that 53 µm net-derived densities (ind. m⁻² 0–400 m) were greater than those from the 100 µm net followed by the 200 µm net (Fig. 2 and Table 2). The ratio of median sample size (abundance and biomass) caught by the different nets was determined across all cruises (Table 3). The overall median abundance

Table 2

Results of Kruskal–Wallis analysis of median values of abundance and biomass caught by 53, 100 and 200 µm Bongo nets with respect to season and station group.

	Abundance Comparison by net mesh		Biomass Comparison by net mesh	
	H ($df=2$)	p	H ($df=2$)	p
<i>Group 1</i>				
Spring	9.92	0.007	4.64	0.098
Summer	17.13	0.000	10.73	0.005
Autumn	18.78	0.000	2.11	0.349
<i>Group 2</i>				
Spring	19.94	0.000	0.69	0.708
Summer	6.31	0.043	0.15	0.926
Autumn	19.64	0.000	2.67	0.263

Data for both abundance and biomass are presented in Fig. 2.

ratio was 1.71 for the 53 µm ($n=58$) to 100 µm ($n=46$) nets, 5.90 for the 53 to 200 µm ($n=46$) nets and 3.44 for the 100 to 200 µm nets (i.e. the 100 µm net caught an average of 58% of the 53 µm net

Table 3
Ratio of median abundance and biomass captured by different net mesh sizes (53, 100, and 200 μm) with respect to season and station group.

Group	Net		
	53/100	53/200	100/200
Abundance			
<i>Spring</i>			
1	4.01	15.57	3.87
2	1.78	5.87	3.31
<i>Summer</i>			
1	1.51	6.70	4.43
2	1.77	2.86	1.61
<i>Autumn</i>			
1	1.92	6.15	3.21
2	1.59	5.73	3.60
Biomass			
<i>Spring</i>			
1	2.18	2.63	1.21
2	1.18	1.14	0.96
<i>Summer</i>			
1	1.87	1.35	0.72
2	0.96	0.99	1.03
<i>Autumn</i>			
1	1.06	1.44	1.36
2	1.31	1.69	1.29

and the 200 μm net 17%). There were no systematic differences in these ratios found between station groups within cruises although both 53/200 and 100/200 were lowest in Group 2 (northern) stations during summer. This was possibly due to the high abundances of appendicularians and calanoid nauplii retained by the larger mesh nets. Biomass net ratios were smaller and more even than abundance ratios, reflecting the largely uniform biomass caught by nets of different mesh sizes (Table 3).

3.4. Community structure

The results of cluster analyses performed on double root transformed abundances (unaggregated) from the 100 and 200 μm mesh nets are shown in Fig. 3. Across all 3 cruises the same basic division of stations was apparent, with a group comprised of stations in the southern part of the Scotia Sea (Group 1) contrasting with a group from further north (Group 2). The limit of the northward extent of the southern group lay at $\sim 58^\circ\text{S}$. Stations Su 6 and Au 6.1 sampled during summer and autumn, respectively (geographically ~ 20 miles apart), were not affiliated with either group and were intermediate in terms of abundance. The same groupings were found in the 53 μm samples (not illustrated). The major separation of groups was robust, although SIMPROF indicated that a few stations could be differentiated within the major groups identified, reflecting the heterogeneity that is apparent in the Scotia Sea (Fig. 3A–C).

Across both groups and all nets, copepods generally comprised $> 90\%$ of total zooplankton abundance, although during summer this proportion fell as low as 80% within Group 2. This was largely a result of the presence of high abundances of appendicularians (10–14% of total abundance) in all net catches within Group 2, where a greater proportion of ‘large’ copepods was also apparent. To summarise this complex data set and to better understand large-scale differences, the number of taxonomic categories was reduced from 122 to 30 through aggregating into various higher order groups such that each category consisted of at least 0.5% of total sample abundance. Although two assemblages were identified, many species and higher order groups had distributions that spanned the Scotia Sea and were present in both groups of stations. Differences between the two groups were

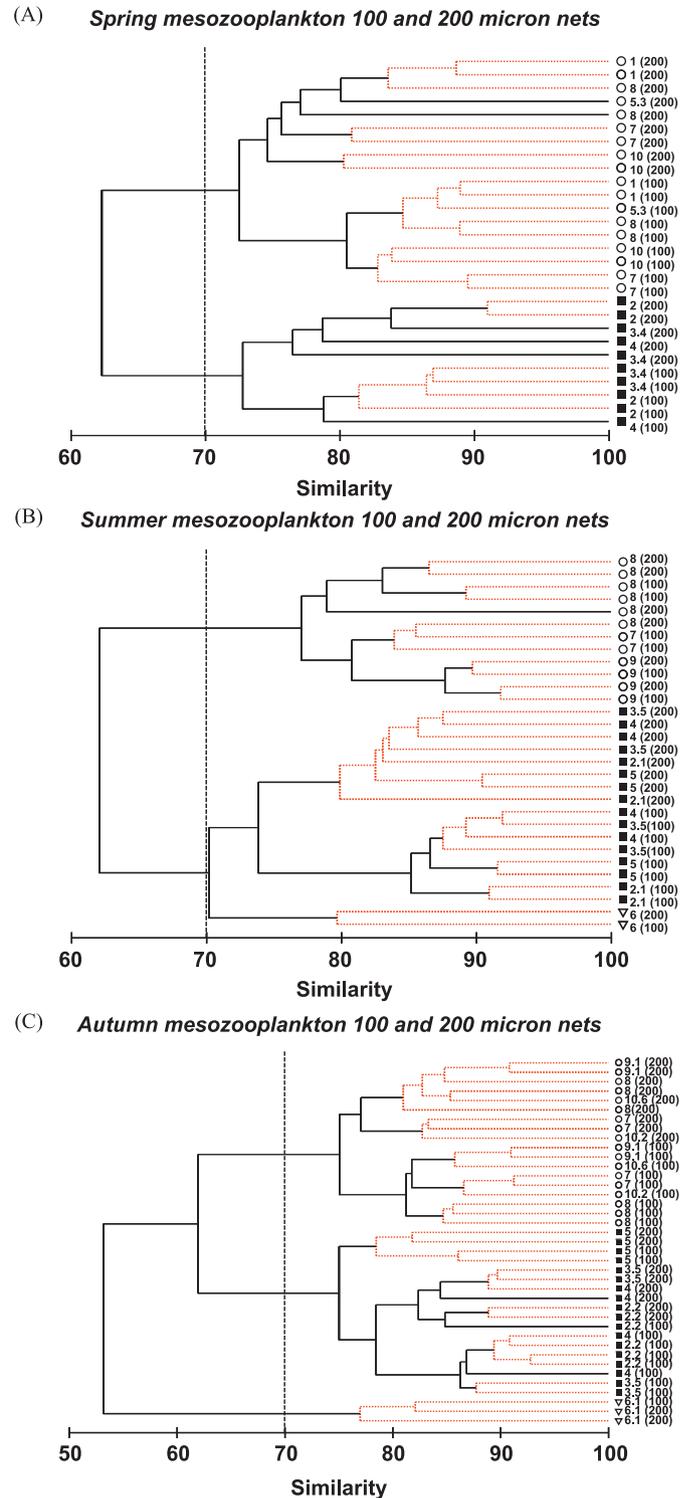


Fig. 3. Results of cluster analysis including SIMPROF (similarity profiles routine) on species data derived from the 100 and 200 μm nets for (A) spring (B) summer and (C) autumn cruises. Black squares represent stations defined as belonging to Group 1, open circles Group 2 and inverted triangle Group 3. Samples connected by pecked lines cannot be significantly differentiated.

examined by the SIMPER routine, which indicated that within cruises and between nets, differences in abundance of broadly the same taxa were responsible for distinguishing between the station groupings, rather than the presence of different taxa *per se*. No single species or taxon dominated the contributions to dissimilarity between the two groups, and the species list was essentially the same, albeit with

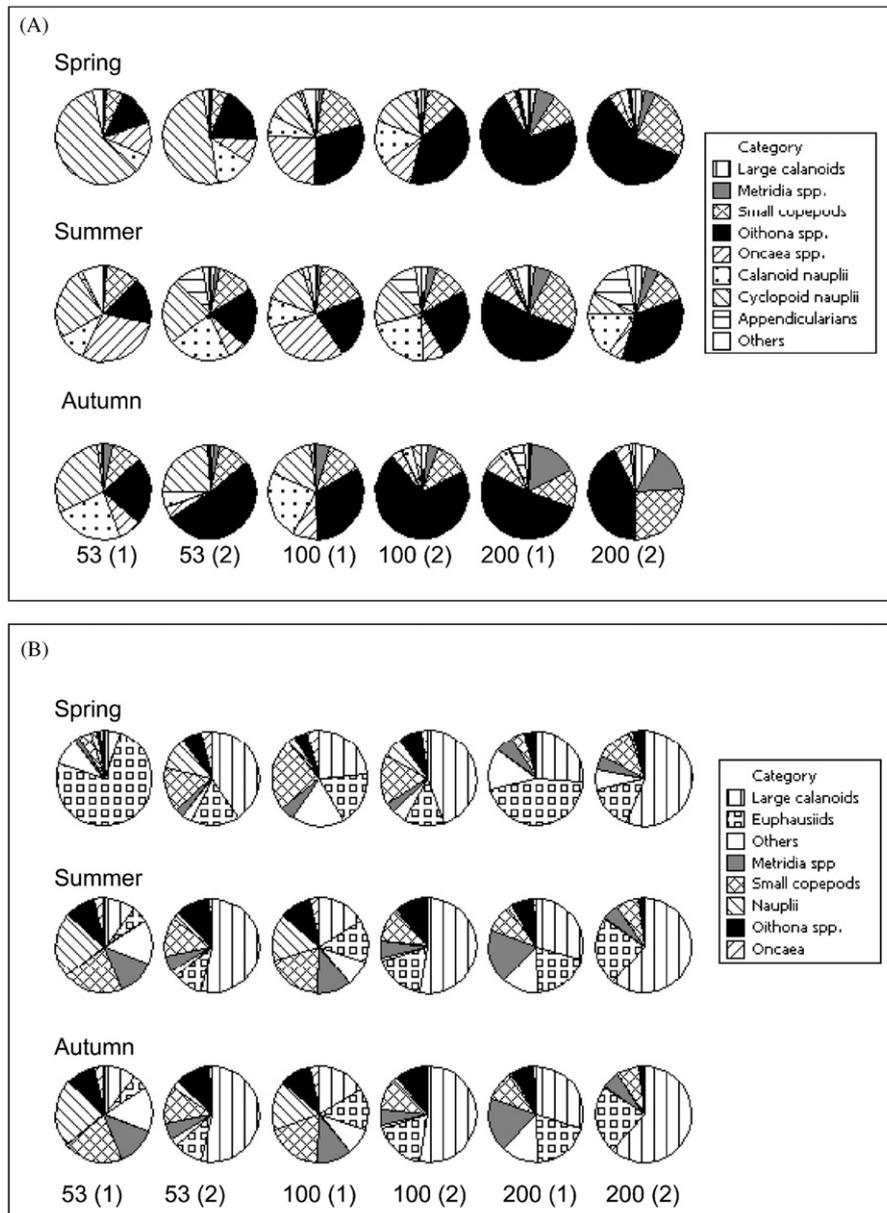


Fig. 4. Pie charts summarising main zooplankton groups contributing to (A) abundance and (B) biomass by net mesh (53, 100 and 200 μm), season (spring, summer, autumn) and station group (1 and 2). Data plotted are medians.

modest changes in rank order between nets and cruises. Within cruises, average dissimilarity between station groups ranged from ~32–41%. Species indicated by SIMPER as contributing most to within-group similarity and between-group dissimilarity are given in Appendix B. Across all nets and cruises the basic patterns of species distribution and dominance within groups were similar. Small species (< 1.5 mm) dominated overall, with *Oithona similis* and cyclopoid nauplii (predominantly *Oithona* spp.) being most abundant, particularly in the 53 and 100 μm mesh nets. As a result of mesh selectivity the 53 μm mesh net retained greater numbers of the smaller copepodite and naupliar stages of numerous small species than the two larger nets.

Despite sampling across different years, some surprisingly clear patterns emerged. Stations to the south of the Scotia Sea had uniformly much lower plankton abundance and biomass than those further north in all seasons. Net catches across all mesh sizes were dominated by small species and stages of copepods. With a few exceptions, such as *Stephos longipes*, a copepod

associated with sea-ice and *Drepanopus forcipatus*, a neritic species encountered downstream of South Georgia, most species and taxa were widely distributed across the Scotia Sea. The consistently higher zooplankton abundances within Group 2, across all 3 cruises, was reflected in many species distributions across most nets, e.g. *Oncaea* spp., *O. similis*, *Ctenocalanus citer* and *Metridia* spp. Some species were present in all seasons at broadly similar densities, e.g. chaetognaths and *Euchaeta antarctica* (carnivores), plus *C. citer* and ostracods. Others were particularly abundant during one or more cruises, such as appendicularians and *C. acutus* (summer) suggesting spring/summer recruitment, *Pelagobia longicirrata* (spring and summer) suggesting early spring/summer recruitment. The shelled pteropod *Limacina helicina* and the copepods *C. similimus* and *R. gigas* had elevated abundances in summer and autumn. *Euphausia superba* calyp- topes were only seen in autumn and were present almost exclusively in the southern Group 1. Although not tabled here salps were also abundant in Group 1 during autumn (autumn).

The occasional presence of salp chains in the Bongo nets did not reflect the higher abundances disclosed by midwater trawl samples, which filtered a vastly greater volume of water (see Ward et al., 2012). Calanoid copepod nauplii were most abundant in Group 2 during spring and summer but by autumn they were more abundant in Group 1 suggesting a later period of recruitment further south. Cyclopoid nauplii (mainly *Oithona* spp.), although more abundant in Group 2, tended to fluctuate in number across cruises, whereas euphausiid eggs and nauplii (non *E. superba*) were present in spring and summer but not in autumn. When data from the 53 μm mesh net are considered some species are seen to be more abundant in one group compared to the other across all cruises, e.g. *Microcalanus pygmaeus*, *Oncaea* spp., *O. frigida* and chaetognaths have a proportionately greater share in Group 1, whereas *C. citer* and *O. similis* have a proportionately greater share in Group 2 (Appendix B).

To summarise major differences in percentage abundance and biomass between seasons, nets and station groups we have further subsumed taxonomic categories into broader groups and have constructed pie charts of both median abundance and biomass (Fig. 4). In terms of abundance these reflect the dominance of small species, particularly *Oithona* spp. and cyclopoid and calanoid nauplii along with *Oncaea* spp. across all seasons. Other taxa tended to be seasonally abundant, e.g. appendicularians in summer and *Metridia* spp. in the autumn. In terms of biomass, large calanoids and euphausiids dominated in the larger

net mesh sizes across all seasons particularly within Group 2. The small taxa formed proportionately more of the biomass in the 53 μm nets and 100 μm nets within Group 1 nets but were correspondingly less important in Group 2 where large calanoids and euphausiids made a greater contribution.

3.5. LHPR sampling

To summarise the population depth distribution of the large calanoid copepod species *C. acutus*, *R. gigas* and *C. simillimus*, we have chosen to illustrate selected stations that are representative of station groups and cruises. Full details of median depth of the population are given in Appendix C.

During spring, *C. acutus* was the most abundant large seasonal migrant within Group 1 and females dominated the population (Fig. 5), which was located at a median depth of ~ 470 m and was entirely absent from the top 200 m (Fig. 6). The less abundant *R. gigas* was also absent from the top 200 m and was dominated by older copepodite stages (Fig. 5). At station Sp 8, the most northerly station sampled, older overwintered copepodite stages again dominated, with *R. gigas* and *C. simillimus* spread throughout the top 500 m. Once again *C. acutus* was largely absent from the top 200 m and had a stage and vertical distribution very similar to that at Sp 2.

In summer within Group 1 the stage structure and depth distribution of *C. acutus* and *R. gigas* appeared very similar to that

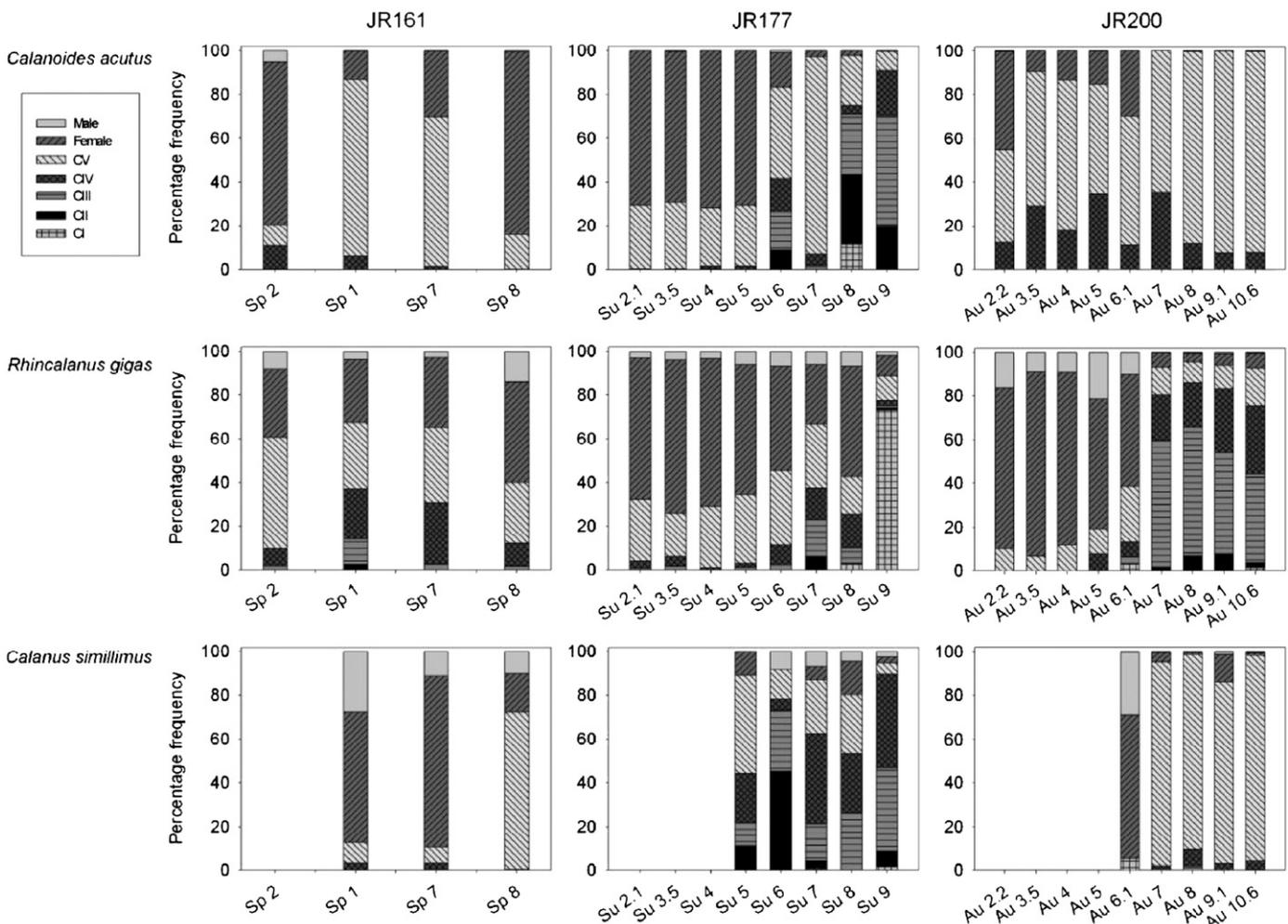


Fig. 5. Population stage frequency data for *Calanoides acutus*, *Rhincalanus gigas* and *Calanus simillimus* obtained from the LHPR profiles (0–1000 m) with respect to season: Spring (JR161), Summer (JR177) and Autumn (JR200).

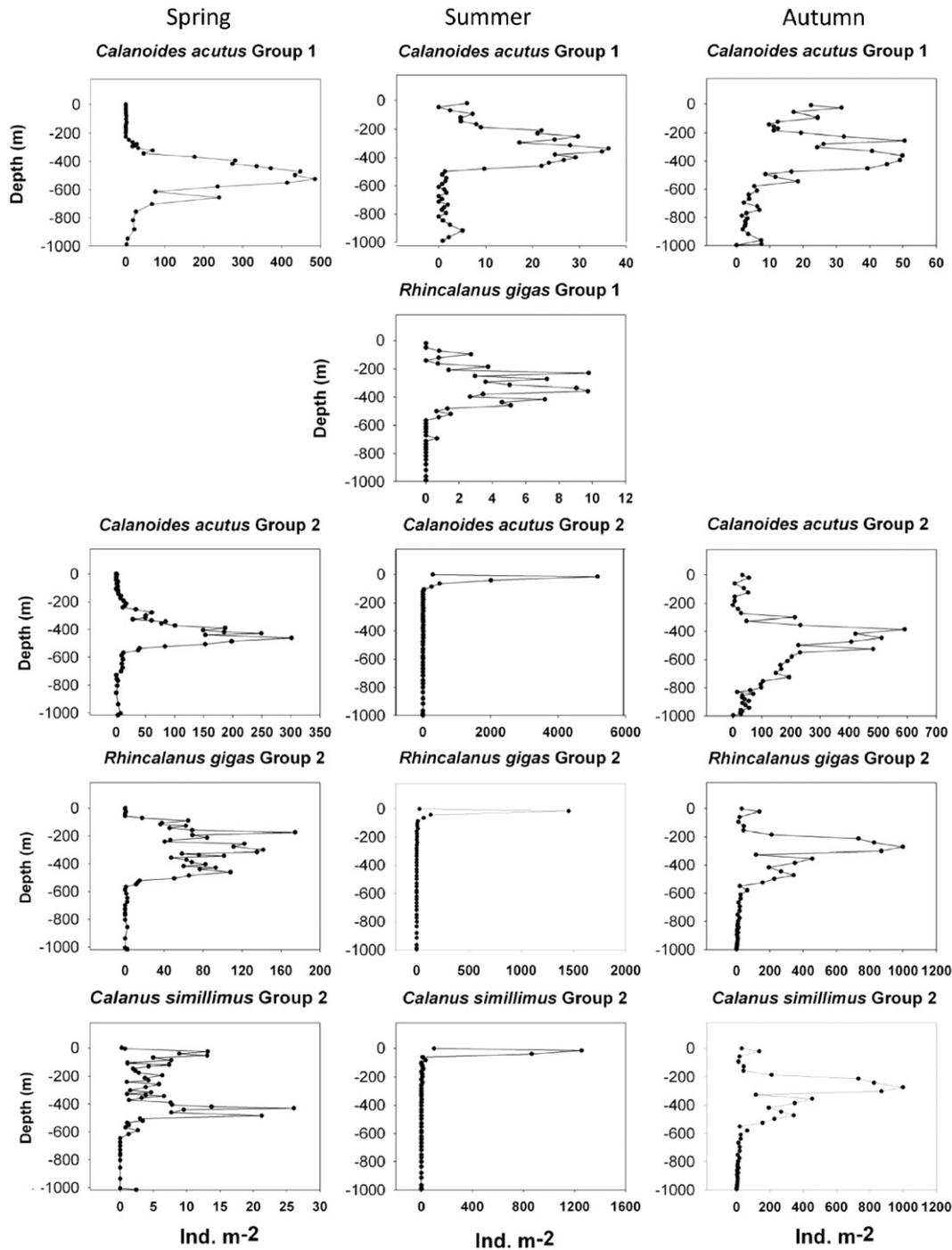


Fig. 6. Representative LHPR profiles of population depth of *Calanoides acutus*, *Rhincalanus gigas* and *Calanus simillimus* with respect to season and station group.

encountered during spring. Overwintered populations, again dominated by females (Fig. 5), were still located at depths of between 200 and 500 m with no evidence that recruitment had commenced (Fig. 6). Within Group 2 stage composition varied between stations. *C. acutus* was dominated by Stage CV at station Su 7 with distributions extending from the surface to 1000 m. Stage CIV, the next most abundant stage, was located in the top 200 m. In contrast both *R. gigas* and *C. simillimus* were located within the top 200 m, with the former being dominated by stages CII and CIII whereas the latter was dominated by stages CIV and CV. Progressing northwards, at stations Su 8 and Su 9 (Fig. 5) younger stages of both *C. acutus* and *R. gigas* were dominant or co-

dominant with older stages and along with *C. simillimus* at station Su 9, were mainly located in the top 100 m (Fig. 6).

During autumn the population stage frequency of *C. acutus* was dominated by older stages at all stations sampled. The major difference between station groups was the presence of females at Group 1 stations in addition to CV and CIV, which dominated Group 2 stations (Fig. 5). Depth distributions generally extended from near surface to 600–800 m, reflected in the interquartile population depth ranges, which were greater overall than during the spring and summer cruises, although population depth was somewhat shallower at Group 1 stations (Appendix C). *R. gigas* and in particular *C. simillimus* were only abundant within Group 2 stations.

The relatively few *R. gigas* present at Group 1 stations were predominantly older stages in contrast to Group 2, where younger stages, particularly CIII, were conspicuous. With virtually all stages present at most Group 2 stations, *R. gigas* was dominated by stages CIII and CIV with population depth distributions that extended from the surface 200 m down to around 400 m (Fig. 6). *C. simillimus* in Group 2 stations was dominated by CVs, which frequently had modal peaks within the top 200 m and further down the water column between 200 and 400 m. The exception was Au 6.1 where the few *C. simillimus* present were dominated by males and females.

4. Discussion

4.1. Mesh selection

The net mesh used in any study of this kind profoundly influences perceptions of community structure (Antaclì et al., 2010; Nichols and Thompson, 1991; Vannucci, 1968). Until recently nets of $\geq 200 \mu\text{m}$ were broadly the norm as far as sampling mesozooplankton in the Southern Ocean (and elsewhere) was concerned. Studies using finer mesh nets and pumps are challenging the view of the Southern Ocean as being simply dominated by large secondary producers and short food chains. Antarctic krill, salps and large calanoid copepods are all conspicuous in net catches but increasingly the contribution made to abundance and biomass by smaller species, particularly cyclopoid and small calanoid copepods, is being appreciated, as is their role in grazing and recycling material (Atkinson, 1998; Dubischar and Bathmann, 1997; Schnack et al., 1985; Tarling et al., 2012; Thompson et al., 2011). In this study small copepods dominated numerically across all stations and nets of all mesh sizes, with *Oithona* spp., *Oncaea* spp. and *C. citer* and *M. pygmaeus* being particularly abundant, as were cyclopoid nauplii in the 53 and 100 μm nets. Within Group 2 mean copepod densities of up to $\sim 8800 \text{ ind. m}^{-3}$ were recorded with the 53 μm net. This estimate was obtained by fishing a 400 m water column in which the majority of organisms were located within the top 100 m (see Hirst and Ward, 2008). From the same stations 20 l water bottle samples from the upper 100 m were analysed for all small species stages and produced maximum densities up to $\sim 40,000 \text{ ind. m}^{-3}$ (Ward unpublished data), which is comparable to catches taken with a 100 μm net reported by Dubischar et al. (2002) and with concurrent optical plankton counter data from within the vicinity of the APF (Pollard et al., 2002).

In absolute terms the standardised abundance (ind. m^{-2} 0–400 m) in the 53 μm nets considerably exceeded that of the other two nets (Table 3). There was less of a difference between nets in terms of biomass although the 53 μm nets generally captured somewhat more. This is a similar result to that of Hopkins (1971) who also compared net catches made with different meshes and concluded that while plankton abundance increased with decreasing mesh aperture, biomass values showed relatively little variation. Within Group 1, median biomass values ranged from 0.73 to 2.99 g dw m^{-2} and from 4.91 to 15.23 g dw m^{-2} within Group 2. The former values are consistent with net estimates for the Antarctic zone whereas the latter reflects the higher biomass captured further north around South Georgia and the Polar Front (Atkinson et al., 2001). Biomass captured by the 53 μm nets ranged from $\sim 10\%$ to 60% (mean 30%) higher than the 200 μm nets and broadly equates to micrometazoan biomass that the larger net loses through its larger mesh. This is clearly significant in the sense that the smaller size fraction has a higher turnover rate and mass-specific energy demand (Atkinson, 1994; Dubischar and Bathmann, 1997; Paffenhöfer, 1971).

Predictions made by Galliène and Robins (2001) using OPC data collected between 50°N and 50°S to derive a 'mean biomass size spectrum' and established relationships for mesh selectivity

(Nichols and Thompson, 1991) suggested that if a 64 μm mesh net retained $> 95\%$ of the community then a 100 μm mesh would retain $\sim 60\%$ of this and a 200 μm mesh only $\sim 7\%$. Our data indicated that mean net abundances for the 100 μm nets averaged 58% of that caught by the 53 μm nets (as predicted), and for the 200 μm net 17%, which is somewhat more than predicted. When treated in the same way, biomass values were closer to those predicted, with mean values for the 100 μm net some 99% (predicted 91%) and the 200 μm net 70% (predicted 78%) of the 53 μm net. It is not possible to discount sampling error but the standardised abundances of copepodite stages big enough to be retained by all net meshes were statistically indistinguishable, suggesting that overall, differences in filtration efficiency were not an issue. Clogging of the finer mesh net was not noticeable during any cruise, for which its better aspect ratio relative to the larger Bongo nets (see the section "Methods") was probably responsible. Community size structure in the Southern Ocean almost certainly differs from that found in the temperate and tropical parts of the Atlantic Ocean where Galliène and Robins (2001) derived their relationship, as there are differences in taxonomic composition between biomes, with polar regions containing proportionately more copepods than either the Westerlies or the Trades (Longhurst, 1998). Higher densities of *Oithona* spp. have been observed within the Polar Frontal Zone (Atkinson, 1996, 1998; Dubischar and Bathmann, 1997) and the much higher densities of *Oithona* spp. captured in the South Polar biome relative to either the Trades, Equatorial or Westerlies biomes, which suggest the potential for a relatively greater abundance of smaller copepods (Woodd-Walker et al., 2002), although biomass may be less affected.

4.2. Seasonal plankton dynamics in the Scotia Sea

Although interannual differences cannot be accounted for, differing seasonal patterns of abundance were suggested by the net catches across cruises. In Group 1 stations, to the south of the SB-ACC, abundance maxima occurred in autumn in all 3 nets. Within Group 2 stations, to the north of the SACCF, the data are more ambiguous, with abundance in the 53 and 100 μm mesh nets varying little across seasons or showing slightly higher abundances in autumn, whereas in the 200 μm net there is a clear maximum in summer (Fig. 2). Hunt and Hosie (2006a, b) investigated the seasonal succession of zooplankton in the Southern Ocean south of Australia using Continuous Plankton Recorder and Norpac nets and found that in the seasonal ice zone ($\sim 62\text{--}66^\circ\text{S}$) along 140°E , abundance and species diversity was low in November, peaked in January and tailed off towards autumn. This coincided with a shift in community composition, with *Salpa thompsoni* and *Euphausia superba* larvae becoming more prevalent, as did the large calanoid copepods *Metridia gerlachei*, *C. propinquus* and *C. simillimus*. Low abundance and diversity in spring and autumn was thought to be partly attributable to the seasonal descent of plankton out of the near-surface layers during and prior to winter. Further north, in the sub-Antarctic and Polar Frontal Zones, there was a north to south shift in the density distribution of common and widely distributed taxa. This shift was interpreted as a latitudinal gradient in the timing of seasonal development across the study area, as suggested by Voronina (1970). Temporal changes in abundance were linked to the respective life-cycles of the species concerned and in the case of small species their 'catchability', which increased as later and hence larger stages developed within the population.

Within the Scotia Sea, differences in the relative abundance of prominent taxa during different seasons are also most likely linked to life-cycles. Within Group 1 increased abundances of *O. similis*, calanoid nauplii, *M. pygmaeus* and cyclopoid nauplii contributed to

the autumn peak in the 53 and 100 μm nets whereas *O. similis* and *Metridia* spp. were responsible for the peak in the 200 μm net. Within Group 2 only the 200 μm net showed a clear summer peak with high abundances, relative to spring and autumn, of calanoid nauplii (mainly *R. gigas*), cyclopoid nauplii and appendicularians. *Euphausia superba* larvae and high abundances of salps were only encountered in Group 1 stations during the autumn cruise. Salps have previously been recorded as particularly abundant in the southern part of the Scotia Sea during January/February (Kawaguchi et al., 2004; Ward et al., 2004) which Kawaguchi et al. (2004) attributed to the spatio-temporal pattern of asexual reproduction by budding proceeding from north to south as the summer progresses. The Scotia Sea is also a key place for krill recruitment particularly its southern regions (Brinton, 1985; Schmidt et al., 2012; Spirodonov, 1995) and the timing of the appearance of larvae in surface waters in autumn is indicative of spawning around 1–2 months previously.

4.3. Copepod stage distribution and vertical distribution

Clear differences in age structure and depth distribution of copepod populations were apparent across seasons with respect to station group. Overwintered stages of *C. acutus* and *R. gigas* were found in Group 1 during spring and summer when populations were still largely below the top 200 m layer. In contrast younger stages were present within Group 2 during summer and populations of all species largely lay in the surface 100 m. By autumn overwintering stages were again dominant across all species within both station groups and undergoing their seasonal descent (Atkinson, 1991; Atkinson et al., 1997; Tarling et al., 2004; Ward et al., 1997).

The timing of ice retreat appears to influence the development and seasonal succession of zooplankton populations, possibly through its influence on primary productivity (Atkinson and Shreeve, 1995; Bianchi et al., 1992; Burghart et al., 1999). Ice-edge stations have often been found to have older overwintered species stages in comparison to ice-free waters where they are in a later phase of development (Atkinson and Shreeve, 1995; Burghart et al., 1999; Ward et al., 2006). During spring the ice-edge lay in close proximity to the southern stations (Fig. 1) and during summer, although ice-free at the time of sampling, two weeks previously ice had covered the region. Low salinity water occasioned by ice-melt was present at the southernmost stations at this time (Whitehouse et al., 2012) and stations were characterised by the presence of cryptophytes, a group characteristically seen in the wake of a retreating ice-edge (Garibotti et al., 2005).

4.4. Community structure and potential controls

Many species are widely distributed throughout the ACC (Atkinson and Sinclair, 2000; Chiba et al., 2001; Mackey et al., 2012; Mackintosh 1936, Pakhomov et al., 2000; Ward et al., 2004, 2006) and they show variations in abundance with latitude, and with respect to frontal features. Differences are usually seen at the level of the population (abundance) and not the community (species composition) level (Marin, 1987; Ward et al., 2004, 2006). SIMPER analysis run on data from the 200 μm Bongo nets indicated that during spring and summer the majority of taxa and species-stages that contributed most to between-group dissimilarity were more abundant in northern Group 2 (54 of a total of 65 and 51 of 59, respectively). During autumn, although still in the majority, a reduced total of 35 of 61 taxa species/stages were more abundant in Group 2. The relative increased abundance to the south likely further reflects later recruitment of many taxa in Group 1. A similar pattern of species distribution was also apparent in the other net mesh sizes. Taxa which were more abundant in the southern group in all seasons were restricted to

Siphonophora (mainly *Diphyes* spp.) and the copepods *Gaidius intermedius* and *C. acutus* females, which collectively only contributed ~2–3% to between-group dissimilarity. This shows that differences in population development and abundance are more important than species differences in defining assemblages. This is further emphasised by the LHPR hauls indicating that new generations of large calanoid copepods were present to the north of the SACCF during spring and summer and absent to the south.

Of the environmental factors likely to influence community structure and composition in the Southern Ocean, the importance of temperature, food availability and the more localised impact of sea-ice are widely cited (Atkinson, 1998; Chiba et al., 2001; Mackey et al., 2012; Mackintosh, 1936; Pakhomov and McQuaid, 1996; Pakhomov et al., 2000). A partitioning of the ACC fundamentally similar to this study was observed by Chiba et al. (2001) who distinguished a northern and a southern ACC grouping of stations in a survey off east Antarctica (90–160°E). Differences in water temperature and silicate concentration were correlated with community changes with higher zooplankton abundance and a dominance of small copepods in the northern ACC region and it was concluded that temperature was probably more important than phytoplankton in influencing distributional limits for a number of species Chiba et al. (2001). The effects of temperature are further discussed in Mackey et al. (2012), and Ward et al. (2012) who note that truly polar species are fewer in number and stenothermal. Fewer species therefore tend to lead to lower overall abundances compared to further north, where diversity is higher and where a greater mix of warmer water and widely distributed species are present.

Differences in food availability may also in part account for some of the differences seen between station groups although evidence is slight. Chl *a* varied across the Scotia Sea in all seasons and blooms were seen along the transect during each cruise (Korb et al., 2012; Whitehouse et al., 2012). Park et al. (2010) have recently examined monthly time-series of satellite-observed ocean colour and defined temporal and spatial patterns of production within the Scotia Sea. Irregular seasonal blooms were found to be the norm in most areas, which confounds simple correlations with plankton community patterns found in this study. Although point estimates of Chl *a* are poor predictors of zooplankton abundance and biomass, seasonally integrated estimates and nutrient deficits often better reflect these properties (Ward et al., 2007). Seasonally integrated Chl *a* biomass along the transect (Whitehouse et al., 2012) was some 50% higher to the north of South Georgia than further south but hardly enough to be commensurate with the 2–5-fold average differences in zooplankton abundance and biomass, which were observed between station groups.

The seasonal advance and retreat of sea-ice is also an important process structuring ecosystems in the Southern Ocean (Flores, 2009; Mackintosh, 1936). During winter in the Scotia Sea mean maximum ice extent is broadly coincident with the position of the SB-ACC, although that of the Marginal Ice Zone, in this case defined as the northern limit of low density melt-water input from the receding ice-edge, can extend 50–250 km beyond (Tréguer and Jacques, 1992). The timing of ice retreat in the spring and early summer appears to influence the timing of community development with a late clearing of ice delaying the onset of reproduction in at least some diapausing copepod species (Ward et al., 2004, 2006, this study).

Temperature, despite seasonal warming in the near surface layers, has a gradient consistent with that observed in the plankton and seems most likely to have a major influence on patterns of abundance and diversity. Alongside stenothermy, the effects of low temperatures on development and growth rates on plankton within the ACC gives rise to differences in the phenology of dominant species (Tarling et al., 2004; Ward and Hirst, 2007) which may be a defining characteristic of community composition within the ACC, resulting in lower abundances of widely

Table A1

Weights applied to taxonomic groups distinguished from net samples in the Scotia Sea, January–February 2008, including the algorithm used where direct measurements were not taken and/or the literature source. DW represents median value. With respect to copepods, a range is given where measurements of more than 1 developmental stage were available. Similarly, for other taxa, a range is given where there was more than 1 recognised species within the respective group. In the case of copepods, only those with either > 0.1% contribution to zone abundance or > 1% contribution to zone biomass are listed. Terms: BL=body length in mm (which is ~23% longer than prosome length); DW=dry weight in mg; CW=carbon weight in mg; WW=wet weight (in g or mg, as specified); SL=standard length (for fish); TL=trunk length in μm (for Appendicularia).

Taxa/species/stages	DW (mg)	Method	Source
Copepods			
Calanoid nauplii	0.0035	DW=0.0026e ^{1.3608BL}	Mizdalski (1988) ^a We measured BL directly
<i>Calanoides acutus</i> (CI–CVI)	0.010–0.515	CI–CIII: DW=0.0026e ^{1.3608BL} CIV–CVI: DW=0.0822e ^{0.4079BL}	Mizdalski (1988) ^a
<i>Calanus propinquus</i> (CI–CVI)	0.010–0.672	CI–CIV: DW=0.0026e ^{1.3608BL} CV–CVI: DW=0.0822e ^{0.4079BL}	Mizdalski (1988) ^a
<i>Calanus simillimus</i> (CI–CVI)	0.005–0.309	CI–CIII: DW=0.0026e ^{1.3608BL} CIV–CVI: DW=0.0822e ^{0.4079BL}	Mizdalski (1988) ^a We measured BL directly
<i>Ctenocalanus</i> spp.	0.011	DW=0.0026e ^{1.3608BL}	Mizdalski (1988) ^a
Cyclopoid nauplii	0.0001	Direct measurement	Sabatini, Kiorboe (1994)
<i>Euchaeta antarctica</i> (CI–CVI)	0.011–3.504	CI–CIII: DW=0.0026e ^{1.3608BL} CIV–CVI: DW=0.0822e ^{0.4079BL}	Mizdalski (1988) ^a
<i>Metridia gerlachei</i> (CVI)	0.372	DW=0.0822e ^{0.4079BL}	Mizdalski (1988) ^a
<i>Metridia lucens</i> (CVI)	0.089	DW=0.0026e ^{1.3608BL}	Mizdalski (1988) ^a We measured BL directly
<i>Metridia</i> spp. (CI–CV)	0.010–0.020	DW=0.0026e ^{1.3608BL}	Mizdalski (1988) ^a We measured BL directly
<i>Microcalanus pygmaeus</i>	0.007	DW=0.0026e ^{1.3608BL}	Mizdalski (1988) ^a
<i>Microsetella nauplii</i>	0.0002	CW=2.65 × 10 ⁻⁶ × BL ^{1.95}	Uye et al. (2002) for <i>M. norvegica</i> . Converted to DW using Wiebe et al. (1975), Wiebe (1988) We measured BL directly
<i>Microsetella norvegica</i>	0.005	As for <i>Microsetella nauplii</i>	
<i>Oithona frigida</i>	0.002	Direct measurement	Metz (1996)
<i>Oithona nauplii</i>	0.0001	Direct measurement	Sabatini, Kiorboe (1994)
<i>Oithona similis</i>	0.0017	Direct measurement	Metz (1996)
<i>Oncaea</i> spp.	0.002	Direct measurement	Metz (1996)
<i>Rhincalanus gigas</i> (CI–CVI)	0.050–1.98	DW=0.0822e ^{0.4079BL}	Mizdalski (1988) ^a
<i>Scolecithricella minor</i>	0.015	DW=0.0026e ^{1.3608BL}	Mizdalski (1988) ^a We measured BL directly
Other taxa			
Amphipods	0.469–3.970	DW=0.002BL ^{2.804}	Pakhomov, Perissinotto (1996). We measured BL directly
Polychaeta	0.001–1.788	Direct measurement	We made direct measurements of <i>Pelagobia</i> sp. DW Mizdalski (1988) for <i>Tomopteris</i> sp.
Appendicularia	0.003	DW=2.24 × 10 ⁻¹⁴ TL ^{4.098}	Aguirre et al. (2006). TL in μm . We measured BL directly (mean—500 μm)
<i>Chaetognatha</i>	0.0072	Direct measurement	Mizdalski (1988)
Euphausiids	0.001–44.108 ^b	Direct measurement ₁ DW=0.04BL ^{2.39}	1. Huntley and Brinton (1991) for <i>Euphausia superba</i> larvae 2. Siegel (1987) ^a for all other euphausiid larvae. We measured BL directly
Decapod larvae	2.359 ^b	DW=0.04 BL ^{2.39}	Used the 'other euphausiid' algorithm, as described above. We measured BL directly
Fish larvae	0.149 ^b	log ₁₀ WW=-5.2708 +3.21570log ₁₀ SL	Flores et al. (2008). WW in g. SL in mm. We measured SL directly
Cnidaria	0.707–0.797	Direct measurement	We made direct measurements of <i>Solmundella</i> spp. WW. Converted to DW using Larson (1986)
Mysidacea	0.362 ^b	DW=0.04 BL ^{2.39}	Used the 'other euphausiid' algorithm, as described above. We measured BL directly
Ostracoda	0.0174	Direct measurement	We measured WW directly. Converted to DW using Wiebe et al. (1975), Wiebe (1988)
Pteropoda	0.01–0.43	Direct measurement	Mizdalski (1988) for <i>Clione</i> sp. We made direct measurements of DW on other pteropods (pers. comm. N. Bednarek)
Salps	0.276	DW=0.0598L ^{2.204}	Huntley et al. (1989). We measured BL directly

^a An exponential function fitted to their data.

^b Original value in wet weight (mg)—converted to dry weight using

$$DW_{(\text{mg})} = 10^{\frac{\log_8(0.001\text{WW}) - 0.139}{1.003}} \quad \text{Wiebe et al. (1975) and Wiebe (1988)}$$

DW values were converted to C using

$$C = 10^{\frac{\log DW - 0.499}{0.591}} \quad \text{Wiebe et al. (1975) and Wiebe (1988)}$$

Table B1

Median abundance ind. m⁻² (0–400 m) of dominant taxa by net, station group and season.

	Spring						Summer						Autumn					
	Gp1 53	Gp2 53	Gp1 100	Gp2 100	Gp1 200	Gp2 200	Gp1 53	Gp2 53	Gp1 100	Gp2 100	Gp1 200	Gp2 200	GP1 53	GP2 53	GP1 100	GP2 100	GP1 200	GP2 200
<i>Rhincalanus gigas</i>	58.9	1729	46.4	2199	33.1	2252	98.2	3929	82.1	3702	97.5	4215	0	3536	58	3285	34.2	3805
<i>Calanoides acutus</i>	354	609	556	623	603	941	432.2	7780	332	6924	380	8156	530	511	383	465	534	356
<i>Calanus</i> <i>simillimus</i>	59	177	0	291	0	265	0	5815	0	6076	0	6869	0	15,402	0	12,592	0	14,344
<i>Calanus</i> <i>propinquus</i>	98.3	0	82.8	13.25	49.7	26.5	39.3	570	34.2	848	30.79	876	314.3	294.7	362.7	273.7	438	246.4
<i>Euchaeta</i> <i>antarctica</i>	668	688	586	821.4	675.6	1007	275	392.9	335.3	383	335.3	739	19.65	196.4	30.8	191.6	13.7	219
<i>Metridia</i> spp.	2613	10,277	2973	8691	1742	10,439	1297	22,986	1539	26,903	1957	32,157	21,492	47,462	19,490	54,309	21,461	47,740
<i>Oithona similis</i>	37,649	180,780	30,311	353,563	26,244	119,232	35,206	225,065	41,599	144,722	18,501	169,244	175,391	898,327	140,810	760,329	62,521	109,056
<i>Oithona frigida</i>	13,912	13,991	7313	9751	8479	10,810	13,674	10,687	9743	5255	9031	5693	10,058	16,345	5913	12,263	5475	10,511
<i>Oncaea</i> spp.	47,081	130,162	41,917	75,461	2332	8479	86,442	84,439	57,801	79,696	5063	27,368	53,120	79,209	41,170	45,550	7117	15,329
<i>Microcalanus</i> <i>pygmaeus</i>	22,362	15,406	21,011	14,838	2756	8055	34,891	20,746	35,250	30,214	8949	11,604	59,092	35,832	38,980	29,782	8541	4818
<i>Ctenocalanus citer</i>	629	77,971	901	62,319	371	50,448	2829	90,529	2901	66,121	1368	41,818	16,030	86,124	10,511	52,557	6132	35,914
<i>Clausocalanus</i> <i>laticeps</i>	0	157	0	265	0	159	0	0	0	27.4	0	109	0	1866	0	849	0	985
<i>Clausocalanus</i> spp. copepodites	0	0	0	0	0	0	0	0	0	0	0	0	0	16,973	0	9636	0	3942
<i>Drepanopus</i> <i>forcipatus</i>	0	0	0	0	0	0	0	393	0	493	0	109	0	3300	0	5913	0	3066
Calanoid nauplii	22,637	237,058	6306	105,984	106	9751	315,91	273,472	23,208	215,879	438	106,845	187,020	72,922	104,239	17,519	4161	1752
Cyclopoiid nauplii	235,486	845,107	10,863	136,507	0	0	79,213	274,101	34,703	117,792	0	22,113	231,025	469,594	72,047	8760	219	0
<i>Microsetella</i> <i>norvegica</i>	314	10,061	238	13,142	0	0	314	25,776	273.7	9196	0	109	314	37,090	0	19,271	0	438
<i>M. norvegica</i> nauplii	0	0	0	0	0	0	0	20,746	0	1752	0	0	0	0	0	0	0	0
<i>Thysanoessa</i> <i>calyptopes</i>	0	707	66	1060	93	424	176.8	904	147.1	1067	195	1095	0	0	0	0	0	0
<i>Thysanoessa</i> spp.	0	20	1.66	53	0	0	0	275	0	164.2	0	109	0	432.2	8.6	492.7	0	493
<i>Euphausia</i> <i>superba</i> calyptopes	0	0	0	0	0	0	0	0	0	0	0	192	1159	0	1553	0	1506	0
Euphausiid egg	766.4	157	533	106	431	212	19.6	550	41.1	1040	27.4	848	0	0	13.69	0	0	0
Euphausiid nauplii	471.6	19.6	467	53	199	0	0	236	10.3	411	12	246.3	0	0	0	0	0	0
Chaetognatha	609	1297	611	1298	629.3	1166	1218	1179	1152.9	1478	834.7	931	1080	727	1033	876	1013	711.7
<i>Pelagobia</i> <i>longicirrata</i>	12,183	33,484	4345	6783	66.2	291	19,017	16,345	3284	11,823	82.1	3284	530	275	335	438	150.6	0
Ostracoda spp.	648	1552	861	1325	901	1325	569.7	825	876	712	622.6	493	727	825	705	766	876	630
<i>Limacina helicina</i>	78.6	0	106	424	0	0	786	6287	0	4817	0	4926	1257	9430	0	1752	0	657
Appendicularians	590	1651	768	2968	265	609	2986	126,363	3832	86,702	1478	88,453	8172	0	7008	0	6789	0
Siphonophore	216	19.6	155.7	0	59.6	0	137.5	550	222.4	383	181.3	109	216.1	39.3	109.5	27.4	205.3	27.37
<i>Auricularia</i> spp.	0	0	0	0	0	0	334	0	554	0	284	0	137.5	0	143.7	0	41.1	0

distributed species towards the southern limits of their range rather than a succession of different species.

Appendix A

See Table A1.

Acknowledgments

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Appendix B

See Table B1.

Appendix C

See Table C1.

Table C1

Median depth (Q1–Q3) of populations of four species of biomass dominant copepods and densities $n\ m^{-2}$ (0–1000 m).

Station	<i>Calanoides acutus</i>	<i>Rhincalanus gigas</i>	<i>Calanus similimus</i>	<i>Calanus propinquus</i>
Spring				
Sp 2				
($n\ m^{-2}$)	4155	174	–	–
Median depth (Q1–Q3)	472 (434–551)	497 (449–579)		
Sp 1				
($n\ m^{-2}$)	1067	1979	116	–
Median depth (Q1–Q3)	112 (63–155)	155 (140–169)	183 (169–195)	
Sp 7				
($n\ m^{-2}$)	2213	4494	979	–
Median depth (Q1–Q3)	327 (124–350)	136 (99–339)	42 (26–57)	
Sp 8				
($n\ m^{-2}$)	2451	2260	226	–
Median depth (Q1–Q3)	429 (371–461)	316 (194–405)	343 (117–429)	
Summer				
Su 2.1				
($n\ m^{-2}$)	1290	121	–	–
Median depth (Q1–Q3)	341 (270–385)	250 (227–341)		
Su 3.5				
($n\ m^{-2}$)	417	85	–	–
Median depth (Q1–Q3)	336 (250–417)	336 (250–417)		
Su 4				
($n\ m^{-2}$)	640	71	–	–
Median depth (Q1–Q3)	347 (270–421)	312 (247–369)		
Su 5				
($n\ m^{-2}$)	400	120	–	–
Median depth (Q1–Q3)	387 (330–438)	330 (271–358)		
Su 6				
($n\ m^{-2}$)	104	161	–	–
Median depth (Q1–Q3)	308 (106–416)	370 (341–434)		
Su 7				
($n\ m^{-2}$)	1414	1001	663	–
Median depth (Q1–Q3)	545 (124–371)	57 (33–104)	33 (33–57)	
Su 8				
($n\ m^{-2}$)	2178	642	56	78
Median depth (Q1–Q3)	7 (7–65)	35 (35–65)	35 (35–167)	133 (133–281)
Su 9				
($n\ m^{-2}$)	8490	1737	2311	653
Median depth (Q1–Q3)	16 (16–42)	16 (16–16)	16 (16–42)	42 (16–64)
Autumn				
Au 2.2				
($n\ m^{-2}$)	476	–	–	98
Median depth (Q1–Q3)	589 (214–831)			153 (61–288)
Au 3.5				
($n\ m^{-2}$)	654	51	–	
Median depth (Q1–Q3)	330 (201–453)	423 (362–476)		
Au 4				
($n\ m^{-2}$)	967	95	–	72
Median depth (Q1–Q3)	316 (116–520)	215 (90–401)		215 (33–316)

Table C1 (continued)

Station	<i>Calanoides acutus</i>	<i>Rhincalanus gigas</i>	<i>Calanus simillimus</i>	<i>Calanus propinquus</i>
Au 5 (n m ⁻²)	850	–	–	178
Median depth (Q1–Q3)	396 (297–447)			178 (136–278)
Au 6.1 (n m ⁻²)	223	68	–	262
Median depth (Q1–Q3)	433 (311–558)	383 (311–488)		197 (111–311)
Au 7 (n m ⁻²)	508	2185	5671	83
Median depth (Q1–Q3)	558 (441–719)	320 (228–358)	16 (19–558)	68 (19–91)
Au 8 (n m ⁻²)	5530	6318	20,447	589
Median depth (Q1–Q3)	498 (417–640)	301 (241–386)	301 (94–472)	185 (126–212)
Au 9.1 (n m ⁻²)	589	1132	1687	146
Median depth (Q1–Q3)	546 (336–786)	101 (49–133)	101 (49–312)	712 (282–857)
Au 10.6 (n m ⁻²)	3475	1033	3661	148
Median depth (Q1–Q3)	485 (399–647)	231 (123–269)	287 (13–374)	37 (13–542)

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Paper 4

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Food web structure and bioregions in the Scotia Sea: A seasonal synthesis

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ABSTRACT

Bioregionalisation, the partitioning of large ecosystems into functionally distinct sub-units, facilitates ecosystem modelling, management and conservation. A variety of schemes have been used to partition the Southern Ocean, based variously on frontal positions, sea ice, productivity, water depth and nutrient concentrations. We have tested the utility and robustness of ecosystem bioregionalisation for the Scotia Sea, by classifying spring, summer and autumn stations on the basis of nutrient concentrations, phytoplankton taxa, meso- and macrozooplankton, fish catches and acoustic data. Despite sampling across different seasons and years, at different spatial scales and taxonomic resolutions, cluster analysis indicated basically consistent spatial divisions across this wide range of trophic levels. Stations could be classified into two main groups, lying broadly to the north and south of the Southern Antarctic Circumpolar Current Front (SACCF). In some aspects the 2 station groups were similar, with both having variable but often high phytoplankton biomass as well as similar biomass of fish. However, the colder water southern group, most of which was covered by seasonal sea ice, had a fundamentally different food web structure to that in the northern Scotia Sea. The cold water community had a depleted, cold-adapted fauna characterised by low zooplankton biomass, *Euphausia superba* and the fish *Electrona antarctica* and *Gymnoscopelus braueri*. In contrast the northern group was richer with higher mesozooplankton biomass and a fauna of warmer or more cosmopolitan species such as *Themisto gaudichaudii*, *Euphausia triacantha* and the fish *Protomyctophum bolini*, *Kreffticthys anderssoni* and *Gymnoscopelus fraseri*. The position of the food web transition, broadly consistent with the position of the SACCF, supports a recent circumpolar-scale bioregionalisation. However, there is little evidence that this relatively weak frontal transition represents a significant barrier either here or elsewhere in the Southern Ocean. We suggest that broader-scale factors, namely temperature and possibly the extent of the seasonal ice-zone, within which most of the southern stations lay, were more likely to influence biological zonation.

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1. Introduction

1.1. Bioregionalisation

Partitioning the Southern Ocean into discrete regional units, based on ecological and physical properties, helps in understanding, modelling and ultimately managing the great biological heterogeneity present (Grant et al., 2006). Such partitioning can help define functionally similar or different sub-systems or foodweb types and their extent, which is also necessary to understand, monitor and conserve marine biodiversity. Consideration of baseline data from

these regions also provides a measure against which future change can be determined.

Because of its great size and biological complexity, regionalisation in the Southern Ocean is clearly scale related. At the global scale it has been described as a single functional province in the context of Large Marine Ecosystems (Sherman and Duda, 1999) and with increasing complexity as comprising ice-free open water, seasonal pack-ice and shelf (permanent pack-ice) regions (Hempel, 1985). Tréguer and Jacques (1992) defined 4 functional units based on phytoplankton and nutrient dynamics encompassing the Polar Front Zone (PFZ), the Permanently Open Zone (POOZ), Seasonal Ice Zone (SIZ) and the Coastal and Continental Shelf Zone (CCSZ). Longhurst (1998) suggested a modification of this scheme based on ocean colour data and knowledge of the response of planktonic algae to physical forcing, that has 4 annular provinces extending from the Sub-Tropical Convergence (STC)

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separated by intervening frontal zones. The circumpolar W–E flow of the Antarctic Circumpolar Current (ACC) and the corresponding distribution of animals (Baker, 1954) tends to mean that community transitions are more apparent when travelling from N to S rather than E to W. More recently the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) concluded that a primary regionalisation of the Southern Ocean comprising 14 sub-units could be achieved using just 4 properties namely, surface temperature, water depth, silicate and nitrate (Grant et al., 2006; SC-CAMLR-XXVI, 2007/para 3.44). These sub-units were again largely annular, reflecting current flow of the water masses involved, particularly the ACC and physical discontinuities within it. By incorporating two additional datasets, sea-ice duration and remotely sensed surface chlorophyll, the number of sub-units was increased to 40 (Grant et al., 2006). However all of the variables used for these various bioregionalisations were selected because of the availability of circumpolar data rather than *a priori* knowledge that they structure ecosystems. The contrasting zonations they produce are thus heavily dependent on the input data used. Grant et al. (2006) also concluded that further work to refine the primary regionalisation should focus on the inclusion of biological data, particularly at regional scales.

Foodwebs are not measurable using satellites alone and ship-based studies are therefore an essential and complementary part of the inclusion of biological data in such ecosystem partitioning. The question of how biological data can be used to enhance what are essentially physical regionalisations, was the focus of a second workshop organised by CCAMLR in 2007 (SC-CAMLR-XXVI, 2007/Annex 9, para 97). Among the methods used to extrapolate often sparse point biological data to the circumpolar domain were various modelling approaches such as boosted regression tree analysis, (Pinkerton et al., 2010) generalised dissimilarity modelling (GDM) (Koubbi et al., 2011) and species habitat modelling. Potential problems associated with these approaches include sparse data availability, sampling bias and extrapolation outside of the range of the data both in geographic and environmental space. Here we used a classification method, clustering physical data and point biological samples to test how well the physically derived clusters distinguished between different biological properties in this synthesis of seasonal food web structure across the Scotia Sea. We have investigated the utility of physically based partitions by assessing how various classes of biota, ranging from phytoplankton to mesopelagic fish, were distributed across the region on a seasonal basis and whether patterns evident at the base of the food-chain could be traced through to higher trophic levels.

1.2. The Scotia Sea

The Scotia Sea is one of the better studied parts of the Southern Ocean and was the focus of the *Discovery Investigations* in the early and mid part of the 20th century (Kemp, 1929) as well as subsequent international expeditions and surveys (e.g. BIOMASS, El-Sayed, 1994; CCAMLR, 2000, Watkins et al., 2004). Its food-web structure has recently been reviewed by Murphy et al. (2007), although largely from a krill centred perspective. It lies downstream of Drake Passage in the Atlantic sector of the Southern Ocean, is some 750 km wide and is bounded on 3 sides by the Scotia Arc (Fig. 1) Seasonal sea-ice of variable extent covers the southern part during winter.

The Scotia Sea is a dynamic region, where following constriction at Drake Passage, mixing and overturning associated with interactions with bathymetry and wind stress significantly affects the circumpolar flow (Naveira Garabato et al., 2004). Embedded within it lie the Southern Antarctic Circumpolar Current Front

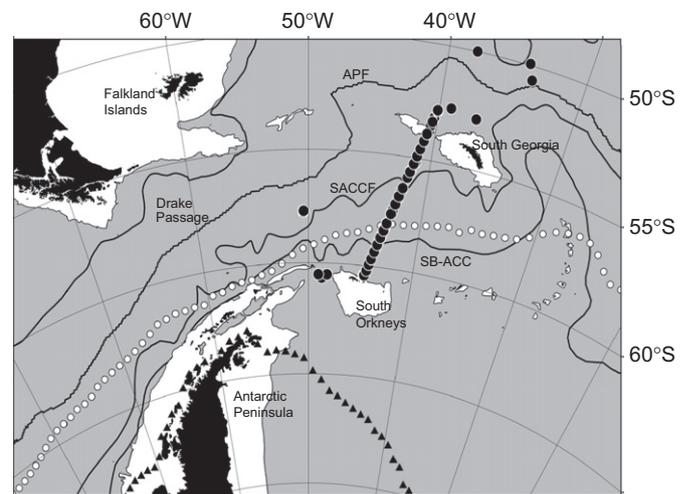


Fig. 1. The Scotia Sea showing the position of the transect along which the majority of stations were sampled during Oct–Nov 2006, Jan–Feb 2008 and March–April 2009. Also shown are mean positions of frontal zones, from north to south APF=Antarctic Polar front, SACCF=Southern Antarctic Circumpolar Current Front and SB-ACC=Southern Boundary of the ACC. Winter (August) and Summer (February) extent of ice edge (15%) shown as open circles and solid triangles, respectively.

(SACCF) and the Southern Boundary of the ACC (SB-ACC) (Brandon et al., 2004; Orsi et al., 1995). The former passes through the Scotia Sea before looping north-westwards around South Georgia, whereas the latter lies to the south and exits the Scotia Sea around the South Sandwich Islands.

Compared to the rest of the ACC the Scotia Sea is a region of high biological production which is generally associated with the interaction of the Antarctic Circumpolar Current (ACC) with bottom topography, particularly the shallow shelf regions of the Scotia Arc. This contrasts with the High Nutrient Low Chlorophyll (HNLC) conditions in the central Drake Passage, where waters from the deep basin of the land-remote SE Pacific enter the Scotia Sea (Whitehouse et al., 2012; Ardelan et al., 2010; Korb and Whitehouse, 2004; Korb et al., 2010; Park et al., 2010). Physical mixing and upwelling, typically in shelf regions, promotes the supply of limiting nutrients, particularly iron, to surface waters, which in turn stimulates phytoplankton production (Blain et al., 2007; Korb et al., 2008; Pollard et al., 2009). Marginal islands hold large concentrations of land based marine predators (Murphy et al., 2007) which are augmented by whale stocks in summer (Reilly et al., 2004) and which exist alongside commercial fisheries (Agnew, 2004). The significance of this region within the Southern Ocean can be gauged from the observations that phytoplankton biomass is much greater in the Scotia Sea and APF region between 10° and 60°W than in other pelagic Antarctic waters (Holm Hansen et al., 2004) and that the Atlantic sector of the Southern Ocean from 0° to 90°W, encompassing the Scotia Sea, contains 70% of the total Southern Ocean krill stock (Atkinson et al., 2004, 2008).

2. Methods

2.1. Scope of the analysis

The data used in this study were all collected during 3 cruises to the Scotia Sea during austral spring 2006 (Cruise JR161, October–December) summer 2008 (Cruise JR177, January–February) and autumn 2009 (Cruise JR200, March–April). The main sampling effort was focussed on a series of stations spaced along a transect ~1000 km long, running north-eastwards from close to the

South Orkneys to the north of South Georgia (Fig. 1). Additional sampling at the Polar Front also took place at various locations during spring and autumn cruises. Station positions are given in Table 1 and figured in Tarling et al. (2012a). Data collected ranged from nutrient concentrations and microplankton cell counts made on samples collected at a series of closely spaced stations during the summer and autumn cruises, to mesozooplankton, macroplankton,

fish and acoustic data collected at more widely spaced stations during all 3 cruises. With the exception of the macrozooplankton and acoustic data, whose treatment and analysis we detail below, all other data were analysed according to methods provided in papers in this volume; physical oceanographic data (Venables et al., 2012), nutrients (Whitehouse et al., 2012), phytoplankton (Korb et al., 2012), mesozooplankton (Ward et al., 2012), fish (Collins et al.,

Table 1

Positions of stations occupied during the spring, summer and autumn cruises. Asterisks indicate stations where different types of data (columns) were collected.

Stations	Latitude (S)	Long (W)	Physics	Phytoplankton	Mesozooplankton	Macrozooplankton	Fish	Acoustics
Spring (JR161)								
Sp1	–57.742	–50.4381			*	*	*	*
Sp2	–60.649	–48.6975			*	*	*	*
Sp3.4	–60.42	–44.6697			*	*	*	*
Sp4	–59.676	–44.0499			*	*	*	*
Sp5.3	–57.438	–42.6173			*	*	*	*
Sp7	–55.206	–41.2462			*	*	*	*
Sp8	–52.858	–40.0974			*	*	*	*
Sp10	–49.999	–38.0007			*	*	*	*
Summer (JR177)								
Su1	–57.685	–50.4423	*	*				
Su2.1	–60.498	–48.1924		*	*	*	*	*
Su3.4	–60.431	–44.5927	*	*				
Su3.5	–60.208	–44.4077	*	*	*	*	*	*
Su3.6	–59.936	–44.239		*				
Su4	–59.688	–44.0544	*	*	*	*	*	*
Su4.2	–59.144	–43.6935		*				
Su4.4	–58.872	–43.5094		*				
Su4.6	–58.598	–43.3309	*	*				
Su4.8	–58.278	–43.141		*				
Su5	–58.023	–42.9843	*	*	*	*	*	*
Su5.3	–57.437	–42.6104		*				
Su6	–57.139	–42.4329	*	*	*			*
Su6.1	–56.843	–42.2566		*				
Su6.2	–56.521	–42.0717		*				
Su6.3	–55.902	–41.7195	*	*				
Su6.4	–55.58	–41.5343		*				
Su7	–55.206	–41.2465	*	*	*	*	*	*
Su7.1	–54.913	–41.1732		*				
Su7.2	–54.591	–40.9966	*	*				
Su7.3	–54.216	–40.813		*				
Su7.4	–53.897	–40.6444		*				
Su7.5	–53.526	–40.4588		*				
Su7.7	–53.155	–40.2755		*				
Su8	–52.858	–40.0971	*	*	*	*	*	*
Su9	–52.626	–39.1148	*		*	*	*	*
Autumn (JR200)								
Au1	–57.69	–50.43				*	*	
Au2.2	–60.5	–49.04			*			*
Au3.4	–60.431	–44.5931	*	*				
Au3.5	–60.209	–44.4085	*	*	*	*	*	*
Au3.6	–59.935	–44.2368		*				
Au4	–59.689	–44.055	*	*	*	*	*	*
Au4.1	–59.356	–43.8365		*				
Au4.3	–59.025	–43.6211	*	*				
Au4.5	–58.694	–43.4042	*	*				
Au4.7	–58.362	–43.1889		*				
Au5	–58.031	–42.9713	*	*	*	*	*	*
Au5.2	–57.585	–42.7023	*	*				
Au6	–57.14	–42.4337		*				
Au6.1	–56.763	–42.2188		*	*	*	*	*
Au6.2	–56.388	–42.0009	*	*				
Au6.4	–55.634	–41.5711	*	*				
Au7	–55.259	–41.3576	*	*	*	*	*	*
Au7.1	–54.912	–41.1741		*				
Au7.2	–54.59	–40.9962		*				
Au7.3	–54.22	–40.8133		*				
Au7.4	–53.897	–40.6441		*				
Au7.6	–53.351	–40.3743		*				
Au8	–52.808	–40.1145	*	*	*	*	*	*
Au9.1	–52.85	–37.1	*		*			*
Au10.2	–49.936	–34.2078			*	*	*	
Au10.6	–50.599	–33.8017			*	*	*	

2012) and acoustics (Fielding et al., 2012). Whilst phytoplankton and mesozooplankton data collected during the 3 cruises are freely summarised below the reader is referred to the primary sources (see references above) for a fuller discussion of specific distribution patterns. Data were analysed using the PRIMER 6 statistical package (Primer-E-Ltd) (Clarke and Gorley, 2006).

2.2. Physical regionalisation

To undertake a physical regionalisation of the Scotia Sea we employed methods outlined in Grant et al. (2006) used in their primary regionalisation of the Southern Ocean. Accordingly, data on silicate and nitrate concentrations from the winter water level (200 m), Sea Surface Temperature (SST) and log water depth from ~12 to 13 stations along the transects during the summer and autumn cruises respectively were normalised. A resemblance matrix was created using the Manhattan distance metric before stations were clustered.

2.3. Macrozooplankton and fish

The RMT 25 is a mid-water trawl with a nominal mouth area of 25 m² and a variable mesh size, 18 mm reducing to 5 mm towards the cod-end. Only night time standard (un-targeted) hauls have been used here, in accordance with Collins et al. (2012). Nominal depth horizons fished were 1000–700 m, 700–400 m, 400–200 m and 200–0 m. RMT 25 catches of macroplankton and fish at each station were pooled to provide a picture of community structure over the whole sampled water column (0–1000 m). At each station the total combined average time for all nets to fish from 1000 m to the surface was 166 ± 16 min. For convenience we have standardised net catches across all cruises to 150 min, i.e. equivalent to 15 min per 100 m depth horizon and not attempted to determine volume swept. This is because of uncertainty regarding the mouth area of the net (nominally 25 m²) presented to the water when it is being hauled. A square root transformation was applied to the fish data before clustering. For the macrozooplankton we selected only those taxa that represented at least 1% of the total abundance to reduce the number and influence of rare species and then applied a stronger double root transformation. Data were subjected to q-type cluster analysis based on the Bray–Curtis similarity and group average linkage classification (Field et al., 1982).

2.4. Acoustic data

Calibrated Volume Backscattering Strength (S_v , dB re 1 m) data were collected at three frequencies (38, 120 and 200 kHz) in a 50 km transect passing through each station in each cruise (Fielding et al., 2012). All acoustic data were processed using EchoviewTM software (ver. 4.20): relevant values for the speed of sound and absorption coefficients were input (derived from station CTD data); surface noise and false bottom echoes were identified and removed; likewise any interference spikes from unsynchronised instruments (using a 3 × 3 matrix convolution algorithm); and time varied gain amplified background noise was subtracted (Watkins and Brierley, 1996). Cleaned data for each frequency were averaged into 5 m (vertical) by 500 m (horizontal) integration cells and imported into MatlabTM where all further manipulation or analysis was undertaken.

The dB difference between two frequencies has been used to distinguish acoustic backscatter between different species of fish and zooplankton (Brierley et al., 1998; Kang et al., 2002; Logerwell and Wilson, 2004; Madureira et al., 1993; McKelvey and Wilson, 2006). Here we apportioned the S_v at 120 kHz ($S_{v120\text{ kHz}}$) to three different general categories based on the dB

120–38 kHz difference ($S_{v120-38}$): where $S_{v120-38}$ between –10 and 2 dB were classified as fish, $S_{v120-38}$ between 2 and 16 dB were classified as macrozooplankton and an $S_{v120-38}$ above 16 were classified as zooplankton (Fielding et al., 2012). These groups were chosen to separate Antarctic krill, the likely dominant scatterer in the Scotia Sea, identified here as macrozooplankton (after Hewitt et al., 2004), from the other common targets such as the myctophid fish *Electrona carlsbergi* (which has a resonating swim bladder) and the smaller zooplankton such as the large copepod *Rhincalanus gigas*. The $S_{v120\text{ kHz}}$ attributable to each group were integrated from 10 m below the surface to either a maximum of 500 m or 2 m above the seabed, resulting in Nautical Area Scattering Coefficient (NASC; m² nautical mile⁻²) values which are used here to describe acoustic biomass. Backscatter data as categorised above were input into a station by backscatter category matrix, standardised and then subjected to q type cluster analysis based on the Bray–Curtis similarity and group average linkage classification (Field et al., 1982).

2.5. Carbon estimation

We have estimated C present in each major planktonic group using published body size to weight algorithms. Estimates of body size were either extracted from the literature or measured directly (see Table A1 Ward et al., 2012). Biomasses are presented as g C m⁻² within the sampled water column. Thus chlorophyll (Chl *a*) has been estimated over the average euphotic zone depth (Korb et al., 2012) and then converted to C using a C:Chl a ratio of 50. Mesozooplankton were integrated from 0–400 m (Ward et al., 2012), macrozooplankton 0–1000 m, and krill biomass 0–500 m (Fielding et al., 2012) and fish 0–1000 m (Collins et al., 2012).

3. Results

3.1. Physics

The positions of the SB and the SACCF were determined after Orsi et al. (1995) and by locating frontal positions in relation to sea-surface dynamic height corresponding to frontal positions determined from Argo float profiles (Venables et al., 2012).

The results of clustering physical and inorganic nutrient data from summer and autumn cruises are shown in Fig. 2. Similar data are lacking for the spring cruise (JR161) as station spacing was coarse by comparison. During both cruises the data fell into two clear groups situated north and south of the SACCF. The SST gradient along transect in both summer and autumn ranged from ~0 to 5 °C and did not appear sharply discontinuous although there was a step change in silicate concentration from 200 m (but not nitrate) associated with the SACCF.

3.2. Phytoplankton cell counts

Data used here were drawn from summer (24 stations) and autumn (21 stations) cruises. Only 5 stations were sampled across the entire transect during spring, which we considered to be too few to adequately define regions. Despite variability in chlorophyll and cell count data (species and biomass) between seasons and across years there were nonetheless similarities between clusters of cell count data from summer and autumn cruises (Korb et al., 2012). Geographically coherent groups of stations were identified during both cruises which comprised those close to the southern end of transect (SOUTH) and a group occupying the region between the SB and the SACCF (MID). Further north a group of stations lay to the south of the Scotia ridge (SW-SG) and a few stations to the north in the Georgia Basin (NW-SG)

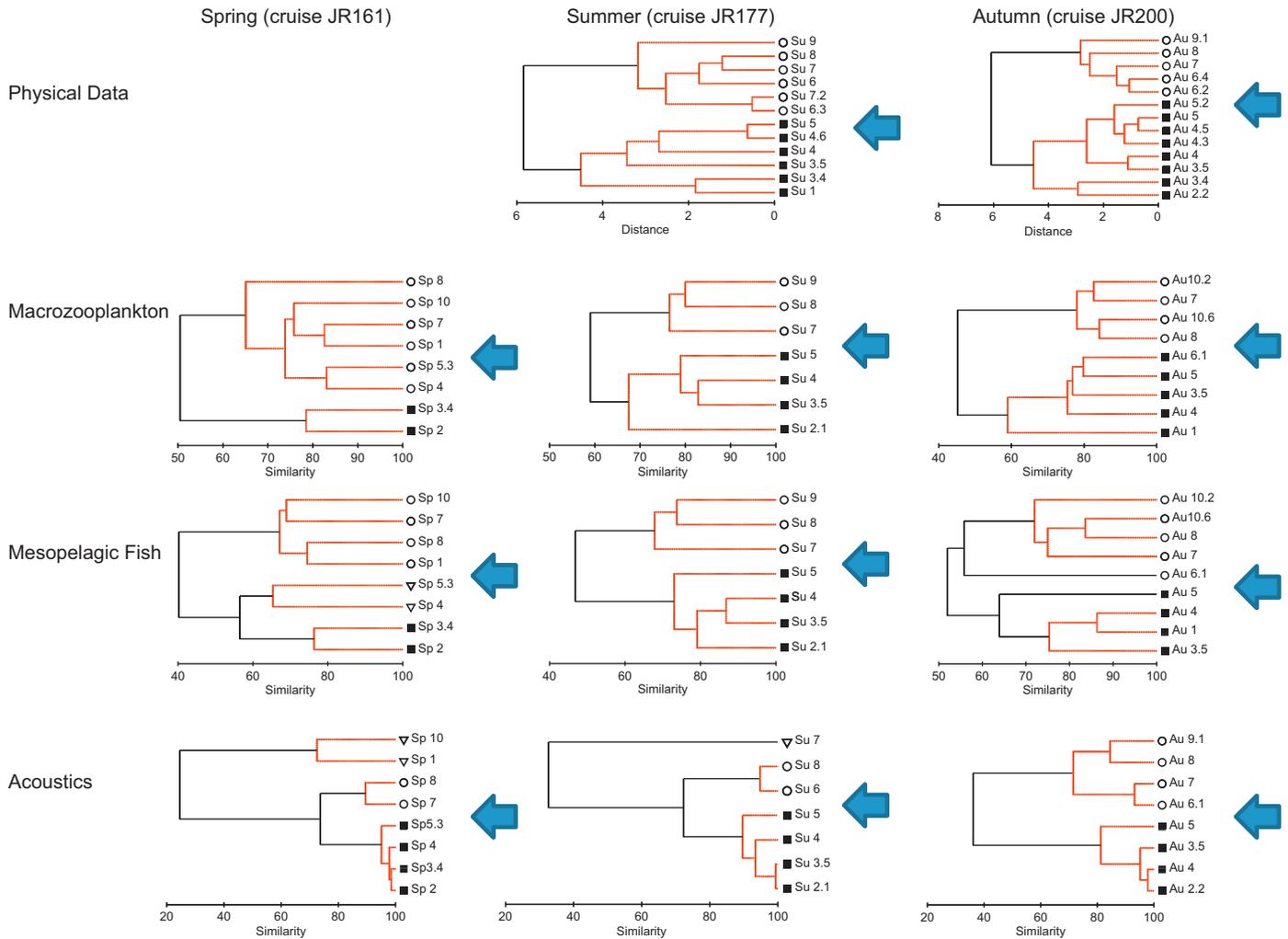


Fig. 2. Results of clustering analysis by season performed on Physical data (silicate and nitrate concentrations from the winter water level (200 m), SST and log water depth), Macrozooplankton data obtained with an RMT25 net from night-time stratified hauls to 1000 m. Mesopelagic fish data obtained with an RMT25 net from night-time stratified hauls to 1000 m. Acoustic data (see text). For the physical data a resemblance matrix was created using the Manhattan distance metric before stations were clustered. In all other cases q-type cluster analysis based on the Bray–Curtis similarity and group average linkage classification was used (Field et al., 1982). Black filled squares = Southern Station Group. Open circles = Northern Station Group. Open triangles = intermediate group. Arrow against each cluster diagram indicates the position of SACCF. The SIMPROF routine was used to look for statistically significant evidence of genuine clusters among stations (linked by red lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Classification of stations by cruises for the phytoplankton cell count data (Korb et al., 2012) and the mesozooplankton data (Ward et al., 2012).

	Station Grouping	Spring	Summer	Autumn
Phytoplankton cell counts (Korb et al., 2012)	SOUTH	Sp 3.4, Sp4	Su 3.5, Su 3.4, Su 3.6, Su 4, Su 4.2, Su 4.4	Au 3.4, Au 3.5, Au 3.6 Au 4, Au 4.2, Au 4.4
	MID	Sp 5.3	Su 4.6, Su 4.8, Su 5, Su 5.1, Su 5.3, Su 6, Su 6.1, Su 6.2	Au 4.5, Au 4.7, Au 5, Au 5.2
	SW-SG	Sp 7	Su 6.3, Su 6.4, Su 7, Su 7.1, Su 7.2, Su 7.3, Su 7.4, Su 7.5	Au 6, Au 6.1, Au 6.2, Au 6.4, Au 7, Au 7.1, Au 7.2, Au 7.3, Au 8
	NW-SG	Sp 8	Su 7.7, Su 8	Au 7.4 ^a , Au 7.6 ^a , Au 8 ^a
Mesozooplankton (Ward et al., 2012)	Southern station group	Sp 2, Sp 3.4, Sp 4	Su 2.1, Su 3.5, Su 4, Su 5	Au 2.2, Au 3.5, Au 4, Au 5
	Northern station group	Sp 1, Sp 5.3, Sp 7, Sp 8, Sp 10	Su 7, Su 8, Su 9	Au 7, Au 8, Au 9.1, Au 10.2, Au 10.6
	Intermediate station group	–	Su 6	Au 6.1

For mesozooplankton data all groups contain 100 µm and 200 µm net samples.

^a Outlying stations which were nonetheless geographically coherent.

(see Table 2 for stations included within groups). Boundaries between groups varied between years and were not entirely consistent with frontal positions (Korb et al., 2012). During

summer the northern boundary of the SOUTH group lay south of the SB and the southern edge of the SW-SG lay north of the SACCF thus the MID group straddled the region between the two

fronts. In autumn (JR200) the boundaries appear coincident with the frontal zones.

In summer the SOUTH grouping was dominated by diatoms although also characterised by the presence of cryptophytes thought to be indicative of a receding ice-edge. The MID zone contained significant proportions of dinoflagellates, whereas diatoms were dominant in the SW-SG and NW-SG groups. In autumn increases in dinoflagellates were seen across all groups and dominant diatom species were different between MID and SWSG (Korb et al., 2012).

3.3. Mesozooplankton

Ward et al. (2012) have described the presence of 2 main zooplankton assemblages occupying the southern and northern parts of the Scotia Sea, respectively, during all 3 cruises (see Table 2 for stations included in groups). Whilst these groupings do not represent distinct communities and are each characterised by many of the same species, they differed greatly in overall abundance and in the case of the copepods *Calanoides acutus* and *R. gigas* age (i.e. stage) structure, irrespective of season. Station spacing was relatively coarse but the northern limit of the southern group appears to be broadly coincident with, or north of, the SB-ACC and the southern edge of the northern group lay between the SB-ACC and the SACCF. Stations Su 6 and Au 6.1, sampled only during summer and autumn, appeared intermediate in character between the northern and southern assemblages and lay within the SACCF (Venables et al., 2012). Ward et al. (2012) suggest that this might be representative of an intermediate zone akin to the 'MID' grouping of stations seen in the analysis by Korb et al. (2012). Both major assemblages were dominated by small organisms with *Oithona similis* and cyclopoid nauplii (mostly *Oithona* spp.) being most abundant along with *Oncaea* spp. and *Microcalanus pygmaeus* sub-dominant in the southern assemblage and *Ctenocalanus citer* and appendicularians in the northern assemblage.

3.4. Macrozooplankton

During spring, stations Sp 2 and Sp 3.4 formed a separate grouping to the south that was characterised by euphausiids (*Euphausia superba* and *Thysanoessa* spp.), siphonophores (*Diphyes* spp.) and the medusoid *Calyropsis* spp. (Fig. 2). Remaining stations to the north were characterised by *Euphausia triacantha* and salps (predominantly *Salpa thompsoni*). During summer, stations Su 2.1–Su 5 formed the southerly grouping and Su 7–Su 9 the northern group; differences between the two being driven by higher abundances of krill in the southern group and the amphipod *Themisto gaudichaudii* and *E. triacantha* in the northern group. During autumn the southern group extended up to and included station Au 6.1 and the more northerly group included the Polar Front stations in addition to those nearer to South Georgia (Fig. 2). High abundances of salps (66% of within group similarity) strongly characterised the southern group during this cruise and *E. triacantha* and *T. gaudichaudii* among others, the northern group.

There were high densities of *E. superba*, *E. triacantha*, *Thysanoessa* spp., salps and the amphipod *T. gaudichaudii* seen at some stations during all 3 cruises. We therefore investigated whether it was these taxa that were driving/shaping the overall community structure by removing them from the data matrix and re-running the analysis. There was no change at all in station affiliation to group during spring and summer but a minor one during autumn, with Au 6.1 changing its affiliation from Group 1 to Group 2. Running the analysis with only the excluded taxa also generally preserved the affiliations of stations to groups although some became divorced from their original grouping because of high

abundances of one or other taxa exerting undue influence on a very restricted group of taxonomic variables. Differences between groups were generally preserved because of higher abundances of *E. superba* in the southern Scotia Sea (except autumn when they were more evenly distributed) and of *T. gaudichaudii* and *E. triacantha* in the north. Salps were particularly abundant to the south during autumn. The separation of groups was therefore underpinned both by the predominantly mesopelagic taxa from the deeper depth horizons and also by organisms that are generally more epipelagic in distribution and in some cases form swarms (Everson and Ward, 1980).

Abundances of taxa within groups and cruises are shown in Table 3 where to ease presentation we have pooled species within lower taxonomic groupings. The large net mesh on the RMT 25 almost certainly does not retain large numbers of many smaller taxa which pass through it but nonetheless, should be consistent across cruises. During spring, median values of all taxa totalled within station groups were essentially equal but higher in the northern group during summer and autumn cruises. Siphonophores and *E. superba* were generally more abundant in the southern group while many other taxa, for example Amphipoda, Mysidacea and Decapoda in addition to *E. triacantha*, *Thysanoessa* spp. and the swarm forming *T. gaudichaudii*, were consistently more abundant in the north.

3.5. Fish

Our analysis of the fish fauna differed somewhat from Collins et al., (2012) insofar as they used depth horizon as the key factor in their analysis and we by contrast pooled data from surface to 1000 m and also used season. Stations Sp 2 and Sp 3.4 separated out from Sp 4 and Sp 5.3 within the southern group during spring and Au 5 and Au 6.1, both lying close to, or within the SACCF, from their nearest neighbours in autumn (Fig. 2). Many species were

Table 3

Macroplankton groups from the RMT25. Median densities (ind. per 150 min haul) of taxa pooled across nets. Generally one haul in each of the following depth horizons (1000–700 m, 700–400 m and 400–10 m) was carried out per station and data standardised to represent densities per 150 min haul from 0–1000 m. n=no. stations per Group.

	Spring		Summer		Autumn	
	Gp1 (n=2)	Gp2 (n=6)	Gp1 (n=4)	Gp2 (n=3)	Gp1 (n=5)	Gp2 (n=4)
Hydromedusae	67	97.1	60.1	89	44.4	126.2
Siphonophora	231.6	22.8	65.1	14	26.6	42.9
Ctenophora	0	0	0	0	0	0
Amphipoda	40.9	66.8	23.3	109.4	17.6	131.4
Chaetognatha	48.6	74.4	88.3	246.8	2	140.2
Ostracoda	0.5	17.9	0.8	11.3	2.6	21.4
Mysidacea	1.9	63.4	8.3	81.5	13.7	35.8
Decapoda	1	6.5	10	16.9	5.3	25
Polychaeta	1	1	5.4	186.3	0	3.8
Pteropoda	2.5	8.3	1.3	8.1	1	10.6
Cephalopoda	2.2	8.3	7.1	5.6	2	14.5
Others	0	2.6	0	0.8	0	2.5
Total*	397	420.3	269.3	887.2	131.4	589.3
<i>Salpa thompsoni</i>	1	84.4	102.5	467.7	12629	75.4
<i>E. superba</i>	669	46	8891	77.4	22.2	8.1
<i>E. triacantha</i>	0	226	45.3	970	41	1653
<i>Thysanoessa</i> spp.	515	78	28.6	450	5.9	40
Euphausiids (other)	0	9.2	0.9	267	1.9	181
<i>Themisto gaudichaudii</i>	21	20.5	0.4	423.6	0.9	1735.9

Total* is the total of taxa excluding salps, euphausiids and the amphipod, *Themisto gaudichaudii*, which are detailed separately.

widely distributed within the Scotia Sea but those typically found within the northern assemblage included *Krefflichthys anderssoni*, *Gymnoscopelus fraseri*, *Protomyctophum bolini* and *E. carlsbergi* and in the southern assemblage *Electrona antarctica* and *Bathylagus* sp. were dominant.

3.6. Acoustic data

Some clear and consistent patterns emerged following clustering of the acoustic data (Fig. 2). Macrozooplankton (krill) were overall the dominant acoustic category at 120 kHz across all stations and cruises whereas small zooplankton contributed least (Fielding et al., 2012). The southernmost stations of all 3 cruises were characterised by the dominant presence of macrozooplankton (krill) and very little else. At northern stations signature backscattering categories were more diverse and evenly divided between macrozooplankton and fish. A third grouping comprising stations Sp 1 and Sp 10 was observed during spring. Although stations were only distantly related both were dominated by fish. Station Su 7 in summer was characterised by acoustic backscatter from fish which distinguished it from Su 6 and Su 8 where macrozooplankton dominated, although not as much as in the southern groups. Across the Scotia Sea krill biomass was similar in spring (weighted mean and (SD)=27.66 (49.68) gm^{-2}) and summer (27.17 (21.14) gm^{-2}) but significantly lower (2.24 (1.35) gm^{-2}) in autumn 2009 (Fielding et al., 2012).

3.7. Carbon estimates within groups

The amount of carbon within each major pelagic taxonomic group has also been estimated for each of the season and station groupings, and is presented in Fig. 3. Phytoplankton carbon averaged around 2–4 g C m^{-2} within the euphotic zone during spring and summer but fell below this in autumn. Differences between station groups were broadly consistent with the findings of Whitehouse et al. (2012) who used SeaWiFS climatologies to establish that the region NW of South Georgia generated approximately 1.5 times higher Chl *a* biomass than other regions defined along the transect. The consistently higher mesozooplankton C in Group 2 contrasts with that of krill C which is considerably less in all seasons within this group but is higher than mesozooplankton C within Group 1 during spring and summer. In autumn krill biomass was uniformly low across the Scotia Sea. Macrozooplankton C (less krill) was low within both station groups across all seasons but probably reflects the coarse mesh of the RMT25 and fish biomass was also uniformly low within both groups across all 3 seasons.

4. Discussion

4.1. Physical regionalisation

Our physical regionalisation of the Scotia Sea using nutrient, temperature and depth data clearly distinguished 2 groups of stations which separated along the line of the SACCF, replicating the circumpolar-scale findings of Grant et al. (2006). There was a clear gradient in SST across the Scotia Sea from close to 0 °C at the southernmost stations in spring, which were influenced by the retreating winter ice-edge, to almost 8 °C at the APF. At the SACCF a temperature change of > 1 °C occurs at 200–300 m in the Upper Circumpolar Deep Water (UCDW) over a relatively short distance, although during our 3 cruises SST profiles alone could not locate the SACCF. Step changes in silicate concentration at the winter water level of 200 m during cruises JR177 and JR200, were also coincident with its position located both by temperature gradient

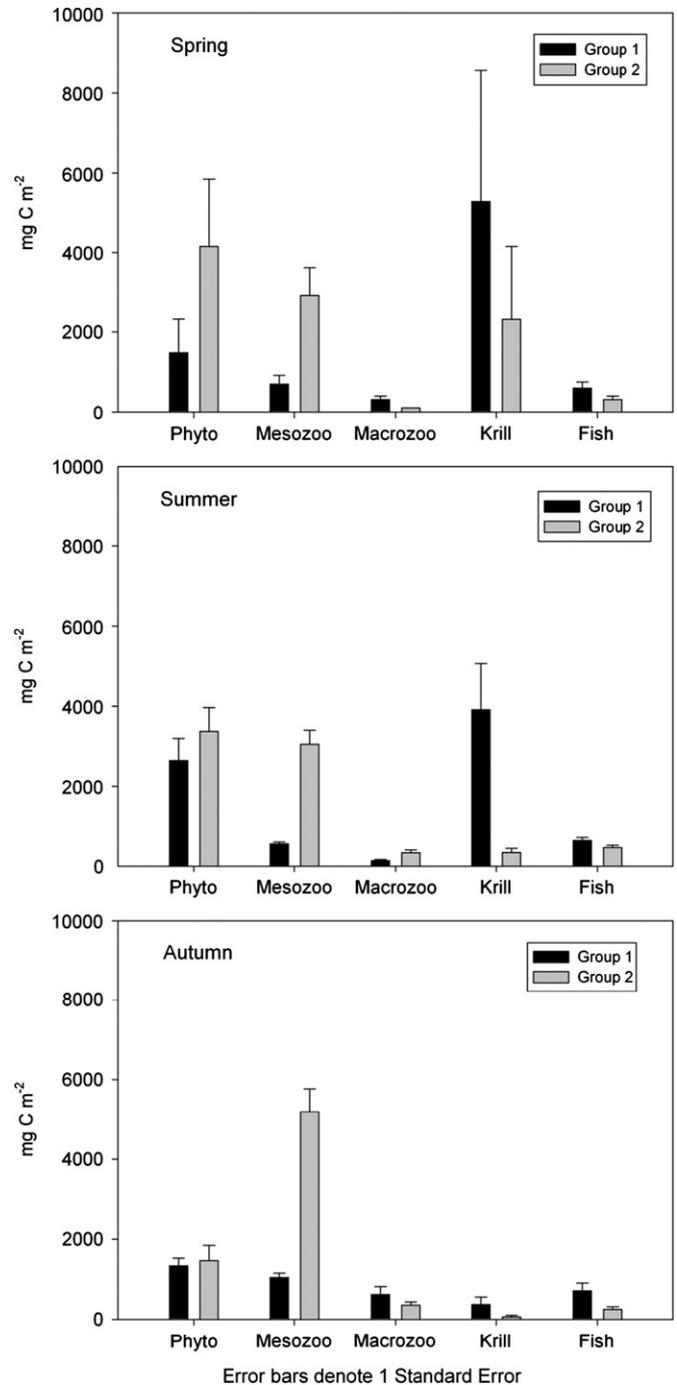


Fig. 3. Mean (SE) Carbon mass (mg C m^{-2}) within phytoplankton, mesozooplankton, macrozooplankton, krill and mesopelagic fish groupings with respect to season and station group. Phytoplankton was integrated over the euphotic zone (Korb et al., 2012), mesozooplankton (0–400 m), macrozooplankton (0–1000 m), krill (0–500 m) and fish (0–1000 m). Phytoplankton carbon was estimated using a C:Chl *a* ratio of 50, mesozooplankton (see Ward et al., 2012), macroplankton, krill and fish (Omori, 1969; Clarke et al., 1985, 1992). Fish and macrozooplankton densities were determined on the assumption that the full mouth area of the RMT25 (25 m^2) was fishing throughout. This is in contrast to the approach used for cluster analysis where time was used to average catches over depth horizons (Table 2). Macrozooplankton densities are probably conservative as the mesh in the front part of the RMT25 net is relatively coarse (see methods).

in the UCDW below the mixed layer (Boehme et al., 2008; Heywood et al., 1999; Orsi et al., 1995) and by use of dynamic height measurements (Venables et al., 2012).

4.2. Community structure within the ACC

We now consider the extent to which the biological data reflects this physical regionalisation. To assist in this, station group designations derived from the clustering analysis of the major taxonomic groups have been superimposed on a plot of dynamic sea surface height (Fig. 4) used by Venables et al. (2012) to define frontal regions during the 3 cruises. Despite sampling across different seasons and years at different spatial scales and taxonomic resolutions, fundamentally similar biotic distribution patterns emerged across a wide range of taxa which were consistent with partitioning using the 4 physical/chemical indices. The envelope occupied by the SACCF was a region where different communities overlapped and this was particularly apparent in autumn, when a greater number of stations were located within the frontal envelope (Fig. 4). With few exceptions communities did not extend beyond the side of the envelope characterising their northern or southern limits. There were however instances of some northern communities penetrating to the south of the SACCF (macrozooplankton in spring) and southern communities to the north (phytoplankton in summer). In the mesozooplankton analysis a third grouping was noted in summer and autumn, characterised by single stations that were intermediate in position between the north and south groups and lay within the frontal envelope. Questions then arise as to whether similar patterns are seen elsewhere in the Southern Ocean and what the principal agents driving these differences in food-web structure in the northern and southern regions of the Scotia Sea might be.

We consider in turn some of these variables, although they will almost certainly be acting upon communities in a synergistic manner. First we examine the extent to which frontal discontinuities across the Scotia Sea might potentially be acting to preserve the differences we see in species distributions and then consider in turn patterns of primary production, ice-cover and temperature.

4.3. Frontal zones

The rise in sea surface temperature from the Antarctic continent northwards is not uniform and the sharp changes in gradients that exist at some frontal zones often mark discontinuities in the distribution of phytoplankton and mesozooplankton (Burghart et al., 1999; Deacon, 1982; Errhif et al., 1997; Hosie et al., 2000; Hunt and Hosie, 2006; Pakhomov et al., 2000; Ward et al., 2003, 2004). Major fronts that are coincident with changes in species distributions appear to be the sub-Tropical Convergence which marks the southernmost distributional limits of many subtropical species (Bradford-Grieve, 1994, 1999), the SAF and APF (Pakhomov et al., 2000; Ward et al., 2003) and the Antarctic Divergence, a continuation of the Weddell front, which runs along the southern edge of the Scotia Sea and separates continental shelf and open ocean communities (Boysen-Ennen and Piatkowski, 1988; Deacon, 1982; Hosie et al., 2000; Longhurst, 1998; Ward et al., 2006).

By comparison the SACCF is not generally recognised elsewhere in the Southern Ocean as being coincident with significant faunal discontinuities. In a study by Koubbi et al. (2011) regions delineated by the SACCF and the SB-ACC were defined using a GDM approach to characterise distributions of myctophid fish species in the Indian Ocean sector. There is however little direct evidence that the SACCF constrains the movement of either krill or other zooplankton. Its surface signal is generally weak and is not visible in satellite SST images. Density changes and corresponding changes in nutrient levels, particularly silicate, are apparent where there are strong currents but overall the surface/mixed layer of the SACCF is unlikely to represent a significant faunal boundary. Neither is it likely to represent a barrier at depth, given the continuity of species distributions across the Scotia Sea (Atkinson and Sinclair, 2000; Mackintosh, 1936; Marin, 1987; Ward et al., 2004). In fact active transport across the front is suggested by Boehme et al. (2008) who have demonstrated that the mean monthly position of the SACCF in the Scotia Sea is quite

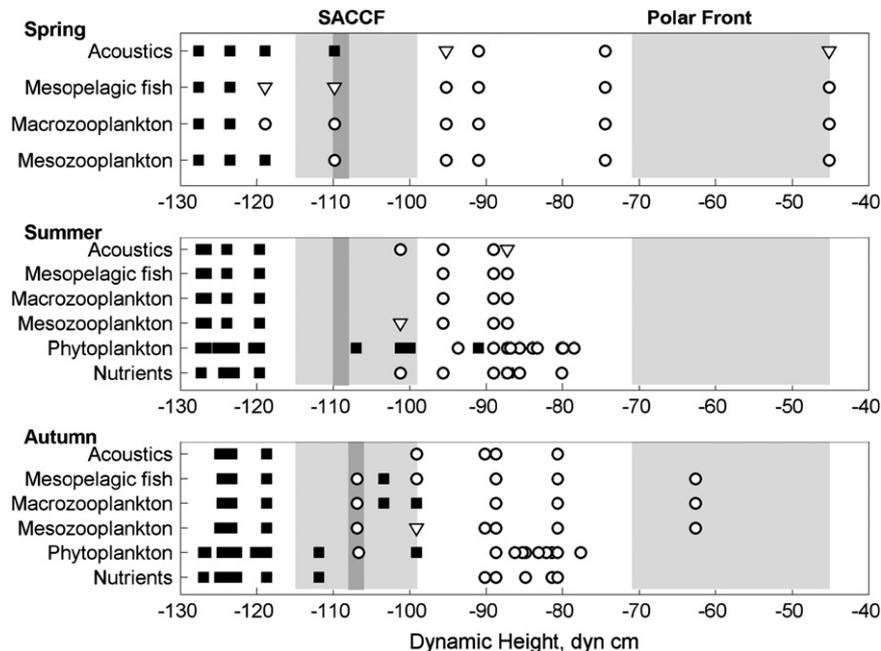


Fig. 4. Stations classified by station group as determined from cluster analyses performed on nutrients, phytoplankton, mesozooplankton, macrozooplankton, mesopelagic fish and acoustic datasets in relation to sea surface dynamic height measurements. The data are presented by cruise. Solid squares represent the Southern station group, open circles the Northern station group and inverted open triangles intermediate station group. The dynamic range (envelope) within which the SACCF and APF were found is indicated (light grey blocking) as is the position of the SACCF on each cruise as determined by temperature, depth and density characteristics (dark grey blocking) see Venables et al. (2012). For clarity the phytoplankton groups SOUTH and MID and SW-SG and NW-SG of Korb et al. (2012) were amalgamated as southern and northern groups respectively in line with the greatest dissimilarity seen in the cluster analyses (Korb et al., 2012).

variable with meandering and eddy fields observed near Elephant Island bringing cold water from south of the SB-ACC northwards. Conversely Meredith et al. (2003) observed eddies from north of the SACCF being transported to the south near South Georgia.

4.4. Other factors

Ward et al. (2012) have considered the likely influence of food, temperature and ice-cover on mesozooplankton distribution across the Scotia Sea. Here primary production is highly seasonal, spatially variable and overall is high relative to elsewhere in the Southern Ocean. Whilst food amounts, type and quality clearly influence zooplankton growth and reproduction (e.g. Ross et al., 2000; Schmidt et al., 2012; Shreeve et al., 2002; Ward et al., 2007) evidence that regional differences in Chl *a* biomass and phytoplankton production underpin the differences observed between regions is slight. Although primary production and phytoplankton biomass were up to 50% greater to the north of South Georgia compared to other regions along the transect, we think this insufficient to account for the 2–9 fold differences in abundance and biomass of taxa observed on either side of the SACCF (Ward et al., 2012). The spatial and temporal variation in food availability suggests it is of lesser importance in determining community patterns. Other taxonomic groups within the mesopelagic macroplankton and fish faunas, neither of which directly consume phytoplankton, also had similar spatial distributions across all 3 cruises, suggesting other factors were more important.

The effect of temperature on plankton distributions in the Southern Ocean was first considered by Mackintosh (1936) who determined temperature preferences for a range of macroplankton across the ACC. Many of those studied were found to have wide distributional ranges but others exhibited preferences for either warmer or colder water (see also Atkinson and Sinclair 2000; Mackey et al., 2012). Within the Southern Ocean plankton diversity also decreases as one moves from warmer to colder waters (Chiba et al., 2001; Mackey et al., 2012; Woodd-Walker et al., 2002), reflecting the fact that truly polar species are fewer in number and stenothermal. Fewer species will therefore almost certainly lead to lower overall abundances compared to further north, where diversity is higher and where there is a greater mix of warmer water and more widely distributed species. Habitat temperature has profound effects on species life-cycles and development rates. At low temperatures egg hatching times and stage durations increase (Hirst and Bunker, 2003; Shreeve et al., 2002; Ward and Shreeve, 1998) and consequently slower growing instars may be subject to higher mortality (Kiorboe and Hirst, 2008). A number of widespread and commonly occurring copepod species within the ACC, such as *C. acutus* and *R. gigas* have been found to have extended life cycles in the colder parts of their range (Atkinson et al., 1997; Marin, 1988; Ward et al., 1997) which means greater exposure to mortality and consequently lower abundances. Others like the sac spawning cyclopoid *Oithona similis*, which is much more abundant in the northern part of the ACC (Atkinson, 1998; Ward and Hirst, 2007) have reduced fecundity at low temperatures because of increased egg hatch times (Ward and Hirst, 2007). Elsewhere in the Southern Ocean Chiba et al. (2001) suggested that temperature was more important than Chl *a* in defining assemblages off east Antarctica. The abundances of the majority of a series of indicator species showed a positive relationship to temperature but not to Chl *a* (Chiba et al., 2001).

The southern part of the Scotia Sea is under the influence of seasonal ice cover which will affect production, particularly if ice persists in the region, and will exacerbate 'seasonal' differences between north and south. Ice-edge blooms resulting from water column stabilisation due to the receding ice-edge are however

unpredictable in their occurrence (Savidge et al., 1996). The northern boundary of the ice-edge in the Scotia Sea is broadly coincident with the SB-ACC at the point where it was crossed by the transect. The marginal ice-zone; the area where dilution effects from a receding ice edge are measurable, extends further beyond this.

It is logistically difficult to sample ice-covered areas and this is largely responsible for our lack of knowledge regarding the impact seasonal sea ice has on pelagic communities. Our understanding of its importance in the lifecycle and population dynamics of Antarctic krill (*E. superba*) is greater than for many other species (Brierley et al., 2002; Daly, 2004; Loeb et al., 1997; Mackintosh, 1972; Siegel et al., 2004) although recent studies are beginning to remedy this (Flores et al., 2009; Hopkins and Torres, 1989; Hopkins et al., 1993; Tanimura et al., 2008). Findings from a number of ice-edge studies parallel this one insofar as older overwintered copepod stages are often dominant in comparison to ice-free waters (Atkinson and Shreeve, 1995; Burghart et al., 1999; Ward et al., 2006; this study). The timing of ice retreat does therefore appear to influence the development and seasonal succession of zooplankton populations.

With our present state of knowledge regarding physiological limits and population controls on polar species it is unsurprising that we do not yet fully understand the interplay of factors that drive differences in assemblages and communities. However the similarities in distribution patterns across the Scotia Sea of a wide range of taxa, which are consistent across seasons, suggests that temperature, which, despite seasonal warming displays a persistent gradient across the ACC and seasonal sea-ice cover, are important.

4.5. Food web structure

Our study suggests strongly that there are differences in the spatial distribution of biota across the Scotia Sea and that it can be effectively partitioned into two main regions either side of the SACCF. Our data are mostly drawn from point samples along an oceanic transect whose geographical position undoubtedly influenced our findings. Had it occupied a different location, either west or east of its actual position, it is likely that we would have obtained different results for a number of taxonomic groups, particularly at the northern end where South Georgia has a significant influence on production processes. Nonetheless the quantitative and qualitative differences seen across a range of primary and secondary producers suggest functionally different foodwebs and although key organisms such as *E. superba* and salps can be common to both, they may undertake different ecological roles depending on where they are found.

We have summarised these observations in Fig. 5 and have also included a summary of the main higher predator species observed in each region during the 3 cruises (A. Black pers. comm.). Chl *a* concentration and size composition were found to be widely variable across both regions in all 3 seasons and qualitative differences in community composition were also seen (Korb et al., 2012; Whitehouse et al., 2012). Within the southernmost group of stations lying within the marginal ice-zone, diatoms were more common in spring and autumn than summer, although overall, dinoflagellates were dominant or co-dominant across all seasons. Within the region encompassing the SACCF an intense spring bloom was observed which it was suggested was sustained by iron rich waters from the vicinity of the Antarctic Peninsula (Whitehouse et al., 2012). Korb et al. (2012) speculated that it was likely that much of the production in the southern part of the Scotia Sea was recycled rather than exported. At lower latitudes the region to the south of South Georgia was largely unproductive although short blooms did occur, whereas to the

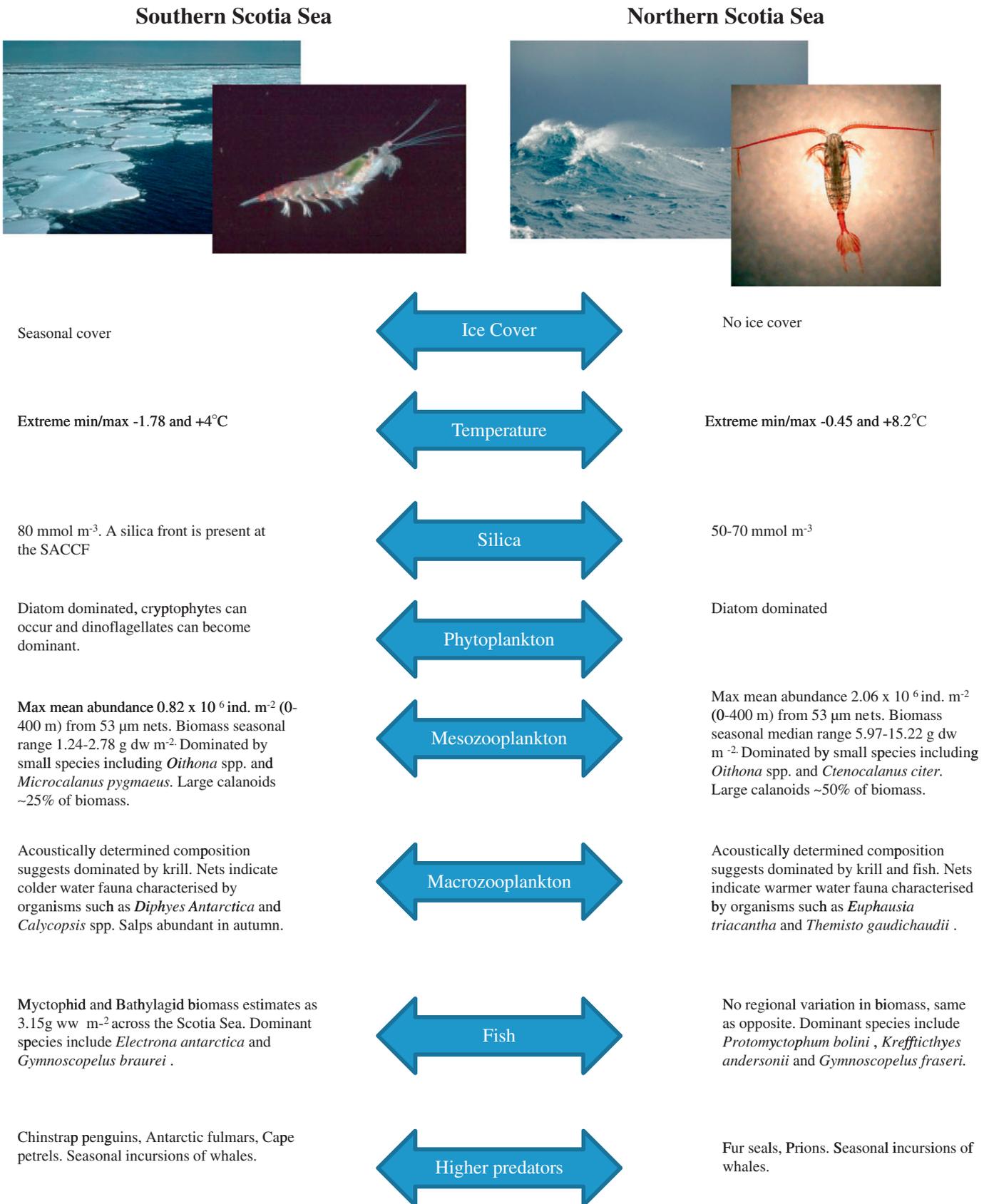


Fig. 5. A summary of the major physical and food-web characteristics in the southern and northern regions of the Scotia Sea as disclosed by this analysis.

north of South Georgia, an iron replete system was consistently the most productive feature of the region (Korb et al., 2012; Whitehouse et al., 2012). Export of carbon was low south of South Georgia, compared to ~10 fold higher values to the north where blooms can be long lasting and intense (Whitehouse et al., 2012).

Consideration of all groups and species is well beyond the scope of this study; for example we have not investigated the dynamics of the microbial web, members of which are significant grazers of phytoplankton (Smetacek et al., 2004). Conversely mesozooplankton (essentially copepods) are not generally thought to be significant grazers of phytoplankton in the Southern Ocean, particularly where blooms occur (Atkinson, 1996; Dubischar and Bathmann, 1997; Zeldis, 2001). However higher copepod abundances found in the northern Scotia Sea may be important in recycling and re-supplying nutrients such as ammonium (Atkinson et al., 2001), as well as forming a resource preyed upon by a variety of predators. High abundances of krill and salps, are however capable of exerting local grazing controls (Dubischar and Bathmann, 1997; Granéli et al., 1993; Mayzaud et al., 2002; Smetacek et al., 2004; Whitehouse et al., 2009) and contribute significantly to carbon export. Atkinson et al. (2012) have noted the variability in krill egestion rates, faecal pellet density and C content and hence the potential for carbon export across the Scotia Sea.

Sampling for macrozooplankton with the RMT25 extended from the surface to 1000 m and therefore included a number of taxa which were essentially epipelagic, in addition to numerous mesopelagic forms. While many species were widely distributed, overall densities were higher to the north. Groups such as the Siphonophora were more abundant to the south whereas species such as *E. triacantha* and *T. gaudichaudii* were dominant to the north. The most conspicuous macroplankton species, *E. superba*, is widespread across the Scotia Sea. Within the Southern Ocean as a whole it has a wide habitat range, with 87% of the total stock living over deep oceanic water (> 2000 m) in areas of moderate productivity, reflecting a balance between advection, migration, top-down and bottom-up processes (Atkinson et al., 2008). About 70% of the population lives in the seasonal ice zone (Atkinson et al., 2008) and the southern Scotia Sea is a noted spawning area (Spiridonov, 1995). During the spring cruise it was found that, away from sea ice, iron-fertilised blooms in the SACCF might be important in facilitating early spawning in krill (Schmidt et al., 2012).

We know little about the controls on mesopelagic fish populations, although along with the mesopelagic macrozooplankton, they are clearly not isolated from processes occurring in the overlying surface waters. In the Scotia Sea they are preyed upon by a range of predators; king penguins (Olsson and North, 1997), fur seals (Daneri and Coria, 1992; Reid and Arnould, 1996) and elephant seals (Daneri and Carlina, 2002). Although myctophid species composition changed with latitude across the Scotia Sea, biomass appeared broadly constant (Collins et al., 2012).

Pakhomov et al. (1996) showed that all myctophid species are opportunistic mesozooplankton feeders exhibiting a high degree of overlap in their food spectrum and consuming primarily the most abundant species of copepods, euphausiids, hyperiids and pteropods. A dietary study carried out in the northern part of the Scotia Sea (Shreeve et al., 2009) indicated the presence of feeding guilds within the myctophid fish population. Principal prey items were larger mesozooplankton and smaller macrozooplankton species, particularly euphausiids, amphipods and calanoid copepods. Similarity analysis disclosed two groups, one dominated by copepod consumers (*P. bolini*, *P. choriodon*, *G. fraseri* and *G. nicholsi*) and the other by consumers of the amphipod *T. gaudichaudii* (*E. antarctica* and *G. braueri*). The size of the fish was found to be a key determinant of diet, with large prey such as

E. superba only being consumed by the largest species. It was also suggested that seasonal and regional differences in diet were likely as predator size and prey fields may differ. At present we have no information regarding fish diet from the present 3 cruises but species previously identified as being predominantly copepod consumers were abundant in the northern Scotia Sea where copepods were consistently more abundant e.g. *P. bolini*, *G. fraseri* as well as *K. anderssoni* which appears to have a broader prey spectrum including many small euphausiids (Shreeve et al., 2009). In the southern Scotia Sea dominant species included *E. antarctica* which preyed extensively upon *T. gaudichaudii* further north and *G. braueri*, an apparently more catholic feeder, which consumed *T. gaudichaudii*, small euphausiids and additionally copepods.

Stowasser et al. (2012) investigated food web dynamics during the summer cruise using stable isotope analysis. A main finding was that across the Scotia Sea the food web spanned 4 trophic levels with *E. superba* and large copepods (the dominant suspension feeding taxa in the Scotia Sea) being on the same trophic level. Myctophid fish which prey on both groups were one trophic level above this. Given that ~90% of energy is lost at each trophic step, myctophid production is therefore likely to be around 10% that of krill. While their relative production was not compared during the cruises, myctophid biomass was estimated by Collins et al. (2012) at ~4.5 million tonnes in the Scotia Sea, much less than krill from a recent survey (Fielding et al., 2012; Hewitt et al., 2004). This is also consistent with acoustically determined krill biomass in the southern part of the Scotia Sea during spring and summer, which was ~6 times higher than net caught myctophid biomass (Fig. 3). In the northern Scotia Sea, biomass estimates for the two groups were closer, particularly during summer and autumn, although there is great regional and interannual variability in krill biomass across the Scotia Sea (Hewitt et al., 2004; Trathan et al., 1993).

Higher predators such as seals and seabirds are extremely mobile for a good part of the year but as central place foragers during spring and summer, breeders are generally constrained to returning to breeding /nesting sites fringing the Scotia Sea to rear young (Reid et al., 2004). This restricts their foraging ranges at these times although it is likely that food availability rather than frontal positions or temperature gradients influences their at sea distribution. Later in the year as predators leave breeding sites they are more widely dispersed. Predator observations undertaken during the cruises indicated that dominant predators to the south of the Scotia Sea in the spring and summer were chinstrap penguins (*Pygoscelis antarctica*) and cape petrels (*Daption capense*). In autumn fur seals (*Arctocephalus gazella*) were encountered more frequently here than further north where they were abundant during spring and summer (A. Black, pers. comm.). This may be due to the krill shortage observed in the northern Scotia Sea during autumn (Fielding et al., 2012). Prions (*Pachyptila spp.*) and blue petrels (*Halobaena caerulea*) were abundant and wide ranging predators in the mid Scotia region during all cruises and cetaceans were also notable in this region with an apparent southward movement of fin whales observed from spring to autumn.

In terms of the distribution of carbon across the various taxonomic groups, consistent patterns were observed. With the exception of krill during autumn the rank order was broadly the same across taxonomic groups, seasons and years. In the northern part of the Scotia Sea mesozooplankton biomass (mainly copepods) was greater than krill biomass during all seasons, echoing the wider findings of Voronina et al. (1994) and Voronina (1998). In the south, krill biomass exceeded mesozooplankton biomass during spring and summer although not in autumn 2009 when krill biomass was low across the whole Scotia

Sea. Macrozooplankton and fish biomass was uniformly low in all seasons. This highlights the present stability of the food-web despite the intense seasonality experienced in the Southern Ocean (see also Tarling et al., 2012b). The relative contribution of copepods and krill to secondary production has implications for energy flux as the two groups have fundamentally different life-history strategies and behaviours and so the fate of secondary production arising from each group may be quite different (see Hill et al., 2012). The latitudinal gradient from copepod to krill dominated communities seen in this study therefore has implications for the whole food web.

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Paper 5

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The summertime plankton community at South Georgia (Southern Ocean): Comparing the historical (1926/1927) 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 A.C., Gunther, E.R., 1935. The plankton of the South Georgia whaling grounds and adjacent waters 1926–1927. Discovery Report 11, 1–456]. 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 1926/1927 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 seven 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 1926/1927, 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 1926/1927, 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 and 1927 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.

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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. How-

ever, 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

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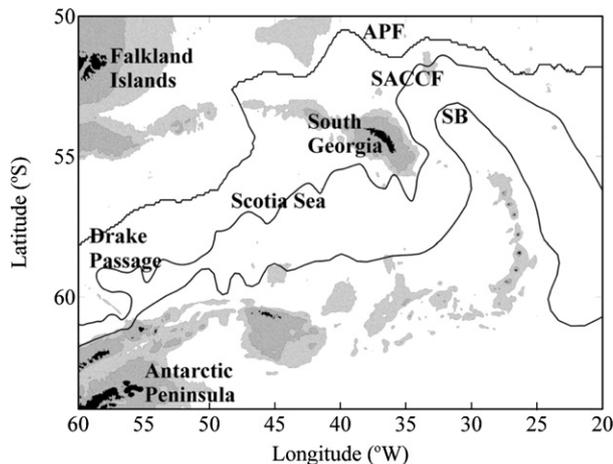
E-mail address: pward@nerc-bas.ac.uk (P. Ward).

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).

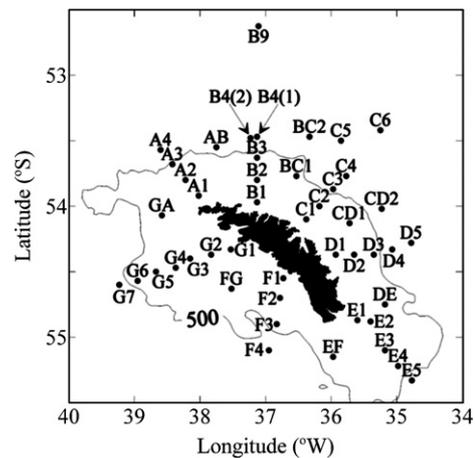
Climate variability in the Southern Ocean is characterised by a number of coupled modes of variability in addition to secular change. Of the former, El Niño-Southern Oscillation (ENSO) events have been particularly highlighted as significant forcing agents of ecosystem change (Stenseth et al., 2002; 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) (Fig. 1).

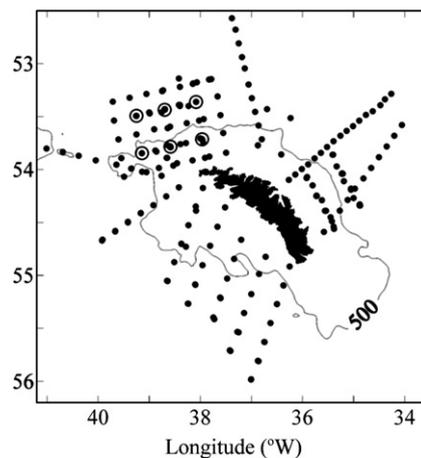
South Georgia is an island located at the northeast limits of the Scotia Sea in the southwest Atlantic sector of the Southern Ocean (Fig. 1a). As such, it sits within the zonation of the Antarctic Circumpolar Current (ACC), with the Southern ACC Front (SACCF) being located particularly close to the island (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., in press).



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.



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 Fig. 13 of Hardy and Gunther (1935, p. 22).



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

Fig. 1. The study area.

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, p. 361) 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'. 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; Vladimirskaia, 1978), with renewed interest in exploiting the living resources of the Southern Ocean (principally fin-fish and krill; Everson, 1977) during the 1970s, 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 1926/1927 survey comprised a series of seven transects (Fig. 1b), along which stations were located at approximately 10 nautical mile intervals. These commenced five 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 (Figs. 1c and 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

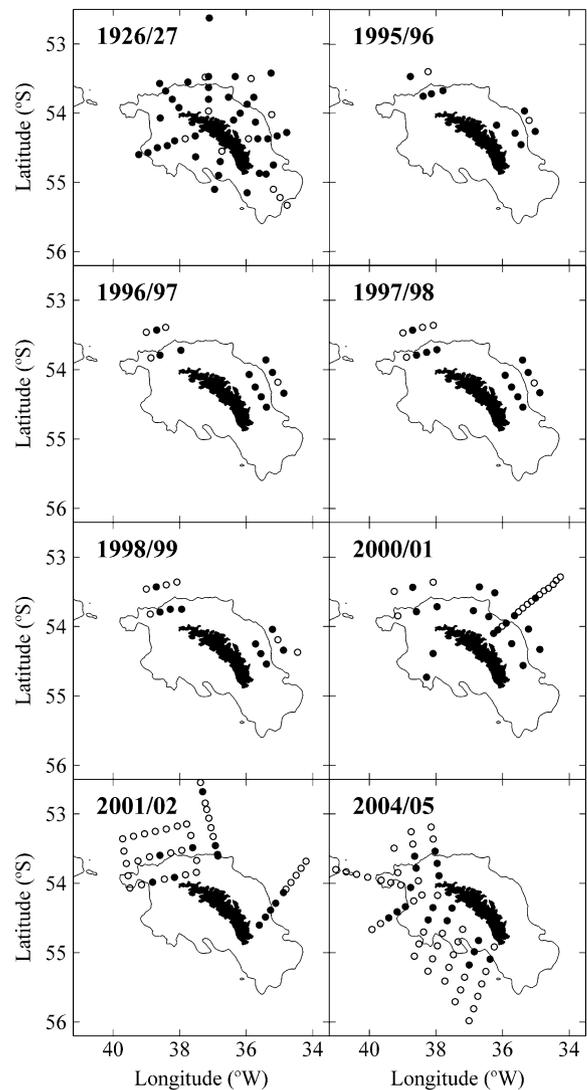


Fig. 2. Stations sampled by cruise. The filled circles on each panel indicate BAS stations that lay within 40 km of the Discovery station positions and also the 36 matched Discovery stations (see methods). Open circles are stations without a match. 1995/1996 – cruise JR11 (11 stations), 1996/1997 – cruise JR17 (14 stations), 1997/1998 – cruise JR28 (16 stations), 1998/1999 – cruise JR38 (17 stations), 2000/2001 – cruise JR57 (39 stations), 2001/2002 – cruise JR70 (45 stations), 2004/2005 – cruise JR116 (57 stations).

same general area. Sample numbers within cruises varied from 11 to 57 with a total of 189 stations across all seven cruises.

2.1. Physical oceanography

At the Discovery stations, hydrographic measurements were made at standard depths using water bottles (Nansen–Peterson 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 °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 Autosol 8400 (prior to 1999)

and 8400B (1999 onwards). CTD potential temperatures and salinities are accurate to $\pm 0.002^\circ\text{C}$ 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 $\sim 60\ \mu\text{m}$, a 70 cm dia net (N70V) used to sample mesozooplankton and made with two grades of silk netting 40 mpi ($\sim 350\ \mu\text{m}$) in the foremost part and 74 mpi ($\sim 200\ \mu\text{m}$) behind, and a coarser net of 1 m 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 three 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 $1\ \text{m s}^{-1}$, 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 six 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 2/3 in objective (equivalent to a primary magnification of $10\times$) or if small forms dominated a 1/6 in objective was used (equivalent to a primary magnification of about $42\times$) (Dr Brian Bracegirdle pers comm.). Coupled with a $10\times$ eyepiece this would have provided $100\times$ and $420\times$ magnification respectively, which is comparable to that used in similar analyses undertaken today. N70V analysis consisted of removing larger organisms ($>2\ \text{mm}$) 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 $200\ \mu\text{m}$ net which was deployed vertically from 200 m (or near bottom if water depth $<200\ \text{m}$) to the surface. Numbers of samples across cruises varied from 11 to 57 (total $n = 189$ across 7 cruises) and were restricted to those taken within the region sampled by the 1926/1927 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 1926/1927 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; Gallienne and Robins, 2001; Ward and Hirst, 2007), was only encountered at one station north of the Polar Front. Hardy and Gunther (1935, p. 189) also thought this curious, 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). *O. 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 1926/1927. 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. *D. pectinatus* at South Georgia is now recognised as *D. 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 1926/1927 is presently widespread in tropical and subtropical waters (Bradford-Griewe 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*

Table 1
N50V phytoplankton hauls (0–100 m)

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

Average abundance (ind. $\cdot 10^3$) with respect to phytoplankton station groups of taxa contributing $\geq 2\%$ to within group similarity or between group dissimilarity in the SIMPER analysis.

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* Chalmers (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 Table 1) 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 1926/1927, 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 $\geq 2\%$ 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 seven BAS cruises (see Fig. 1c). Data from only five of these stations were available for cruise years 1995/1996 and 1996/1997. 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_ε , 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 1926/1927 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 1926/1927 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 1926/1927 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. $m = m_1$ ($j = 1$; 1926/1927 cruise) and $m = m_2$ ($j = 2, \dots, 8$; 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 *D. forcipatus* had a marked effect on the subsequent calculation of PSI. We know that this species was present over the shelf in 1926/1927 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

$$\text{PSI} = 100 - 0.5 \sum |A_i - B_i| = \sum \min(A_i, B_i),$$

where A_i , B_i = the percentage of species i in samples A and B , respectively.

3. Results

3.1. Physical oceanography

Fig. 3 shows the potential temperature/salinity characteristics of the 1926/1927 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 °C 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 °C 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 °C at the very surface, but is more often closer to 2 °C. 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 po-

tential temperatures close to South Georgia lie in the range –1 to 1 °C, with salinities of approximately 33.9–34.0 (Fig. 3).

With regard to changing water mass properties close to South Georgia, it is immediately obvious from Fig. 3 that the 1926/1927 Discovery Investigations data are cold in the upper layers, specifically the surface waters and WW layer. The 1926/1927 data compare most closely with data collected during January–February 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 (Fig. 4).

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). Gp 1 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 1926/1927 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 (Fig. 5).

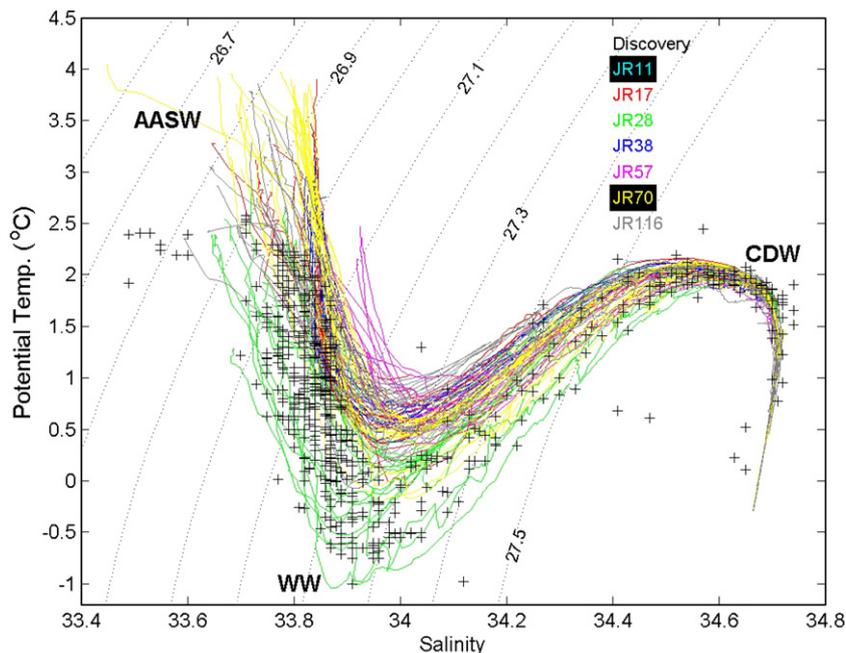
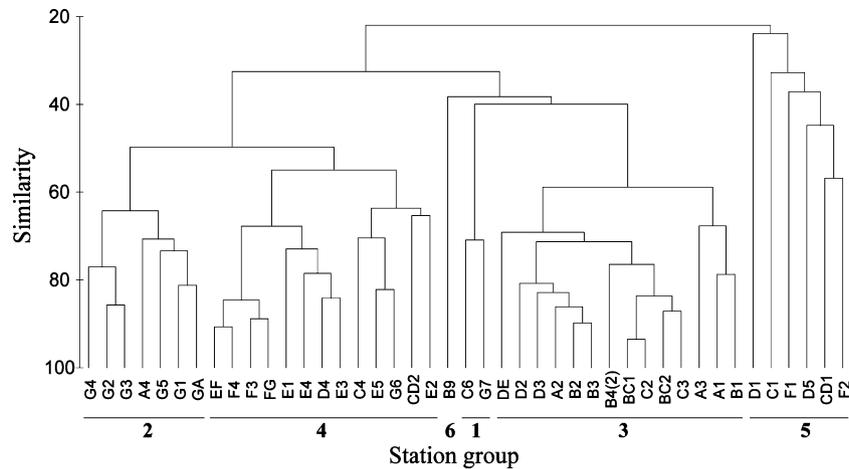
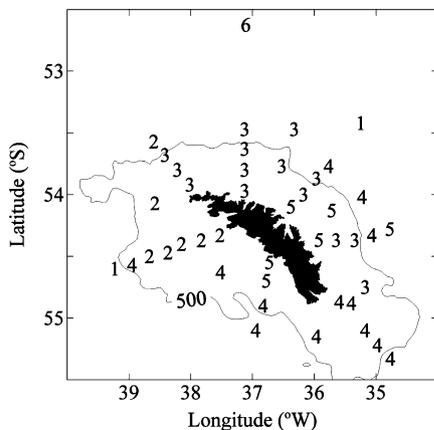


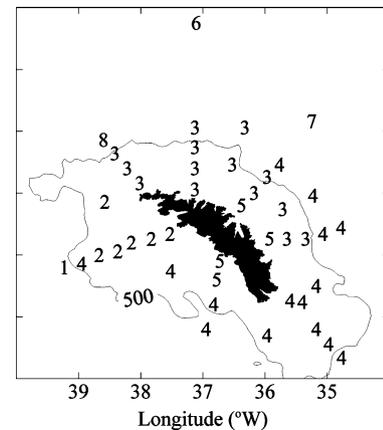
Fig. 3. Potential temperature/salinity characteristics of waters sampled during the 1926/1927 Discovery Expedition around South Georgia (black crosses), plotted alongside more recent data (1996–2001) collected from this same region by the British Antarctic Survey (coloured lines). Discovery data are 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.



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



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



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

Fig. 4. Results of hierarchical clustering of Phytoplankton counts.

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 b.

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 *D. 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 three main groups.

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

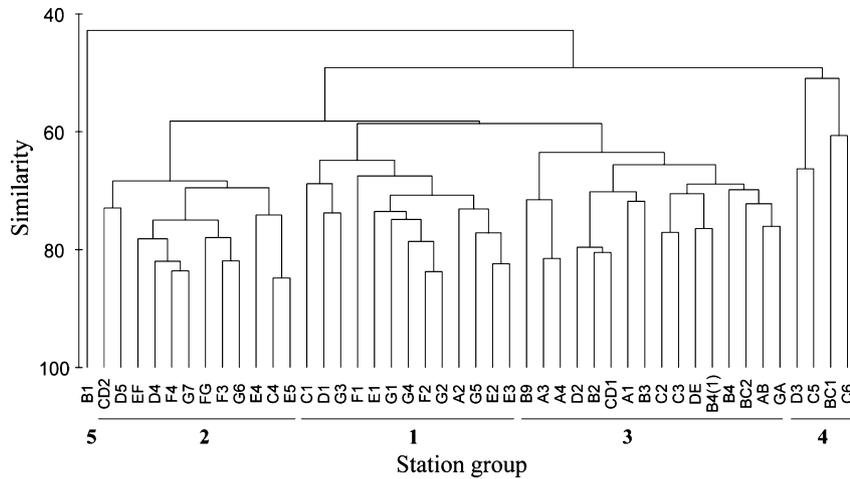
The relative abundance of zooplankton ($ind. m^{-3}$) within the survey area is shown in Fig. 4c. Highest abundances were seen at near-coastal stations towards the southeast of the island (mainly station group 1) where *D. forcipatus* was abundant. Elsewhere, lower abundances were seen, particularly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

3.4. Interannual variability and a comparison between Discovery and BAS data

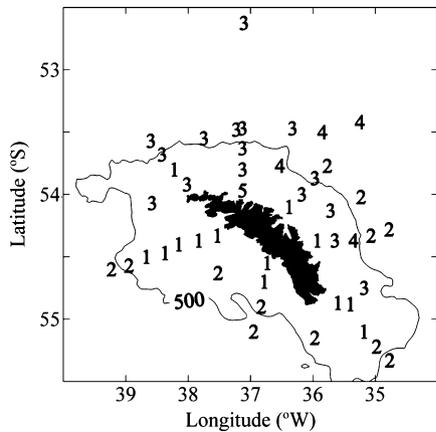
Of the total variation in log abundance at the 6 stations sampled across 7 BAS cruises, 32% was attributable to cruise, 9% to station and 59% to residual variation (Table 3) i.e. of the two components (cruise and station), cruise, although not as large as residual variation, was proportionately larger 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



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



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

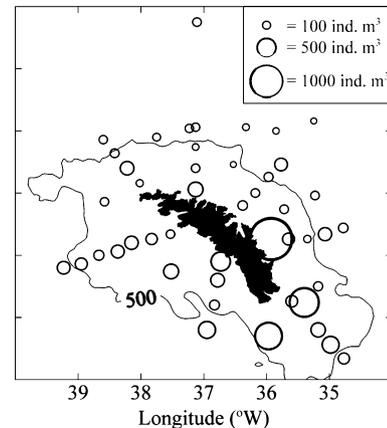
5c. Zooplankton abundance (ind. m⁻³) during the 1926/27 summer season.

Fig. 5. Results of hierarchical clustering of Zooplankton counts.

approximate as it ignores the uncertainty in the estimated variance components. A more conservative approach based on the six 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 Fig. 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 six 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 1926/1927 and finishing in 2005. With one exception, mean PSI value for all cruises ranged between 70% and 80%. PSI is strongly influenced by the most abundant species (Rebstock, 2001) and the decline in the average PSI during 1998/1999 was largely due to the presence of higher proportions of pteropods (*Lima-*

cina 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 1926/1927 ($\sim 1.5^\circ\text{C}$ < contemporary cruise data; Whitehouse et al., in press) may have influenced the development of zooplankton populations. In the absence of stage frequency data in 1926/1927 we compared the rank order of abundance of 4 species of large calanoid copepods across all cruises and found it differed in 1926/1927. *C. propinquus*, second in rank order in 1926/1927, 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 1926/1927 season compared to 1990, although it appeared not to have impacted upon the other three species. With the exception of *Rhincalanus gigas*, which had a lower average percentage in the top 250 m in Discovery samples, the remaining three species had similar proportions of the population present in both years (Table 5).

Table 2
N70V zooplankton hauls (0 ≤ 250 m)

	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 <i>Calanus</i>	1.3	0.9	0.5	0.4	0.1
<i>simillimus</i>					
<i>propinquus</i>	2.2	4.7	1.2	4.2	1.3
<i>calanoides acutus</i>	7.4	16.3	3.3	1.3	1.1
<i>Rhincalanus gigas</i>	0.5	0.7	1.8	0.6	1.3
<i>Metridia</i> spp.	0.2	1.7	0.8	6.3	3.1
<i>Clausocalanus laticeps</i>	0.1	1.3	0.3	0.8	0
<i>Clausocalanus</i>	0	0	0	0.17	0
<i>arcuicornis</i>					
<i>Drepanopus forcipatus</i>	294.0	24.3	14.5	0.1	237.0
<i>Scolecithricella minor</i>	0.1	1.0	1.0	0.5	0
<i>Ctenocalanus vanus</i>	7.6	28.7	11.3	8.8	13.5
<i>Microcalanus pygmaeus</i>	0.05	0.7	0.9	0.1	7.7
<i>Microcalanus</i> sp.	0	0.1	0	0.2	0
<i>Oithona</i> spp.	80.0	159.0	73.0	6.8	0
<i>Oncaea</i> spp.	1.2	6.1	0.8	0.7	81.0
<i>Chaetognatha</i>	0.2	1.1	1.0	0.3	0.8
<i>Polychaeta</i>	1.3	3.4	0.8	0.8	0
<i>Pelagobia longicirrata</i>	0.6	2.1	0.3	0	0.03
<i>Ostracoda</i>	0	0.5	0.2	0.2	0
<i>Euphausiacea</i>	0.45	1.1	0.2	0.3	0
<i>Thysanoessa</i> spp.					
Thecate Pteropoda	0.4	.4	0.2	0.02	0
<i>Limacina</i> spp.					
Tunicate <i>Salpa fusiformis</i>	0	0.2	0.1	0.6	0
Appendicularians	0.9	2.2	0.03	0	0

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.

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 1926/1927 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 1926/1927 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.

Table 3
Summary of models and data used to test for differences within BAS cruises and between BAS cruises and Discovery data from 1926/1927

Data/model	Difference 1926 – BAS (se)	W	p	Variance component (% of total)			Total
				Cruise	Station	Residual	
(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
(c) 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

W – Wald test.

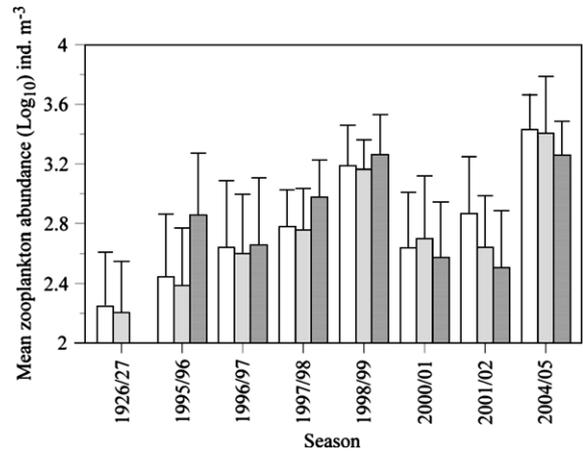


Fig. 6. Log zooplankton abundance (ind. m⁻³ ± SD) by cruise. Open-fill for all stations sampled during a cruise, mid-tone for stations with a 40 km match to Discovery stations, dark tone for six stations sampled to the NW of South Georgia during BAS cruises.

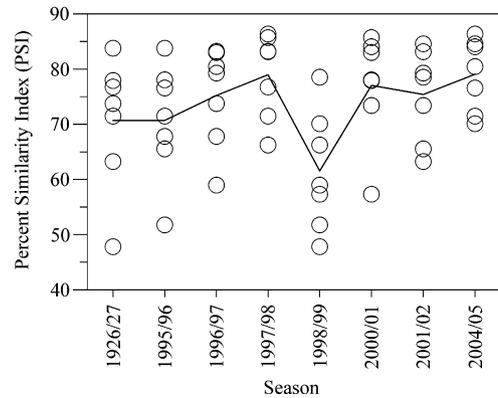


Fig. 7. Percentage Similarity Index (PSI) based on a common matrix of 45 taxa (see Section 2.5) Open circles represent PSI comparisons for that year and every other year in the series. Solid line is the mean across all comparisons.

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 January–February 1998 compared with other recent cruises around South Georgia, and concluded that they were caused by the strong El Niño event of 1997/1998. 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 1926/1927 is equivocal. Using various proxies, Quinn et al. (1987) have found evidence for an El Niño during 1925/1926, and the timescales of the oceanic teleconnection are such that this could feasibly have influenced the region around South Georgia in 1926/1927. However, examinations of various atmospheric measures of ENSO (including the Southern Oscillation Index, and individually the Darwin Mean

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

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

Table 5
Depth distribution of four large calanoid species during austral summer 1926/1927 and 1990 near South Georgia

	<i>Calanoides acutus</i>	<i>Rhincalanus gigas</i>	<i>Calanus simillimus</i>	<i>Calanus propinquus</i>
Discovery 1926/1927 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

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.

Sea Level Pressure) shows little evidence for such an event (Phil Jones, Climatic Research Unit, University of East Anglia, personal communication).

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 1926/1927, 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 200 m 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 1926/1927 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 1926/1927 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 1926/1927 nonetheless fell within the range displayed by contemporary data.

Low abundance in 1926/1927 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 $\sim 350 \mu\text{m}$ 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 1926/1927, 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 from 1926/1927. With the exception of cruise JR38 (1998/1999) 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% and 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 1920s. 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, *C. 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 1926/1927. The significance of this finding is unknown. Its higher relative abundance in 1926/1927 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 *C. 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 years 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 *C. 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.

Acknowledgements

We acknowledge our many BAS colleagues who over the years have contributed to the planning and execution of numerous research cruises to South Georgia and beyond. We also thank Geraint Tarling who kindly carried out the PSI analysis. The foundations of so much of the marine research carried out at South Georgia and elsewhere in the Southern Ocean were laid by the Discovery Investigations. We dedicate this paper to those prescient scientists who laboured under very difficult conditions and made this comparison possible. It forms a contribution to the BAS LTMS-B programme and the Discovery 2010 CEMI project.

Appendix I

Phytoplankton taxa taken in the N50V net during the 1926/1927 survey around South Georgia and listed in the phytoplankton tables (Appendix 1 of Hardy and Gunther (1935))

Phytoplankton taxa from the N50V net series identified in Hardy and Gunther's 1926/1927 survey of South Georgia	Phytoplankton Taxa contributing $\geq 2\%$ at any one station	Present classification according to Scott and Marchant (2005) and vanLandingham (1967–1999)
<i>Coscinodiscus bouvet</i> Karsten	+	<i>Coscinodiscus bouvet</i>
<i>C. curvulatus</i> Grunow	+	<i>C. curvulatus</i>
<i>C. kerguelensis</i> Karsten		<i>C. kerguelensis</i>

Appendix I (continued)

Phytoplankton taxa from the N50V net series identified in Hardy and Gunther's 1926/1927 survey of South Georgia	Phytoplankton Taxa contributing $\geq 2\%$ at any one station	Present classification according to Scott and Marchant (2005) and vanLandingham (1967–1999)
<i>C. lineatus</i> Ehrenberg		<i>C. lineatus</i>
<i>C. oculoides</i> Karsten	+	<i>C. oculoides</i>
<i>C. opposites</i> Karsten	+	<i>C. opposites</i>
<i>C. sub-bulliens</i> Jørgensen		<i>C. sub-bulliens</i>
<i>Asteromphalus brookei</i> Bailey		<i>A. brookei</i>
<i>A. hookeri</i> Ehrenberg		<i>A. hookeri</i>
<i>A. regularis</i> Karsten		<i>A. hookeri</i> Ehrenberg
<i>Thalassiosira antarctica</i> Karsten	+	<i>Thalassiosira antarctica</i>
<i>Dactyliosolen laevis</i> Castracane		<i>D. antarcticus (laevis form)</i>
<i>Corethron valdiviae</i> Karsten	+	<i>Corethron pennatum</i>
<i>Rhizosolenia alata</i> Brightwell	+	<i>Proboscia alata</i> Sundström 1986
<i>R. curva</i> Karsten		<i>R. curvata</i> O. Zacharias 1905
<i>R. obtusa</i> Hensen		<i>Proboscia inermis</i> Castracane
<i>R. styliformis</i> Brightwell	+	<i>R. styliformis</i>
<i>Chaetocerus atlanticus</i> Cleve		<i>Chaetocerus atlanticus</i>
<i>C. criophilum</i> Castracane	+	<i>C. criophiles</i> Castracane
<i>C. curvatus</i> Castracane		<i>C. curvatus</i>
<i>C. dicaeta</i> Ehrenberg	+	<i>C. dicaeta</i>
<i>C. socialis</i> Lauder	+	<i>C. socialis</i>
<i>C. schimperianus</i> Karsten	+	<i>C. bulbosus</i> Ehrenberg
<i>Biddulphia striata</i> Karsten		<i>Odontella weisflogii</i> Grunow
<i>Eucampia antarctica</i> Castracane	+	<i>Eucampia antarctica</i>
<i>Fragilaria antarctica</i> Castracane	+	<i>Fragilariopsis kerguelensis</i> Hustedt
<i>Thalassiothrix antarctica</i> Schimper	+	<i>Thalassiothrix antarctica</i>
<i>Pleurosigma directum</i> Grunow		<i>Pleurosigma directum</i>
<i>Nitzschia seriata</i> Cleve	+	<i>Nitzschia seriata</i>
<i>Peridinium</i> spp.	+	<i>Peridinium</i> spp.
<i>Ceratium pentagonum</i> Gourret	+	<i>Ceratium pentagonum</i>
<i>Distephanus speculum</i> Ehrenberg	+	<i>Dictyocha speculum</i> Ehrenberg

Taxa used in Simper analysis following 2% selection, indicated by +. Present classification of species after Scott and Marchant (2005) and vanLandingham (1967–1999).

Appendix II

The species lists used for the analysis

Taxa identified in Hardy and Gunther's 1926/1927 survey of South Georgia that occurred in the top 250 m	Grouping of taxonomic categories compatible with BAS analysis and input into data matrix and subject to cluster analysis	Taxa contributing $\geq 2\%$ at any one station	Taxonomic categories used in the Discovery/BAS comparison
Foraminifera	Foraminifera	+	
Radiolaria	Radiolaria	+	
Medusae	Medusae		+
Beroe	Beroe		
Ctenophora	Ctenophora		+
Siphonophora	Siphonophora		+
Chaetognatha	Chaetognatha (all species)	+	+
<i>Eukrohnia hamata</i>			
<i>Sagitta maxima</i>			
<i>S. planktonis</i>			
<i>S. gazellae</i>			
<i>Pelagobia longicirrata</i>	<i>Pelagobia longicirrata</i>	+	+
Polychaete juv	Polychaete juv	+	+
<i>Tomopteris</i> spp.	<i>Tomopteris</i> spp.		+
Ostracoda juv	Ostracoda (all species)	+	+
<i>Conchoecia hettacra</i>			
<i>Conchoecia</i> sp.			
<i>Calanus simillimus</i>	<i>Calanus simillimus</i>	+	+
<i>Calanus propinquus</i>	<i>Calanus propinquus</i>	+	+
<i>Calanoides acutus</i>	<i>Calanoides acutus</i>	+	+
<i>Rhincalanus gigas</i>	<i>Rhincalanus gigas</i>	+	+
<i>Eucalanus acus</i>	<i>Subeucalanus longiceps</i>		+
<i>Clausocalanus laticeps</i>	<i>Clausocalanus laticeps</i>	+	+
<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus</i> spp.	+	+
<i>Ctenocalanus vanus</i>	<i>Ctenocalanus vanus</i>	+	+
<i>Microcalanus pygmaeus</i>	<i>Microcalanus pygmaeus</i>	+	+
<i>Microcalanus</i> sp.			
<i>Drepanopus pectinatus</i>	<i>Drepanopus forcipatus</i>	+	+
<i>Paraeuchaeta antarctica</i>	<i>Paraeuchaeta antarctica</i>		+
<i>Paraeuchaeta</i> sp. juv			
<i>Aetideus armatus</i>	<i>Aetideus</i> spp.		+
<i>Gaidius tenuispinus</i>	<i>Gaidius tenuispinus</i>		+

(continued on next page)

Appendix II (continued)

Taxa identified in Hardy and Gunther's 1926/1927 survey of South Georgia that occurred in the top 250 m	Grouping of taxonomic categories compatible with BAS analysis and input into data matrix and subject to cluster analysis	Taxa contributing $\geq 2\%$ at any one station	Taxonomic categories used in the Discovery/BAS comparison
<i>Heterorhabdus</i> sp.	<i>Heterorhabdus</i> sp.		+
<i>Haloptilus</i> spp.	<i>Haloptilus</i> spp.		+
<i>Candacia</i> sp.	<i>Candacia</i> sp.		+
<i>Euchirella</i> spp.	<i>Euchirella</i> spp.		+
<i>Scolecithricella minor</i>	<i>Scolecithricella minor</i>	+	+
<i>Scaphocalanus echinatus</i>	<i>Scaphocalanus</i> spp.		+
<i>Racovitzanus antarcticus</i>	<i>Racovitzanus antarcticus</i>		+
<i>Pleuromma robusta</i>	<i>Pleuromma robusta</i>		+
<i>Metridia gerlachei</i> <i>M. lucens</i>	<i>Metridia</i> spp.	+	+
<i>Oithona frigida</i> <i>Oithona</i> sp.	<i>Oithona</i> spp (mainly <i>O. similis</i> see methods)	+	+
<i>Oncaea conifera</i> <i>Oncaea curvata</i> <i>Oncaea notopus</i> <i>Oncaea</i> juv	<i>Oncaea</i> spp.	+	+
<i>Parathemisto gaudichaudii</i>	<i>Parathemisto gaudichaudii</i>		+
<i>Primno macropa</i>	<i>Primno macropa</i>		
<i>Vibilia antarctica</i>	<i>Vibilia antarctica</i>		
<i>Cylopus</i> sp.	<i>Cylopus</i> sp.		+
Amphipoda	Amphipoda		+
Mysidae	Mysidae		+
<i>Euphausia frigida</i> (adult)	<i>Euphausia frigida</i> (adult)		+
<i>E. frigida</i> cyrtopia	<i>E. frigida</i> cyrtopia		
<i>E. frigida</i> furcilia	<i>E. frigida</i> furcilia		+
<i>E. frigida</i> calyptopis	<i>E. frigida</i> calyptopis		+
<i>E. superba</i> (adult)	<i>E. superba</i> (adult)		+
<i>E. superba</i> cyrtopia	<i>E. superba</i> cyrtopia		
<i>E. superba</i> furcilia	<i>E. superba</i> furcilia		+
<i>E. superba</i> calyptopis	<i>E. superba</i> calyptopis		+
<i>Thysanöessa macrura</i> (male)	<i>Thysanoessa</i> spp. (both species, sexes and furcilia)	+	+

Appendix II (continued)

Taxa identified in Hardy and Gunther's 1926/1927 survey of South Georgia that occurred in the top 250 m	Grouping of taxonomic categories compatible with BAS analysis and input into data matrix and subject to cluster analysis	Taxa contributing $\geq 2\%$ at any one station	Taxonomic categories used in the Discovery/BAS comparison
<i>Thysanöessa vicina</i> (male)			
<i>Thysanöessa</i> sp (female)			
<i>Thysanöessa</i> cyrtopia			
<i>Thysanöessa</i> furcilia			
<i>Thysanöessa</i> calyptopis	<i>Thysanöessa</i> calyptopis		+
<i>Limacina balea</i>	<i>Limacina</i> spp. (all species)	+	+
<i>L. helicina</i>			
<i>Limacina</i> juv			
<i>Salpa fusiformis</i>	<i>Salpa thompsoni</i>	+	+
Appendicularia	Appendicularia	+	+

First column: list of species present in the upper 250 m of the water column derived from Appendix II Table I and the text of Hardy and Gunther (1935). Second column: Species list compatible with BAS taxonomic categories derived from column one by aggregating species and stages within higher taxonomic categories. NB Foraminifera and Radiolaria not routinely counted in BAS samples but input into the data matrix for the PRIMER analysis. Third column: Species list remaining in the PRIMER analysis following the selection of taxa in the data matrix that contributed $\geq 2\%$ by abundance to any one station. Fourth column: Taxonomic categories used in the Discovery/BAS comparison and with the exception of *D. forcipatus* the PSI analysis.

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Paper 6

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Comparing Bongo net and N70 mesozooplankton catches: using a reconstruction of an original net to quantify historical plankton catch data

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Abstract If Southern Ocean plankton communities are changing in response to climate, biases in various nets need to be evaluated to help understand regional and temporal differences between historical and contemporary sample collections. A comparison of the catching ability of a Bongo net (mesh aperture 200 μm) and a reconstructed version of an N70 net (upper mesh aperture 445 μm , lower mesh aperture 195 μm) as used by the *Discovery Investigations* was therefore undertaken. Forty Bongo and forty N70 samples were obtained from 10 stations in the Southern Ocean during December 2009. Bongo net catch abundance was ~ 3 times greater than the N70 and ~ 4 times greater when only copepod instars < 0.5 mm body length were considered. The Bongo net captured more plankton at all chlorophyll *a* (Chl *a*) concentrations encountered, although the difference was less at high Chl *a* when the N70 appeared to filter all size classes of copepod more efficiently, as well as retaining a relatively greater proportion of non-copepod plankton. Application of these findings was made to a previous study in which N70 samples from 1926/1927 were compared to a series of Bongo net hauls made post-1995. By ‘correcting’ abundances for net bias among a common set of 45 taxa, N70 data were within the range of variability seen in the Bongo net samples. Making such inter-net comparisons allows us

to use historical collections and better judge the nature and magnitude of change in these plankton communities.

Keywords Bongo net · N70 net · Zooplankton · Southern Ocean · *Discovery Investigations* · Net comparison

Introduction

It is well documented that the Southern Ocean has warmed rapidly over the last half of the twentieth century (Gille 2002; Levitus et al. 2005; Gille 2008). Warming has not been spatially uniform (Gille 2008), but in the Atlantic sector, temperatures have increased by as much as 1°C in the near surface waters over the last 80 years (Whitehouse et al. 2008). The response of the marine ecosystem to these and associated physical changes (e.g. climate anomalies and sea-ice trends) is currently being investigated, particularly among the higher trophic levels (Smith et al. 2003; Weimerskirch et al. 2003; Forcada et al. 2005, 2006; Trathan et al. 2007). Further down the food chain, changes in phytoplankton communities along the Antarctic Peninsula have been observed (Moline et al. 2004) and, within the Atlantic sector, Antarctic krill (*Euphausia superba*) has undergone a decline in abundance over the last 40 years (Atkinson et al. 2004). Understanding how a changing environment influences plankton composition and distribution requires sampling at appropriate spatial and temporal scales. Understanding biases in various net systems is therefore important if we are to compare and understand regional and temporal differences between sample collections. Quantitative differences between sample sets may not be so important when defining community boundaries (e.g. see Ward et al. 2012) but where absolute abundances,

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biomass or stage composition, particularly of the smaller size fractions, are being considered, we need a sense of how different net systems may bias our interpretations.

Although some biological time-series are beginning to illustrate relationships with the physical environment at ~decadal scales (Ross et al. 2008; Loeb et al. 2010), the remoteness of the Southern Ocean, harsh climate and limited seasonal access have, in general, resulted in a lack of long-term plankton time-series to compare with changes in the physical environment. To date, one of the most comprehensive collections of plankton samples taken in the Southern Ocean was made by the *Discovery Investigations* in the period 1925–1950. During the time they were active in the field, many thousands of plankton samples were obtained, principally from stations in the South Atlantic sector. Samples were largely collected during the late 1920s to early 1930s and therefore have limited temporal extent, although nonetheless can serve as a basis against which present day collections may be compared. Various net types were used during the *Discovery Investigations* (Kemp et al. 1929) with the N100 and the N70 nets being the most commonly used. They closely resemble the WP2 type ring nets employed by many contemporary expeditions to collect mesozooplankton. The original N70 was a 70-cm dia. ring net constructed with an upper section of coarse mesh netting (1/4 inch) and two subsequent sections of different grades of silk netting and possessed a closing throttling mechanism. It was deployed whilst the ship was stationary and hauled vertically through various depth horizons and closed by a messenger weight to obtain samples within selected depth horizons.

Several recent studies have used original N70 sample data and compared them with results from contemporary collections to try and assess any changes. In so doing, it has been seen as necessary either to reconstruct N70 nets to collect contemporary samples (Kawamura 1986, 1987) or to use a net similar to the N70 in design and net size (Vuorinen et al. 1997; Ward et al. 2008). In this study, we have reconstructed an N70 net and compared its catching ability with that of a paired Bongo net that we have routinely used in the Southern Ocean. We quantify differences, including how both nets responded to phytoplankton clogging in terms of size selectivity and use this information to make a comparison between modern day plankton samples (Ward et al. 2008) and those collected in 1926/1927 (Hardy and Gunther 1935) as part of the *Discovery Investigations*.

Samples arising from the *Discovery Investigations* are currently being maintained by the Natural History Museum in London and represent the largest and most comprehensive collection of plankton samples made in the early part of last century which are still curated and available for study. More information is available at: <http://www.nhm.ac.uk/>

[research-curation/research/historical-marine-collections/nhm-collections/discovery/index.html](http://www.nhm.ac.uk/research-curation/research/historical-marine-collections/nhm-collections/discovery/index.html).

Materials and methods

Net construction

The specification for the construction of the original N70 net is detailed in Kemp et al. (1929). The N70 was a 70-cm dia net used to sample mesozooplankton and constructed with coarse netting and two grades of silk mesh. The upper part of the net was 21 inches (~53 cm) of ¼ inch (~6 mm) knotted mesh followed by a canvas band and then two finer mesh sections both made from Messrs Staniers' Quadruple Extra Heavy Quality Double Twist Swiss Silk bolting cloth, the first 3 feet 2" (96.5 cm) of 40 threads per inch (TPI) and the bottom section 4 feet 5" (~136 cm) of 74 TPI. The N70 was equipped with a throttling rope and messenger system and when hauled vertically was used to sample discrete depth horizons. 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.

We have constructed an N70 net as close as possible to the specifications of Kemp et al. (1929). A similar reconstruction carried out by Kawamura (1986) used nylon netting in the upper section (specified as 210D/15F/2 but aperture not given), and silk mesh of apertures 0.473 and 0.222 mm for the lower sections, these specified as Nippon Bolting Cloth grades GG40 and GG73, respectively. This was based on the original specification of Kemp et al. (1929) although Kawamura (1986) gives the equivalent mesh apertures of Staniers' Quadruple Extra Heavy Quality Double Twist Swiss Silk bolting cloth of 40 TPI and 74 TPI as 0.569 and 0.239 mm, respectively. No explanation was provided for this conversion or for the fact that the mesh used in the reconstructed net differed significantly in aperture from the inferred metric equivalent of the original specification. There is a problem in deducing the actual mesh apertures in the original net because silk gauze supplied by Messrs Staniers was provided in a range of thread widths such that the mesh aperture varied with thread width at a stated TPI, and these various silk mesh types are no longer manufactured. Using the oldest Staniers' product description leaflet (dated 1975) that we have obtained, the heaviest grades of silk mesh are designated XXX-GG grade. The 40XXX-GG is listed as 455 µm aperture and 38 and three-quarters TPI and the 74XXX-GG as 190 µm aperture and 71 and three-quarters TPI. We concluded that the original silk mesh would have had apertures and open areas similar to these and selected the nearest polyamide (nylon) equivalents as follows: meshes of 440 and 195 µm

aperture, for the lower parts of the net. The former having a 46% open area, 41 TPI and a thread thickness of 195 microns and the latter a 43% open area, 86 TPI and a thread thickness of 100 microns. The TPI of the equivalent monofilaments are greater because the threads are thinner compared with silk, but the primary filtration characteristic is the mesh apertures that are broadly equivalent. The upper part of the net was constructed of knotted mesh (5 mm knot to knot). Comparative details of net characteristics are provided in Table 1.

Our comparison was made with a paired Bongo net of 0.61 m diameter equipped with a 200 μm mesh net which has been a standard piece of equipment used by us to sample mesozooplankton in the Southern Ocean over the last 15 or so years (Shreeve et al. 2002; Ward et al. 2006, 2007). The nets are mounted side by side, and the towing wire is attached to a motion compensating mechanism operated through coiled springs that damp movement imparted by rolling of the ship as the net is deployed from the mid-ship gantry whilst the ship is stationary.

Sampling

Net deployments from 200 m to surface were carried out at 10 stations, 5 located within Marguerite Bay at the base of

Table 1 Net mesh characteristics of the reconstructed N70 and Bongo net used in this comparison

	Mesh (μm)	Threads per inch	Thread thickness (μm)	Open area (cm^{-2})	Open area as % of total net area
N70	440	41	195	7,894	46
	195	86	100	4,539	43
Bongo net	200	80	120	14,806	38

Table 2 Station positions at which samples were obtained with Bongo and N70 nets

Date	Latitude ($^{\circ}\text{S}$)	Longitude ($^{\circ}\text{W}$)	Nominal grouping
03/12/2009	67.99	68.40	Marguerite Bay
04/12/2009	67.12	69.48	Marguerite Bay
06/12/2009	66.26	70.43	Marguerite Bay
08/12/2009	67.82	70.82	Marguerite Bay
09/12/2009	67.74	70.17	Marguerite Bay
16/12/2009	55.21	41.10	South Georgia
20/12/2009	52.72	40.15	South Georgia
20/12/2009	53.49	39.26	South Georgia
21/12/2009	53.79	38.59	South Georgia
22/12/2009	53.36	38.09	South Georgia

the Antarctic Peninsula and 5 in the Scotia Sea and north of the island South Georgia (Table 2). At each station, two Bongo net deployments were carried out resulting in 4 samples, followed by four N70 deployments each resulting in a single sample. Thus, a total of 40 Bongo net and 40 N70 samples were collected over a range of environmental conditions. Nets were lowered open to 200 m and hauled slowly to the surface at $\sim 0.22 \text{ m s}^{-1}$. The *Discovery Investigations* did not use flow-meters when collecting plankton samples, and as any comparison with their samples will therefore rely on estimating volume swept, we used net diameter and the length of water column sampled to obtain a filtration volume for the two net types. Calculations based on mouth area indicate that, over a 200 m water column, the Bongo net would filter 58.46 m^{-3} of water and the N70 76.98 m^{-3} . All net deployments were carried out during hours of daylight.

Samples were fixed in seawater formalin (4%W:V) and later split using a Folsom plankton splitter. Split fractions ranged from 1/2 to 1/512 depending on plankton numbers. Two separate splits were used to count larger and smaller organisms respectively and, for each split, both halves were enumerated. In this way, between 200 and 600 organisms per split were identified and counted. Counts were standardised to ind. m^{-3} based on the estimated volume filtered. Published body size to body weight algorithms were used to convert from abundance to biomass. Estimates of body size were either extracted from the literature or measured directly (see Table A1, Ward et al. (2012)).

Data treatment

A fundamental difference between the two sampling devices is that the paired Bongo net captures two plankton samples simultaneously, whilst the N70 captures just one. In making a comparison between the devices, some thought must be given as to whether treating the two Bongo samples as independent affects the comparison with N70 data. We approached this issue through simulation analyses, as follows.

For the Bongo data, two simulated datasets were generated through random selection from the original sample set of copepod abundance, the difference between the two being the method of random selection: Method 1: each Bongo sample (i.e. both the left and the right nets) was treated as an independent sample and any could be randomly selected from the original dataset; Method 2: the left and right samples from a Bongo deployment were treated as non-independent samples such that only the left or the right net samples from a pair could be selected from the original dataset. Thirty replicates of N70 data were also generated from the original N70 sample set of copepod

abundance to compare with the 2 simulated Bongo datasets. Statistical tests showed that both the Method 1 and Method 2 simulated Bongo datasets were significantly different to the N70 dataset ($p < 0.001$). Furthermore, Method 1 and Method 2 datasets were not significantly different from each other ($t = -0.226$, 58 *df*, $p = 0.822$), with a 1.2% difference between their respective means. We concluded that treating the paired Bongo nets as independent or non-independent samples does not affect the comparison with the N70 dataset. We have treated them as independent samples so that the full set of nets can be used in the analysis.

Data analysis

Our main aim was to determine species- and size-specific catch efficiency ratios for the N70 versus the Bongo net. We can then apply these ratios to previously analysed datasets to determine the effect (if any) on their interpretation. In particular, Ward et al. (2008) presented results from a comparison of N70 net samples taken in 1926/1927 with modern (post-1995) Bongo net samples. In that comparison, it was assumed that the catch efficiency for the two nets was equal across all species and sizes. We applied the catch efficiency ratios established by the present study and then performed a percentage similarity analysis (PSI analysis: Whittaker 1952; Whittaker and Fairbanks 1958; Rebstock 2001), as also performed by Ward et al. (2008).

$$\text{PSI} = 100 - 0.5 \sum |A_i - B_i| = \sum \min(A_i, B_i)$$

where A_i , B_i = the percentage of species i in samples A and B , respectively.

The analysis was carried out using a total of 45 species in which the depth integrated abundance of species i was converted to percentage composition relative to the summed abundance of all other species within the sample. Each ‘sample’ was the mean product of a series of individual samples taken during each season and for which a mean abundance for each species was derived. There were a total of 9 samples, 7 obtained using modern Bongo nets (1995–2005) and 2 using N70 nets (1926/1927 *Discovery* campaigns). Of the two N70 datasets, one was the same as presented in Ward et al. (2008), whilst the other was a new dataset that incorporated the catch efficiency ratios derived by the present study. All the Bongo net samples were the same as presented in Ward et al. (2008).

The PSI was performed between all pairs of the 9 ‘samples’ to derive a similarity matrix. The outcome of the analysis was presented so as to illustrate how similar any one particular sample was to all others through plotting a whisker plot, showing the mean level similarity \pm SD for each of the 9 samples.

Results

Abundance and biomass data showed consistent differences between the two types of nets and between sites. We have therefore summarised results with respect to both (Table 3). Bongo nets captured an average of ~ 3.2 times more plankton (by abundance) than the N70, which translated to ~ 1.6 times more biomass. These differences with respect to net type were statistically significant at both sites ($p < 0.01$ for abundance and $p < 0.05$ for biomass).

Copepods have instar stages that are easily measured compared to non-crustacean plankton and generally comprise some 80–90% of plankton abundance, in this case an average of 90.67% ($\pm 6.78\%$) by abundance and 50.8% ($\pm 25\%$) by biomass. As expected, the majority (85–90%) of copepod instars were below 0.5 mm in length, and it was within this size class that the Bongo net caught ~ 4 times more than the N70 (Fig. 1a). In the other size classes, although the Bongo caught more than the N70 in absolute terms, the catch ratio (the Bongo abundance/N70 abundance) was closer to parity.

Copepod biomass exhibited several modal peaks over the range of body length. These were observed in the smallest categories (<0.5 and 0.5 – 1 mm) and comprised all *Oithona* spp. stages, *Ctenocalanus citer*, *Microcalanus pygmaeus* and many early copepodite stages of larger species such as *Metridia* spp. and *Calanus simillimus*. The next mode at ~ 2 – 2.5 mm comprised younger copepodite stages of *Pareuchaeta* spp., *Calanoides acutus* and *Rhincalanus gigas* and older stages of *C. simillimus*. Finally, the > 7 mm size classes contained older copepodite stages of *Calanus propinquus*, *Paraeuchaeta* spp. and *R. gigas*. Although the Bongo net retained more biomass than the N70 across all size classes, it was only in the two smallest classes (<0.99 mm) that the difference was significant (Fig. 1b).

Across both sites and nets, just 4 taxa comprised $\sim 80\%$ of total zooplankton abundance, those being the copepods,

Table 3 Mean total abundance and biomass m^{-3} (\pm SD) captured by Bongo and N70 nets at stations in Marguerite Bay and close to South Georgia

Net Type (No. samples)	Marguerite Bay Mean Abundance ind. m^{-3}	Net Type (No. samples)	South Georgia Mean Abundance ind. m^{-3}
Bongo (20)	289.3 (± 221)	Bongo (20)	3,875 ($\pm 1,805$)
N70 (19)	96.7 (± 99.6)	N70 (20)	1,147 (± 559)
	Mean Biomass mg m^{-3}		Mean Biomass mg m^{-3}
Bongo (20)	5.1 (± 3)	Bongo (20)	86.8 (± 55)
N70 (19)	2.15 (± 1.0)	N70 (20)	54.4 (± 35.4)

Oithona similis, *Ctenocalanus citer* and *Metridia* spp. and a taxon containing all appendicularians (Table 4). The Bongo net consistently captured a greater proportion of

Oithona similis, the single most abundant copepod species across all stations. Conversely, appendicularians had a higher mean percentage occurrence in the N70 net. There was no consistent difference in the percentage contributions of either *Ctenocalanus citer* or *Metridia* spp. Average body length of *O. similis* fell into the smallest class recorded (<0.5 mm) which was ~4-fold more abundant in the Bongo net relative to the N70. This largely accounted for the overall difference in abundance seen between the two types of nets.

Figure 2 shows the relationship of the log10 abundance ratio (Bongo:N70) versus the maximum Chl *a* concentration (Chl *a* max) recorded in the top 100 m at each of the 10 stations. There was a wider variability in the ratio at lower Chl *a* max concentrations but overall the catch ratio decreased at higher Chl *a* max ($F_{26,23}, p = 0.000$) indicating that any clogging of the nets may potentially affect the catching ability of the Bongo net more than the N70.

We examined this relationship by using catch ratios in relation to copepod body size with respect to whether the Chl *a* max was low (<2 mg m⁻³), or high (>2 mg m⁻³) (Fig. 3). Within all size classes, the ratio was always lower at high Chl *a* max concentrations. The ratio at Chl *a* max concentrations >2 mg m⁻³ was between 56 and 87% (mean 73 ± 10%) of the ratio at lower Chl *a* concentrations.

Both the Bongo and N70 nets showed a similar negative relationship with increasing Chl *a* max values, with the slope of the fitted regressions not showing any statistical differences (Fig. 4). The fitted regressions did show significantly different elevations (Fig. 4), indicating that there was a greater proportion of copepods in Bongo samples across all Chl *a* max concentrations. The r^2 value for both nets indicated that Chl *a* potentially accounted for a significant proportion of the variability in the proportion of copepods in the catches of both nets. High Chl *a* may

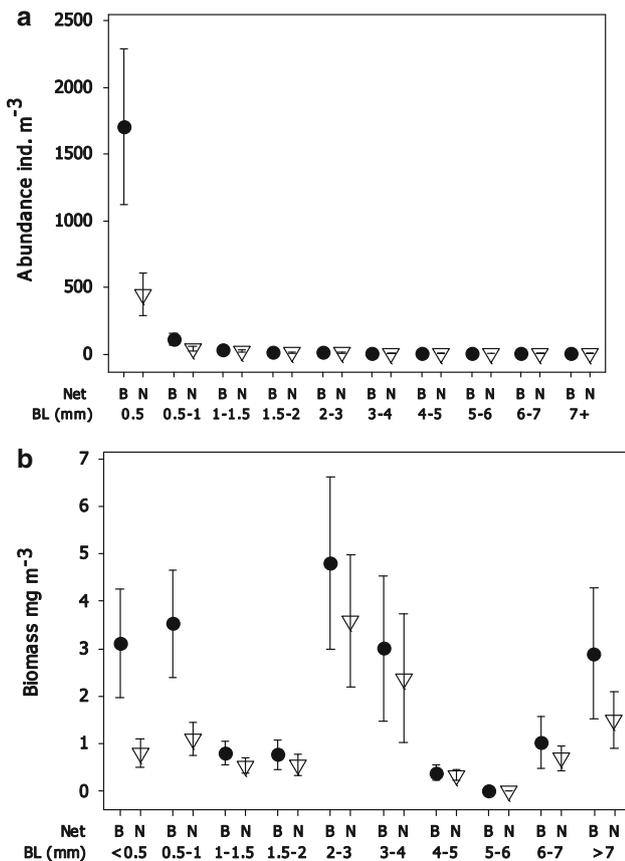


Fig. 1 a Mean copepod abundance (ind. m⁻³) and 95% confidence interval with respect to body length captured by the Bongo and N70 nets. b Mean copepod biomass (dw mg m⁻³) and 95% confidence interval with respect to body length captured by the Bongo and N70 nets. B = Bongo (solid circles), N = N70 (inverted triangles)

Table 4 Mean abundance ind. m⁻³ (±SD) and percentage contribution % (±SD) of the four most abundant zooplankton taxa at both sites and within both nets

	<i>Oithona similis</i>	<i>Ctenocalanus citer</i>	Appendicularians	<i>Metridia</i> spp.
Bongo: Marguerite Bay				
Ind. m ⁻³	208.5 (±134.8)	26.5 (±26.9)	15.5 (±32.2)	12.9 (±14.5)
%	77.6 (±8.9)	7.2 (±4.0)	2.8 (±4.6)	3.4 (±2.2)
N70: Marguerite Bay				
Ind. m ⁻³	56.3 (±50.7)	12.3 (±14.8)	7.8 (±14.9)	7.7 (±9.4)
%	65.4 (±9.7)	9.9 (±4.8)	3.8 (±4.9)	5.8 (±3.6)
Bongo: South Georgia				
Ind. m ⁻³	1,860 (±781)	480.4 (±304.5)	287.7 (±218.2)	130.8 (±78.2)
%	52.0 (±10.6)	12.8 (±3.9)	6.4 (±4.8)	3.6 (±1.5)
N70: South Georgia				
Ind. m ⁻³	480.4 (±256.2)	124.4 (±78.2)	139.1 (±115.0)	44.3 (±27.2)
%	44.7 (±12.2)	11.9 (±4.6)	10.4 (±8.8)	4.0 (±1.3)

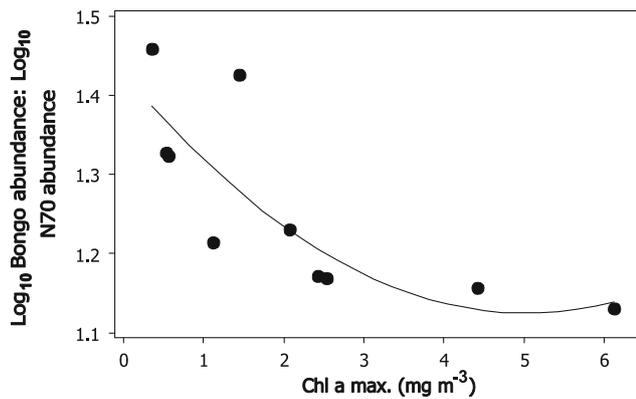


Fig. 2 Ratio of mean Log_{10} Bongo and Log_{10} N70 abundance (ind. m^{-3}) in relation to Chl *a* maximum in the top 100 m of water column at respective stations. Fitted line Ratio Log_{10} Bongo: Log_{10} N70 = $1.441 - 0.1492 \text{ Chl } a + 0.0244 \text{ Chl } a^2$. $r^2(\text{adj}) = 49.1\%$

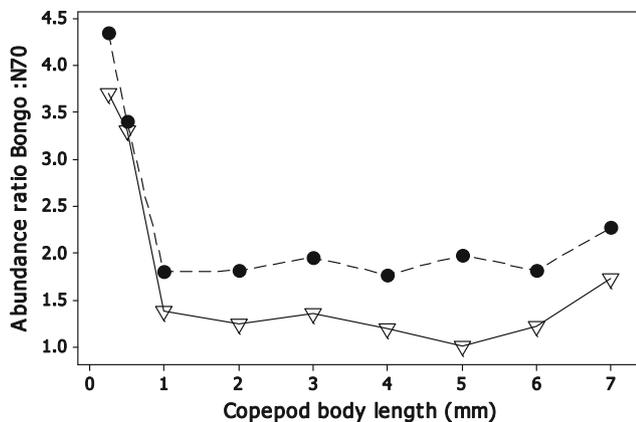


Fig. 3 Mean Bongo:N70 copepod catch ratio in relation to body length. Pecked line with solid circles is low Chl *a* ($<2 \text{ mg m}^{-3}$), solid line with inverted triangles is high Chl *a* ($>2 \text{ mg m}^{-3}$)

enhance the opportunities for some non-copepod taxa to increase in numbers relative to copepods. The most abundant non-copepod contributor to catches at both sites was appendicularians (Table 4), which were overall 4 times more abundant than all other non-copepod taxa combined. Although they were far more abundant at the South Georgia stations, they were strongly and positively related to Chl *a* at both sites ($p < 0.0001$).

Discussion

Despite being superficially similar in appearance and being fished in the same manner, the catching ability of the two nets under comparison differed considerably. The overall open area of the Bongo net mesh was some 19% greater than the N70, although around 2/3 of the open area of the N70 was accounted for by the coarse (440 μm mesh as

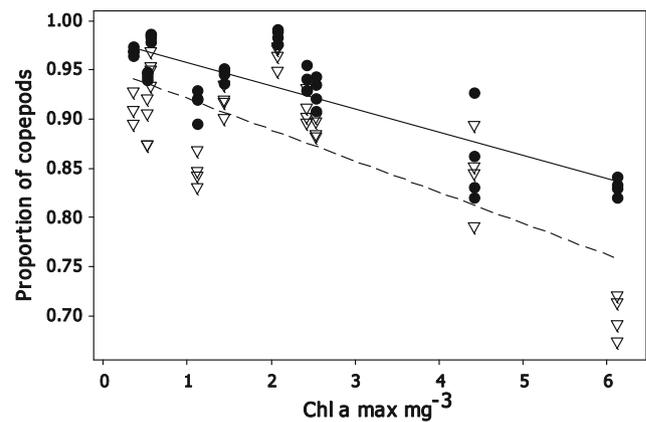


Fig. 4 Copepods as a proportion of all mesozooplankton in relation to Chl *a* maximum. Solid line and solid circles = Bongo net, pecked line and inverted triangles = N70. Bongo: $y = 0.9806 - 0.0234x$ ($r^2 = 0.683$, $F = 81.96$, 39 df , $p < 0.0001$). N70: $y = 0.9526 - 0.0317x$ ($r^2 = 0.570$, $F = 49.06$, 39 df , $p < 0.0001$). Bongo versus N70 regressions. For slope: $t = 1.993$, $v = 75$, not significantly different. For elevation: $t = 4.992$, $v = 75$, significantly different at $p < 0.001$

used in the re-constructed net) upper section. The area of the finer 195 μm mesh lower section is only $\sim 31\%$ of the area of the broadly equivalent 200 μm Bongo mesh. Thus, a priori we might expect a ~ 3 -fold difference in retention efficiency. This is close to what was found, with the Bongo net capturing an average of ~ 3.1 – 3.6 times more plankton than the N70, although the difference was largely confined to the smallest size classes. Above $\sim 1 \text{ mm}$ body length, the difference in the catching ability of the two nets was far less, the difference in favour of the Bongo net averaging 1.39, more in line with the difference in the open area between the two nets (1.19 see Table 1).

Although we did not use flow-meters in this study, there were measurable effects of Chl *a* on species composition and the catch ratio. Although the Bongo net captured more than the N70 across the range of Chl *a* measured, the difference between the two reduced considerably at higher Chl *a* concentrations (Fig. 2). Although the open area of the Bongo net was greater than the N70, the venting effect of the coarser mesh in the N70 will retain a better filtering efficiency under clogging conditions than the Bongo. Clogging appeared to affect all size classes to broadly the same extent (Fig. 3). The share of non-copepod plankton in both nets also increased with increasing Chl *a*, albeit with a relatively greater proportion in the N70 (Fig. 4). This was largely due to the strong positive relationship between Chl *a* and appendicularians, the dominant non-copepod taxon at both sites. At higher Chl *a* concentrations, the N70 appears better able to filter all size classes of copepod more efficiently than the Bongo, as well as retaining a relatively greater proportion of non-copepod plankton, here mainly in the form of appendicularians. Overall, however, the N70

results underestimate plankton abundance compared with the Bongo net, particularly for the smaller size class of plankton (<0.5 mm body length) over the range of Chl *a* measured.

In reconstructing the N70 net, we naturally wished to get as close to the original specification as possible. In choosing an equivalent mesh, we were mindful that mesh size is determined by two factors, namely thread thickness and number of threads per unit distance. The properties of silk mesh also differ from those of nylon equivalents inasmuch as silk shrinks after use will attract debris more than nylon nets (since silk mesh is made from a slightly ‘hairy’ multi-filament thread rather than a smooth mono-filament thread in nylon mesh) and any swelling and fraying with use will serve to reduce mesh aperture (Vanucci 1968). It is not feasible to account for these latter effects, and so we selected a nylon mesh that we deduced was close to the original specification in terms of aperture and open area. Whilst the mesh sizes chosen may not exactly match the originals, we believe they offer a valid means of exploring differences between contemporary plankton collections and the historical sample sets of the *Discovery Investigations*.

Case study

We have applied some of the above findings regarding net performance to a study comparing data obtained during a survey carried out during the *Discovery Investigations* around South Georgia in the summer season of 1926/1927 (Hardy and Gunther 1935) with samples collected post-1995 (Ward et al. 2008). Details of sampling and data manipulation are given in Ward et al. (2008), but briefly the comparison was made on the basis of a common set of 45 taxa, which emerged following taxonomic harmonisation between the two datasets. Here, we have taken those same 45 taxa from the *Discovery* N70 net and multiplied their abundances by the appropriate factor determined in our size-based comparison of net performance. In this way, we have derived abundances corrected for net type to match with the post-1995 Bongo estimates. In the case of copepod life stages in the <0.5 mm and 0.5–0.99 mm size classes, which numerically dominated the plankton, we determined the Bongo:N70 ratio for each individual taxon and applied this to the data. Other taxa in size groups >1 mm have had the average factor of 1.7 (determined by averaging the ratio of the remaining size classes) applied. Where stage structure of a species was not specified in the original study by Hardy and Gunther (1935), we have summed abundances of all stages and used an average factor.

In the original study (Ward et al. 2008), abundance was much lower in the N70 samples from the 1926/1927 survey

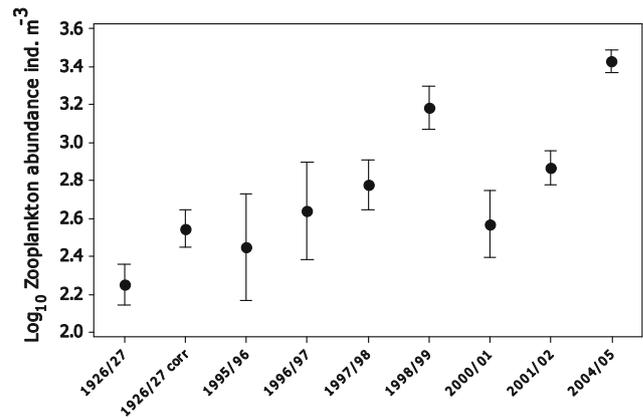


Fig. 5 Data from a study by Ward et al. (2008) showing average Log₁₀ zooplankton abundance (ind. m⁻³ ± SE) from different years sampling around South Georgia. 1926/1927 is the average of N70 data collected by *Discovery Investigations* (Hardy and Gunther 1935), the remainder being Bongo net data collected post-1995, except 1926/1927 corr. which is the original 1926/1927 data with the Bongo:N70 catch ratio corrections determined in this study applied

than post-1995 (Fig. 5). However, the high interannual variability within the sample set as a whole meant that no significant differences were detected. Nonetheless through applying the factors derived from this study, the adjusted abundance values for the *Discovery* cruise of 1926/1927 now lie more within the range of abundances determined from the post-1995 samples although still somewhat at the lower end. Likewise, when considering the PSI analysis from the original study, no changes were seen (Fig. 6). The mean PSI value for the season 1998/1999 fell to just over 60% due to high abundances of the pteropod *Limacina* spp. in that year. It was the only year that differed markedly as in all other years it was consistently between 70 and 80%.

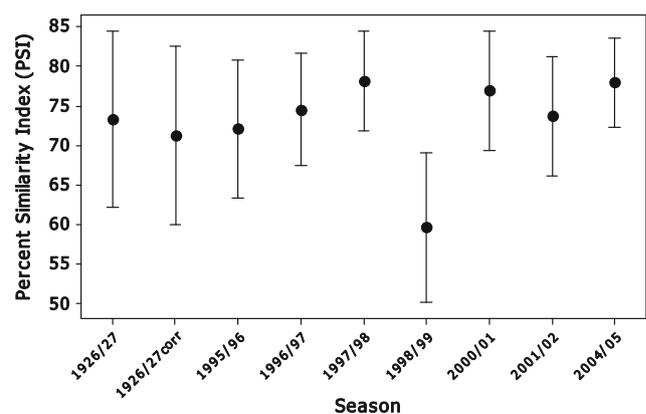


Fig. 6 Data from a study by Ward et al. (2008) showing PSI analysis carried out on samples obtained during different years of sampling around South Georgia. 1926/1927 is the N70 data collected by *Discovery Investigations* (Hardy and Gunther 1935), the remainder being Bongo net data collected post-1995, except 1926/1927 corr. which is the original 1926/1927 data with the Bongo: N70 catch ratio corrections determined in this study applied

Ward et al. (2008) argued that this pattern indicated a relatively robust species composition in this part of the Southern Ocean despite the fact that the region has warmed by over a degree in the last 80 years (Whitehouse et al. 2008). The present study with updated calibration factors further supports this view. However, more subtle changes in species demography such as timing of lifecycles and changing regional distributions (see Mackey et al. 2012) cannot be ruled out, and it may be that change is more readily observed in other sectors of the Southern Ocean.

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Paper 7

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Spatial distributions of Southern Ocean mesozooplankton communities have been resilient to long-term surface warming

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Abstract

The biogeographic response of oceanic planktonic communities to climatic change has a large influence on the future stability of marine food webs and the functioning of global biogeochemical cycles. Temperature plays a pivotal role in determining the distribution of these communities and ocean warming has the potential to cause major distributional shifts, particularly in polar regions where the thermal envelope is narrow. We considered the impact of long-term ocean warming on the spatial distribution of Southern Ocean mesozooplankton communities through examining plankton abundance in relation to sea surface temperature between two distinct periods, separated by around 60 years. Analyses considered 16 dominant mesozooplankton taxa (in terms of biomass and abundance) in the southwest Atlantic sector of the Southern Ocean, from net samples and in situ temperature records collected during the *Discovery Investigations* (1926–1938) and contemporary campaigns (1996–2013). Sea surface temperature was found to have increased significantly by 0.74°C between the two eras. The corresponding sea surface temperature at which community abundance peaked was also significantly higher in contemporary times, by 0.98°C. Spatial projections indicated that the geographical location of community peak abundance had remained the same between the two eras despite the poleward advance of sea surface isotherms. If the community had remained within the same thermal envelope as in the 1920s–1930s, community peak abundance would be 500 km further south in the contemporary era. Studies in the northern hemisphere have found that dominant taxa, such as calanoid copepods, have conserved their thermal niches and tracked surface isotherms polewards. The fact that this has not occurred in the Southern Ocean suggests that other selective pressures, particularly food availability and the properties of underlying water masses, place greater constraints on spatial distributions in this region. It further demonstrates that this community is thermally resilient to present levels of sea surface warming.

KEYWORDS

adaptation, Antarctic, copepods, ocean warming, pelagic, polar

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1 | INTRODUCTION

Biogeographic changes in the distributions of populations and communities are a widely reported outcome of recent rapid climatic shifts (Parmesan & Yohe, 2003). The single most important physical variable affecting marine systems is temperature, as manifested in the close alignment between the distribution patterns of marine ectotherms and latitudinal and vertical thermal gradients (Somero, 2010). These patterns are no doubt influenced by the strong relationship between temperature and physiological performance (Pörtner, 2002). However, other ecological aspects such as species interactions, trophic efficiency and community composition are also strongly related to temperature gradients (Richardson, 2008). The rate and extent of ocean warming is therefore of critical importance to the viability of future marine populations (Richardson, 2008).

Recent biogeographic shifts in marine zooplankton have most commonly been associated with the warming of the sea surface (Beaugrand, Reid, Ibanez, Lindley, & Edwards, 2002; Hinder et al., 2014). In the northeast Atlantic, Beaugrand et al. (2002) reported that members of warm water assemblages of crustacean mesozooplankton (the southern shelf-edge assemblage and the pseudo oceanic assemblage) moved more than 1,100 km polewards over the past 50 years (approximately 200 km per decade) although Chust et al. (2013) determined these translocations to have been considerably lower (8–16 km per decade for *Calanus finmarchicus*). Similarly, Lindley and Daykin (2005) determined *Centropages chierchiae* and *Temora stylifera* to have both moved north from the vicinity of the Iberian Peninsula in the 1970s and 1980s to the English Channel in the 1990s (6° of latitude, amounting to around 300 km per decade). In both of these instances, the reported distributional shifts took place over periods where sea surface temperature warmed by 1°C although the shifts may also be partially influenced by stronger northward currents on the European shelf edge.

The Southern Ocean has undergone some of the world's most rapid regional ocean warming, with a summertime increase at the sea surface of more than 1°C recorded west of the Antarctic Peninsula between 1951–1998 (Meredith & King, 2005) and an increase in the upper 100 m of –0.9°C in January at South Georgia between 1925–2006 (Whitehouse et al., 2008). This long-term shift in sea surface temperature must be placed within the context of seasonal temperature variation, which is just a few degrees in the surface layers (Venables, Meredith, Atkinson, & Ward, 2012). Individuals in contemporary times may therefore be experiencing average water temperatures towards the upper limits of historical seasonal temperature fluctuations. Furthermore, the potential for a biogeographic shift polewards in the Southern Ocean is limited because of the Antarctic continental landmass, strong circumpolar currents and extensive sea-ice. The resilience of Southern Ocean marine taxa to ocean warming must therefore contend with both a geographic narrowing of their temperature envelope, and a seasonal temperature experience that is comparatively small in relation to species found in more temperate regions. If such temperature changes cannot be

tolerated, a contraction of their range and replacement with more temperate species will result, with ecological consequences both to the secondary productivity of the system and its foodwebs.

Nevertheless, sea surface temperature is not the only constraint on biogeographic patterns in mesozooplankton. Much of the Southern Ocean is characterized as being a high nutrient low chlorophyll environment since iron deprivation frequently limits levels of primary productivity (Boyd, 2002; Korb & Whitehouse, 2004). Large phytoplankton blooms persist where iron is naturally enriched through sea-ice melt and continental run off or entrainment from sediments (Pollard et al., 2009) and their location can be a major influence on zooplankton productivity and abundance (Atkinson et al., 1996). Furthermore, some biomass-dominant polar zooplankton species, such as the large calanoid copepods, have multiyear lifecycles and spend much of the year in deeper water masses, some in a state of diapause, occupying the surface layers only during the productive season (Atkinson, 1998; Tarling, Shreeve, Ward, Atkinson, & Hirst, 2004). Conditions in the surface layers may therefore not be the ultimate influence on the distributions of some of these species in the context of their lifecycles.

Here, we consider how Southern Ocean mesozooplankton populations have responded to a period of substantial ocean warming that has continued since the early part of the twentieth century. We compare the distributions of a number of key taxa between two periods, the first sampled by the *Discovery Investigations* between 1926 and 1938 and, the second, by contemporary campaigns between 1996 and 2013. The analyses were performed on net samples and in situ sea surface temperatures collected during the summertime period within the southwest Atlantic sector of the Southern Ocean. Both datasets encompassed more than a decade of sampling (13 and 18 years respectively) in order to synthesize across intradecadal climatic cycles and minimize the influence of interannual variability on comparative analyses (Loeb & Santora, 2015; Murphy et al., 2007; Steinberg et al., 2015). Our analyses establish relationships between the distributions of key taxa and prevailing sea surface temperature to determine how individual species, and the mesozooplankton community as a whole, have responded to the intervening period of ocean warming. Although our findings must be placed within the unique set of circumstances that are faced by open ocean communities in the Southern Ocean, they also provide a wider case study of the potential resilience of such communities to climatic change.

2 | MATERIALS AND METHODS

2.1 | Mesozooplankton species composition and abundance

We analysed net samples from 155 stations south of the Polar Front in the southwest Atlantic sector of the Southern Ocean, collected as part of the *Discovery Investigations* (1926–1938, Figure 1a). The samples were obtained via a series of N70V plankton

nets deployed vertically between 250 m and the surface (see Kemp, Hardy, & Mackintosh, 1929). Mesh sizes in this net decrease in stages from 5 mm in the upper part, to 440 μm and then 195 μm in the mid and lower parts respectively (measurements are metric equivalents of the original imperial units). A further 451 samples were analysed from nets taken in the same ocean sector in contemporary times (1996–2013, Figure 1c). The contemporary samples were obtained from deployments of either RMT1 nets (330 μm mesh) fished obliquely from 200–0 m or Bongo nets (200 μm) fished vertically from either 200–0 m or 400–0 m. During sample analysis, larger organisms were either enumerated from complete samples, or the whole sample placed in a Folsom plankton splitter and fractionated into replicate aliquots until countable numbers (~200 individuals) were estimated to be present. For smaller, more numerous organisms, the sample was further fractionated until countable replicates (~500–800 organisms) were obtained. Abundances of taxa were standardized according to the split fraction, and the amount of water each net filtered was estimated

based on mouth area and distance towed, to derive individual species concentrations (ind./m^3).

2.2 | Sea surface temperature

Sea surface temperature was measured at the zooplankton sampling sites and additional locations using water bottle samples during the *Discovery Investigations* (Kemp et al., 1929) and with high resolution conductivity temperature depth (CTD) instruments during the contemporary cruises (Whitehouse et al., 2008; Figure 1).

To determine the change in sea surface temperature between the 1920s–1930s and present day, data from all available stations from the *Discovery Investigations* and contemporary cruises between the months of October and April and located south of the Polar Front in water depths >500 m were analysed for the region 65–49°S, 80–20°W (Figure 1). Stations were identified as being south of the Polar Front from their vertical temperature profile (Gordon, Georgi, & Taylor, 1977). Duplicate temperature measurements,

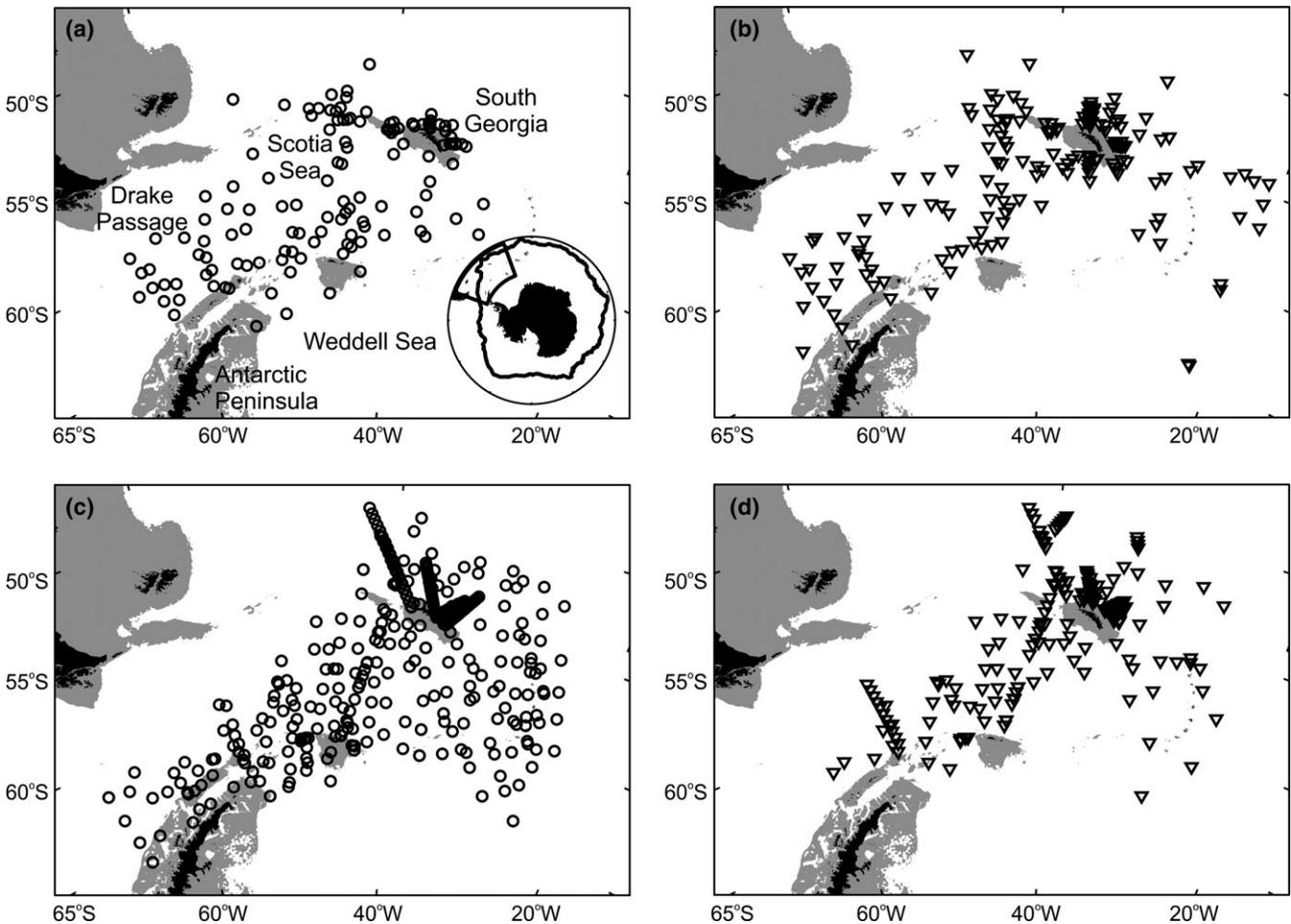


FIGURE 1 Distribution of sample stations. Distribution of zooplankton abundance estimates and sea surface temperature measurements used to determine warming in the Atlantic sector of the Southern Ocean. (a) *Discovery Investigations* (October to April 1926–1938) zooplankton abundance. (b) *Discovery Investigations* sea surface temperature. (c) Contemporary cruises (October to April 1996–2013) zooplankton abundance. (d) Contemporary cruises sea surface temperature. Ocean depths <500 m shaded grey. Only stations south of the Polar Front, as determined from the vertical temperature profile at each station, were used. Inset shows study region and 7-year mean (1987–1993) position of the Polar Front (Moore et al., 1999)

defined as measurements taken within 1 day and 5 km of another sample, were excluded. The surface temperature datasets were compared with the World Ocean Atlas (WOA) 2013 v2 monthly mean 1° surface climatology for 2005–2012 (Locarnini et al., 2013). For each dataset, nearest neighbour interpolation was used to extract the WOA temperature at each station from the corresponding mean monthly objectively analysed field at 0 m depth. WOA grid cells with zero contributing data points were excluded (Meredith & King, 2005). The resulting differences between the station data points and the WOA temperature fields were averaged at 1° spatial resolution to remove geographic bias from the station coverage. The median offset from the WOA data for the gridded data from the *Discovery Investigations* and contemporary data was -0.78°C and -0.04°C , respectively ($N = 106$ for *Discovery*, $N = 91$ for contemporary).

We used these offsets to produce mean October–April sea surface temperature fields for the *Discovery Investigations* and contemporary eras. WOA monthly mean 2005–2012 climatological temperature fields at 0 m for October to April were averaged and the corresponding offset applied uniformly. In this case, all grid cell values were retained to provide a spatially complete coverage for the study region.

2.3 | Numerical methods

Mesozooplankton data analyses focussed on the crustacean fraction which made up approximately 90% of all organisms within net samples. Analyses considered 16 taxa from this fraction chosen because they were major contributors to either the abundance or the biomass of the samples (biomass was determined through multiplying abundance by typical dry weight and was calculated only for the purpose of identifying species that were less abundant but still major contributors through their large individual size). Analyses were restricted to net samples taken between October and April. The datasets were normalized such that each taxon made an equal contribution to the metric of community response (*CRel*, see below) and that the influence of less abundant species was the same as more abundant ones. This ensured that the response metric was not dominated by a small number of highly abundant taxa.

The first stage in this process was to derive relative abundance for each taxon, as follows:

$$Rel_{x,y} = \frac{Abs_{x,y}}{\sum_{y=1}^{y=n} Abs_x} \quad (1)$$

where *Rel* is relative abundance, *Abs*, absolute abundance (ind/m^{-3}), *x*, taxon, *y*, the sample station and *n*, the total number of sampling stations. For the contemporary sample set, it was necessary to determine *Rel* separately for three different types of net deployment (RMT1 200-0 m, Bongo 200-0 m and Bongo 400-0 m). The resulting three matrices were subsequently concatenated into a single matrix before further analysis. Community relative abundance (*CRel*) was calculated as:

$$CRel = \sum_{x=1}^{x=16} Rel_y \quad (2)$$

Cumulative probability curves were generated for (i) cumulative station rank as a function of sea surface temperature and (ii)

cumulative *Rel* or *CRel* as a function of sea surface temperature. Medians and percentiles of *Rel* were calculated, from which the corresponding temperatures were determined to ascertain the relationship of each taxon to temperature. For *CRel*, the residual difference between (i) and (ii), the community relative abundance anomaly ($CRel_A$), was calculated to derive a metric of abundance that normalizes for the distribution of sample stations between sea surface temperatures. $CRel_A$ trajectories were fitted by a Gaussian distribution function ($G_{(T^{\circ}\text{C})}$) where the inflection point, X_0 , denotes the sea surface temperature at which peak relative abundance occurs. The respective $G_{(T^{\circ}\text{C})}$ functions were plotted spatially, using the sea surface temperature fields described above, to identify regions of peak $CRel_A$. A bootstrapping analysis was performed to determine the level of difference in X_0 between the *Discovery Investigations* and contemporary datasets, following Hilborn and Mangel (1997). $CRel_A$ was resampled through selecting 148 datapoints with replacement from either the *Discovery Investigations* or contemporary datasets 30 times. $G_{(T^{\circ}\text{C})}$ and the value of X_0 was derived for each resampled dataset. The significance level of the difference in X_0 between *Discovery Investigations* and contemporary datasets was tested by a two tailed t test, having first passed tests for Normality (Shapiro–Wilk) and Equal Variance. It was not possible to fit a Gaussian distribution to the temperature distributions of a number of individual taxa since they were not normally distributed, so the median temperature of occurrence (termed M_0) was derived for all individual taxa for comparative purposes (Table 1).

2.4 | Influence of extreme values

A potential confounding influence on the statistical comparisons made between eras is that a small number of extreme values in one or other dataset is responsible for the observed significant differences. This would mean the differences between eras may be the result of including or excluding anomalous instances in one or other dataset rather than reflecting a change in the mean situation. We approached this issue through considering three of the main sources of variability within the datasets, namely (i) interannual variability, (ii) differences between taxa, (iii) the degree of spatial overlap between eras. Our null hypothesis was that exclusion of extreme values within these sources of variability reduces the difference between the respective X_0 values to the point that they are no longer significantly different. Rejection of this hypothesis means that analyses are not overly influenced by extreme values and that all data could be included when testing for the difference in X_0 between eras. The datasets were prepared as detailed above but, prior to the generation of the cumulative probability curves, certain net samples or taxa were excluded according to the respective test. Exclusions for: (i) interannual variability, were the years with either the highest or lowest mean sea surface temperatures; (ii) differences between taxa, those taxa with the highest or lowest X_0 values; and (iii) the degree of spatial overlap, those areas that had extremely high or low sea surface temperatures. Further details are given in Appendices S1 and S2. Once the particular subset of data had been excluded,

TABLE 1 Median rank order of 16 dominant taxa of net-caught mesozooplankton in the Atlantic sector of the Southern Ocean during the *Discovery Investigations* (October to April 1926–1938) and contemporary era (October to April 1996–2013) with respect to median temperature (M_0) (left) and relative abundance rank (right). In descending order, rankings are from lowest to highest temperatures and from highest to lowest relative abundance. Note that Contemporary relative abundance ranks were based only on Bongo 200-0 m samples. All taxa are arthropods belonging to the subclass Copepoda

Temperature rank					Relative abundance rank		
Taxon	Discovery Investigations		Contemporary era		Taxon	Discovery Investigations	Contemporary era
	M_0 (°C)	Rank	M_0 (°C)	Rank		Rank	Rank
<i>Microcalanus pygmaeus</i> (Micro)	0.43	1	2.00	2	Oitho	1	1
<i>Metridia gerlachei</i> (M. ger)	0.89	2	2.04	3	Cteno	2	2
<i>Calanoides acutus</i> (C. acu)	1.08	3	2.51	7	Oncae	3	3
<i>Oncaea</i> spp. (Oncae)	1.08	4	2.50	6	C. acu	4	5
<i>Pareuchaeta antarctica</i> (P. ant)	1.14	5	2.00	1	Micro	5	8
<i>Racovitzanus</i> (Racov)	1.21	6	2.27	4	C. pro	6	8
<i>Calanus propinquus</i> (C. pro)	1.26	7	2.36	5	C. sim	7	3
<i>Ctenocalanus vanus</i> (Cteno)	1.47	8	2.89	10	R. gig	8	7
<i>Scolecithricella minor</i> (S. min)	1.70	9	2.59	8	M. ger	9	12
<i>Metridia lucens</i> (M. luc)	1.85	10	3.45	13	S. min	10	9
<i>Oithona</i> spp. (Oitho)	1.88	11	2.68	9	P. ant	11	11
<i>Clausocalanus laticeps</i> (C. lat)	1.90	12	3.48	14	M. luc	12	9
<i>Rhincalanus gigas</i> (R. gig)	2.37	13	3.29	12	C. lat	13	12
<i>Clausocalanus breviceps</i> (C. brev)	3.24	14	3.08	11	Racov	14	15
<i>Calanus simillimus</i> (C. sim)	3.44	15	4.30	16	C. brev	15	14
<i>Subeucalanus longiceps</i> (S. lon)	3.86	16	4.27	15	S. lon	16	15

community relative abundance ($CRel_A$) trajectories were generated and the X_0 value determined. This was compared to the original value of the opposing era and tested statistically to determine if the difference in X_0 between eras remained significant.

2.5 | Comparison of relative abundance ranks between eras

To establish whether community structure had altered between eras, rankings in relative abundance of individual taxa were compared. For contemporary samples, only the Bongo nets that fished from 200-0 m were used for the comparison, given that they were the closest in sampling method to the N70V nets. Differences in the sampling efficiencies of the nets were accommodated through conversion factors derived from corresponding in situ net trials (Ward, Tarling, Coombs, & Enderlein, 2012). Briefly, when both nets were fished to a depth of 200 m, the Bongo net captured ~3 times more copepods overall than the N70V and ~4 times more if the <0.5 mm body length size class alone was considered. Above a body length of 1 mm, the difference in favour of the Bongo net was broadly invariant, averaging 1.7 across all other classes. Therefore in the case of copepod life stages in the <0.5 mm and 0.5–0.99 mm size classes, which numerically dominated the plankton, we determined the Bongo: N70V ratio for each individual taxon and applied this factor to the N70V data. For size groups >1 mm, the average factor of 1.7

was applied. Where stage structure of a species was not distinguished, we have summed abundances of all stages and used an average factor. In the present study, the N70V nets routinely divided the 250-0 m water column into three depth strata (250-100, 100-50 and 50-0 m) and so, for each station, the contents of each net were summed and averaged over the entire 250 m.

3 | RESULTS

In an examination of the summer (October to April) sea surface temperature in our two sampling periods, we determined a significant degree of warming with a median increase of 0.74°C from the *Discovery Investigations* (1920s–1930s) to contemporary times (Mann–Whitney, $T = 11,545$, $n = 91, 106$, $p < .001$, Figure 2).

The median value of X_0 (i.e. the sea surface temperature at which community relative abundance peaked) was 1.27°C (SD 0.29°C) during the 1920–1930s and 2.26°C (SD 0.22°C) during contemporary times (Figure 2). Bootstrap analyses determined these peaks to be significantly different (t test, $t = -14.989$, 58 df , $p < .001$) with X_0 being 0.98°C warmer in contemporary times compared to the 1920–1930s.

We found the significant difference in X_0 between eras was not altered by (i) the influence of extreme years, (ii) peripheral spatial regions and (iii) taxa with affinities to comparatively high or low

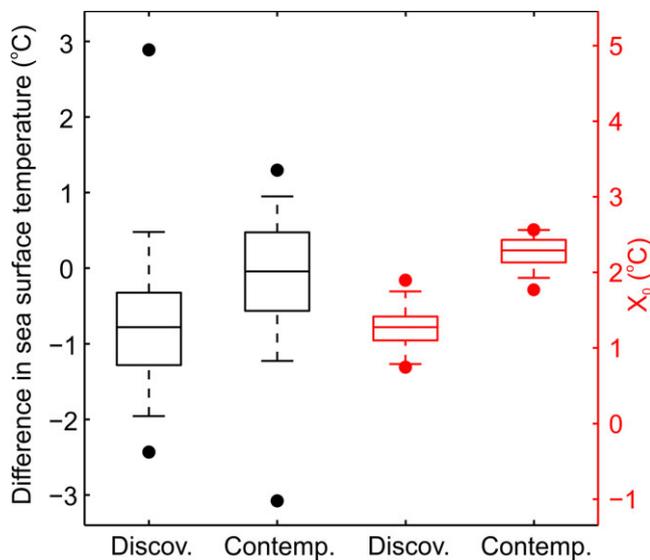


FIGURE 2 Comparison of sea surface temperature offset (black) and the temperature of peak mesozooplankton community abundance (X_0 , red) between October and April in the Southern Ocean Atlantic sector (65–49°S, 80–20°W) during the *Discovery Investigations* (October to April 1926–1938) and contemporary times (October to April 1996–2013). The horizontal line within each box denotes, respectively, the median value of temperature offset and the median X_0 , upper and lower box limits, the 25th and 75th percentiles, whiskers, 5th and 95th percentiles, and dots, maximum and minimum. Sea surface temperature offset values represent the difference between sample station values and the World Ocean Atlas (WOA) 2013 v2 monthly mean 1° surface climatology over 2005–2012. Differences were averaged for every grid cell containing at least one sampling station

temperatures (Table 2, see also Appendix S1). Therefore, all data were included in the final analysis. Compared to a warming in X_0 between eras of 0.98°C when analysing the entire dataset, the three exclusion tests found the smallest degree of such warming in X_0 to be 0.64°C and the largest, 1.24°C. Across all three exclusion tests, there was a consistent trend towards warming in X_0 to within $\pm 0.3^\circ\text{C}$ of the mean level. The level of warming in X_0 was most sensitive to the inclusion or exclusion of peripheral spatial regions. The taxa chosen to represent the mesozooplankton community was found to have less of an influence on X_0 , which reflects that the difference between eras was not overly dependent on including or excluding any one taxon in the analysis.

Nevertheless, each taxon showed a different distributional relationship to sea surface temperature (Figure 3). In the contemporary era, species such as *Metridia gerlachei* and *Calanus propinquus* had values for M_0 (the median temperature of occurrence) close to 2°C while those of *Calanus simillimus* and *Subeucalanus longiceps* were around 4°C. This reflects differing biogeographic affinities of these species, with the former pair being considered as true Antarctic inhabitants, rarely found north of the Polar Front, while the latter pair span both Antarctic and sub-Antarctic water masses. Despite these different temperature distributions, we found a high degree of uniformity in the response to ocean

warming, with the M_0 values of 15 out of the 16 taxa being higher in contemporary times than in the 1920s–1930s, with the difference being between 0.4 and 1.6°C (Figure 3). The ranking of taxa according to M_0 values did alter between the eras (Table 1) with species such as *Pareuchaeta antarctica* and *Clausocalanus breviceps* showing below average increases between the 1920s–1930s and contemporary times, moving them towards colder rankings and others, such as *Calanoides acutus*, above average increases, making their rankings warmer. We did not observe species replacement or a major shift in rank of the dominant zooplankton taxa in terms of relative abundance between the two sampling periods (Table 1). Those taxa that did increase in rank abundance between eras, such as *Calanus simillimus* and *Metridia lucens*, were more associated with warmer waters while taxa which decreased in rank abundance by a similar order, such as *Microcalanus pygmaeus* and *Metridia gerlachei*, had colder temperature distributions. Nevertheless, the median place shift in abundance rank order between eras was 1, signifying only a marginal biogeographic change in community composition.

Geographic projections of CRE_A show that community peak abundance occurred in much the same locations in both eras (Figure 4), which was around 60°S to 62°S in the Drake Passage, then broadening and moving northwards across the Scotia Sea to envelope South Georgia, before narrowing into a band between 52°S and 55°S east of South Georgia. Comparatively, the distribution of peak abundance was slightly wider in 1920s–1930s (Figure 4a) than in contemporary times (Figure 4b), which reflects the broader temperature relationship function ($G_{(T^\circ\text{C})}$) in the former era (See Appendix S2). In Figure 4d, we assume that the mesozooplankton community maintains its relationship to surface temperature as observed in the 1920s–1930s and project this relationship onto the surface temperature conditions of the contemporary era. This predicts that peak community abundance would occur further south by approximately 500 km, occurring below 62°S in Drake Passage and remaining south of South Georgia and below 55°S further east. This projection severely underpredicts mesozooplankton community abundance levels in the northern half of the survey region and overpredicts it to the south, compared to contemporary observations (Figure 4e).

4 | DISCUSSION

We found that, in the intervening period between the *Discovery Investigations* (1926–1938) and contemporary times (1996–2013), the relationship between mesozooplankton community abundance and sea surface temperature changed, with the temperature of peak community abundance (X_0) being 0.98°C warmer in contemporary times compared to the 1920s–1930s. In spatial terms, this changed thermal relationship was manifested in peak community abundance remaining in approximately the same location between the two eras despite a poleward shift in surface isotherms. The observed warming did not alter community composition, with the

TABLE 2 Tests to determine the effect of the exclusion of certain subsets of data on X_0 , namely years or spatial regions that were either extremely warm or cold, or those species whose distributional ranges were the warmest or the coldest (*Calanus simillimus* and *Microcalanus* spp. respectively). Mean X_0 represents the mean (± 1 SD) surface temperature at which peak community relative abundance occurs. The mean difference to the opposing dataset was calculated as the modulus difference in X_0 values between the dataset from which a subset had been excluded and the original dataset of the opposing era. All differences were found to be statistically significant at $p < .05$

Excluded data	1920s–1930s		Contemporary	
	Mean X_0 (°C)	Mean difference to contemporary era (°C)	Mean X_0 (°C)	Mean difference to <i>Discovery investigations</i> era (°C)
None	1.27 (0.29)	0.98	2.26 (0.22)	0.98
High temperature year	1.05 (0.30)	1.21	2.38 (0.17)	1.11
Low temperature year	1.50 (0.36)	0.76	2.38 (0.19)	1.11
Warmest sectors	0.97 (0.29)	1.29	2.25 (0.20)	0.98
Coldest sectors	1.62 (0.49)	0.64	2.40 (0.33)	1.13
<i>Microcalanus</i> spp.	1.25 (0.26)	1.00	2.31 (0.21)	1.04
<i>Calanus simillimus</i>	1.02 (0.38)	1.24	2.28 (0.33)	1.00

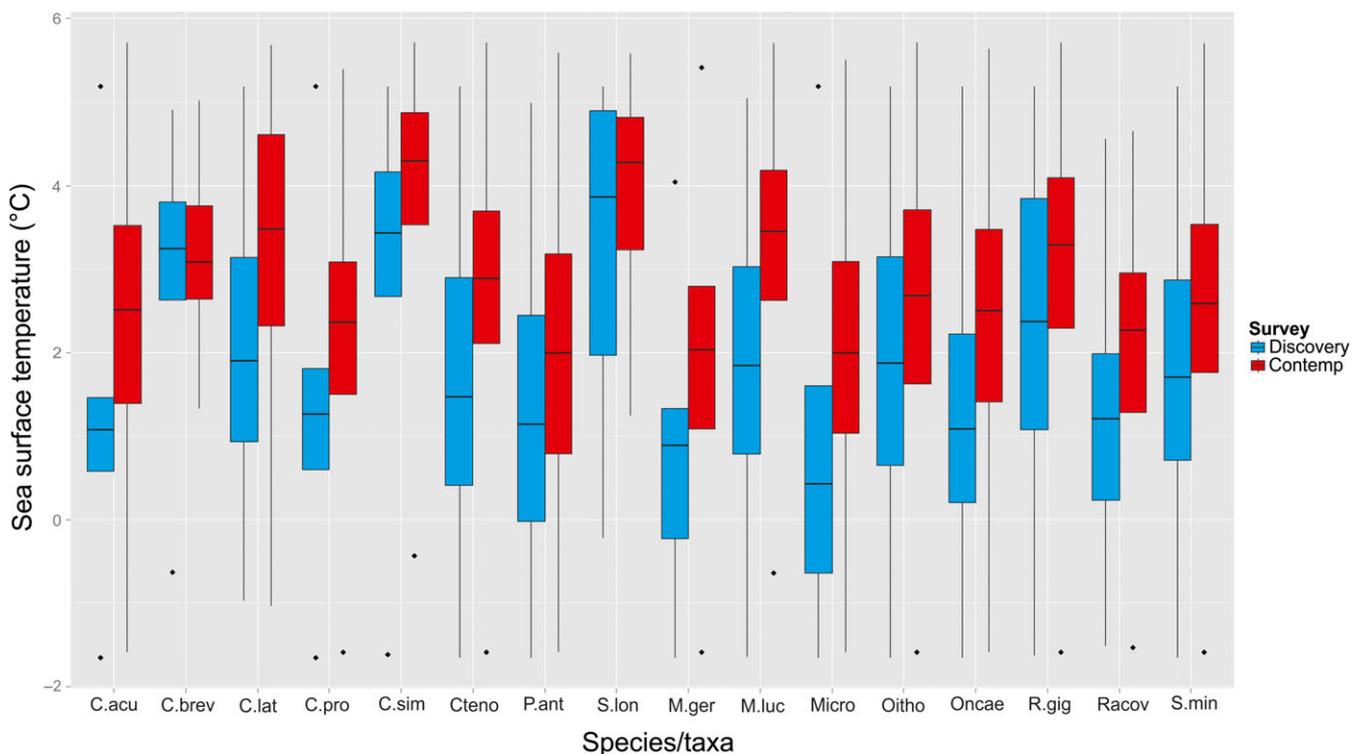


FIGURE 3 Sea surface temperature ranges of individual mesozooplankton taxa between eras. Sea surface temperature ranges of 16 dominant taxa (in terms of abundance and biomass) in the Southern Ocean Atlantic sector ($65\text{--}49^\circ\text{S}$, $80\text{--}20^\circ\text{W}$) during the *Discovery Investigations* (October to April 1926–1938) and contemporary times (October to April 1996–2013). The horizontal line in each box represents the median temperature of occurrence (M_0). Upper and lower box limits denote the 25th and 75th percentiles, whiskers, 5th and 95th percentiles, and dots, maximum and minimum. The names of taxa have been abbreviated, as detailed in Table 1

species assemblage and the relative abundance of key species within the community remaining principally unchanged with the exception of two warmer water species that became marginally more abundant in contemporary times. Individually, as well as combined, key mesozooplankton in the Southern Ocean now peak in abundance at surface temperatures towards the outer limits of the 1920s–1930s thermal envelope.

When we assumed that the mesozooplankton community maintained the same relationship with temperature as seen in the 1920s–1930s, peak abundance in contemporary times was predicted to be up to 500 km further south. This was a severe overprediction of contemporary abundance observations in that region, in contrast with abundances further north, which were underpredicted. The assumption that communities remain within their thermal envelope,

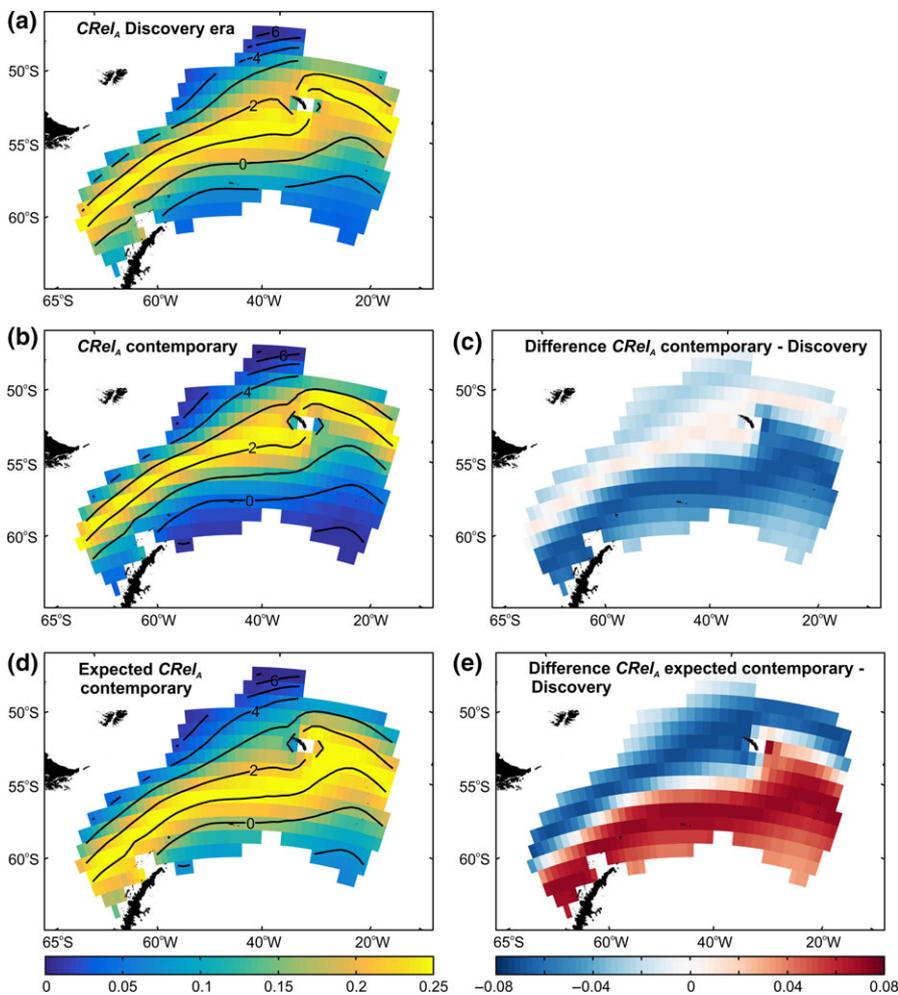


FIGURE 4 Projected distributions of observed and predicted mesozooplankton community abundance between eras. Zooplankton community relative abundance anomaly ($CRel_A$) as f(sea surface temperature) in the Southern Ocean Atlantic sector during the *Discovery Investigations* (October to April 1926–1938) and contemporary times (October to April 1996–2013). (a) $CRel_A$ for *Discovery Investigations*. (b) $CRel_A$ for contemporary times. (c) Difference between $CRel_A$ for contemporary times and *Discovery Investigations*. (d) Expected present day $CRel_A$ assuming the zooplankton community maintained a fixed relationship with sea surface temperature since the *Discovery Investigations*. (e) Expected difference in $CRel_A$ from *Discovery Investigations* era to contemporary times had the relationship to sea surface temperature remain fixed (d–a). Mean sea surface isotherms ($^{\circ}C$) for October–April for the *Discovery Investigations* (a) and contemporary times (b, d) are plotted

or within the limits of other key environmental variables, and shift their distribution accordingly is one that is widely made in attempts to predict the impacts of future climate change (Guisan & Thuiller, 2005; Helaouet & Beaugrand, 2007) and is supported by a wide body of empirical evidence (Parmesan & Yohe, 2003). In a consideration of multidecadal range changes in the *Calanus finmarchicus* and *C. helgolandicus* populations of the North Atlantic and adjacent subarctic regions for example, Hinder et al. (2014) found that the abundance vs. sea surface temperature relationships of both species remained relatively fixed over time. In the Southern Ocean, Mackey et al. (2012) assumed a fixed relationship between macrozooplankton species distribution and sea surface temperature and predicted a general poleward movement as a result of a $1^{\circ}C$ rise. Our findings show that a fixed relationship between species distribution and sea surface temperature cannot be assumed in the case of the Southern Ocean mesozooplankton community.

The changed relationship between Southern Ocean mesozooplankton and sea surface temperature between the 1920s and 1930s and contemporary times is likely to reflect the particular set of circumstances faced by zooplankton communities in this polar region. Unlike the northern hemisphere, where there is geographic scope to move polewards to comparatively high latitudes, the potential for poleward displacement in the Southern Hemisphere is limited

because of the Antarctic continental landmass, strong circumpolar currents and extensive sea-ice. Specifically, within the Atlantic sector, surface waters of the Antarctic Circumpolar Current flow in a northeastward direction and are bounded to the south by the cyclonic Weddell Gyre, where sea-ice persists until late in the Antarctic summer. Large-scale poleward range shifts are therefore not presently possible for Southern Ocean populations.

Furthermore, factors other than temperature may dominate distribution and abundance in this region, particularly the availability of phytoplankton. Park, Ohb, Kim, and Yoo (2010) have shown that regular and predictable phytoplankton blooms occur in only a small proportion of the southwest Atlantic sector of the Southern Ocean, but primary production is generally high throughout much of the region that we identified to contain peak abundances in mesozooplankton. Primary production in this region generally occurs from November onwards, facilitated variously by the supply of limiting nutrients to the upper mixed layer via deep mixing, topographic upwelling or water column stabilization particularly in the region of the retreating ice-edge (Park et al., 2010). This would facilitate zooplankton recruitment and underpin the distribution patterns we observe through the summer months. We cannot quantitatively assess whether chlorophyll distribution and periodicity has changed appreciably in the 60 years between sampling eras but it is unlikely

given that mixing and topographical supply of limiting nutrients are so important within the region. In particular, there is strong evidence that iron availability controls the distribution and biomass of phytoplankton in the southwest Atlantic sector, since high Chl-*a* concentrations are mainly associated with temperature and density profiles that indicate mixing between Antarctic Circumpolar Current waters and iron enriched waters originating from coastal regions or from upwelling of deeper waters associated with bathymetric features (Holm-Hansen et al., 2004). By contrast, the distribution of primary productivity in the Arctic is tightly coupled to the extent and timing of sea-ice, which affects the availability of light and nutrients (Tremblay, Michel, Hobson, Gosselin, & Price, 2006) meaning that zones of high productivity are much less likely to be geographically fixed. Consequently, ocean warming and sea-ice retreat will have a large impact on the distribution of high productivity zones in the Arctic (Popova et al., 2012).

Another major factor that influences the distribution of many polar mesozooplankton species is their lifecycle patterns, particularly for those that spend parts of their life in deeper water masses. Over seasonal cycles, many mesozooplankton taxa change vertical distribution, moving between overlying water masses (Atkinson, 1990). During spring and summer, the majority of Southern Ocean mesozooplankton have a modal depth that is centred in Antarctic Surface Water (AASW, between 0 and 100 m). However, by autumn, taxa such as *Calanoides acutus*, *Calanus simillimus*, *Rhincalanus gigas* and *Eucalanus longiceps* descend to the Winter Water layer between 100 and 250 m and, by winter, they have largely descended beyond 250 m where they occupy Circumpolar Deep Water (CDW). Although there has been reported warming of the CDW over recent decades (Gille, 2008; Schmidtko, Heywood, Thompson, & Aoki, 2014), it is an order of magnitude lower than that of the AASW. From a physiological perspective therefore, the temperature experienced by mesozooplankton species inhabiting the CDW during winter has essentially remained unchanged over the last century. Wintertime occupancy of the thermally invariant CDW may allow seasonally migrating species to complete their lifecycles successfully despite the physiological challenge of occupying the increasingly warm AASW during summer. For some deep diapausing species, such as *Calanoides acutus*, the overwintering phase of the lifecycle may be even more influential, with the species spending up to 8 months a year in the CDW at depths of around 1,000–1,500 m (Andrews, 1966). Spending only a limited period within the surface layers may explain how this species was able to tolerate one of the largest degrees of warming in M_0 (the median sea surface temperature of occurrence) between the two eras.

Even for those mesozooplankton taxa that largely remain in the surface layers year round, such as *Oithona* spp., *Clausocalanus laticeps* and *Ctenocalanus vanus*, there is marked seasonality in temperatures that are likely to condition their physiology. A flexibility and responsiveness to changing environmental conditions allows species to optimize their performance over annual cycles. For instance, in the Arctic, Freese, Søreide, and Niehoff (2016) found distinct seasonal oscillations in digestive enzyme activity in the copepod *Calanus*

glacialis with much lower activity levels during winter, while Lischka, Giménez, Hagen, and Ueberschär (2007) found differing seasonal patterns in digestive enzyme between two further Arctic copepod species, *Pseudocalanus minutus* and *Oithona similis*, with a spring activity peak in the former and a lower level of seasonal oscillation in the latter. The differing patterns of activity in each species reflect the diversity in their respective lifecycle strategies, both in terms of timing of reproduction and peak energy demand and their optimal diets. A community level response to ocean warming will typically be comprised of such a mixture of responses at the species level.

In the southwest Atlantic sector of the Southern Ocean, seasonal oscillations in sea surface temperatures between summer and winter range between 3 and 5°C (Venables et al., 2012). This is considerably less than the 10°C seasonal change experienced by subpolar and temperate pelagic species. Nevertheless, even a 3°C seasonal oscillation means that higher temperatures in contemporary Southern Ocean sea surface environments were at least within the experience of the populations that existed in the 1920 and 1930s, if at the outer limits. This Southern Ocean region is also notable for the high numbers of mesoscale eddies and large meanders of oceanographic fronts, particularly the Polar Front and the Southern Antarctic Circumpolar Current Front, which result in short-term oscillations in sea surface temperatures of several degrees across much of the survey area of the present study (Barré, Provost, Renault, & Sennéchal, 2011; Boehme, Meredith, Thorpe, Biuw, & Fedak, 2008; Moore, Abbott, & Richman, 1999; Venables et al., 2012). Only species that are resilient to such variability in sea surface temperature will succeed within these Southern Ocean environments, which may further precondition them to longer term thermal changes.

Our finding that the spatial distributions of Southern Ocean mesozooplankton communities have not advanced polewards despite surface layer warming in the Atlantic sector over at least the past six decades has meant that the lower trophic levels of this system have remained relatively stable in the face of at least one facet of environmental change. This is key not only to our understanding of the resilience of marine food webs to climatic change but also to decision making regarding the location and timing of fisheries while accounting for the wider ecosystem impacts (Constable et al., 2014; Watters, Hill, Hinke, Matthews, & Reid, 2013). At present, most projections of ecosystem response do not factor in the capacity of the resident communities to be resilient to change and retain locations and distributional ranges (Angilletta, 2009). Efforts to parameterize potential resilience in a mechanistic way must be increasingly undertaken if we are to predict the future distributional ranges of species and communities in a robust manner.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Paper 8

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Temporal changes in abundances of large calanoid copepods in the Scotia Sea: comparing the 1930s with contemporary times

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Abstract

To investigate whether impacts of reported climate change in the Antarctic marine environment have affected mesozooplankton populations, we compared the summertime abundances of four species of large calanoid copepods from samples taken during the *Discovery Investigations* (1926–1938) and contemporary times (1996–2013). *Discovery* samples were obtained using an N70V closing net fished vertically through three depth horizons encompassing the top 250 m of the water column, whereas contemporary samples were obtained using a Bongo net fished vertically through 200–0 m. Data from a previous study comparing catch efficiencies of the two nets were used to generate calibration factors which were applied to the N70V abundances. Following further corrections for net depth differences and seasonal biases in sampling frequency, three of the four species, *Calanoides acutus*, *Rhincalanus gigas* and *Calanus simillimus*, were found to be between ~20–55% more abundant in contemporary times than they were 70 years ago. *Calanus propinquus* was marginally more abundant in the *Discovery* era. These results were robust to sensitivity analyses for the net calibration factor, seasonal bias and net depth corrections. Although near-surface ocean temperatures within the Scotia Sea have increased by up to 1.5 °C during the last 70 years, we conclude that the most likely causes of increased copepod abundances are linked to changes in the food-web. In particular, we discuss the reported decrease in krill abundance in the South Atlantic that has potentially increased the amount of food available to copepods while at the same time decreasing predator pressure.

Keywords *Discovery Investigations* · Calanoid copepods · Scotia Sea · Climate change · Trophic cascades

Introduction

The impacts of climate change are being felt worldwide in the marine environment. Species and communities are responding to complex interactions of environmental forcing factors such as increasing temperature, ocean acidification and ocean-atmospheric coupling, which exert their effects over a range of spatial and temporal scales (Richardson 2008; Hátún et al. 2009; Burrows et al. 2011; Richardson et al. 2012; Poloczanska et al. 2013).

In the Southern Ocean, warming has been taking place for at least the last 50–70 years (Gille 2002; Meredith and King 2005; Whitehouse et al. 2008) and has been attributed to near-surface ocean–atmosphere–ice interactions (Turner

et al. 2013). Consequences of warming have included regional changes in sea-ice extent and duration (Stammerjohn et al. 2008) which has subsequently been suggested as a major factor in the recent decline of Antarctic krill and increases in salp abundance (Loeb et al. 1997; Atkinson et al. 2004; Flores et al. 2012).

Impacts of environmental change on other planktonic groups are however less well understood (Constable et al. 2014). Copepoda are the dominant mesozooplankton group in the Southern Ocean but the factors affecting their distribution and abundance have been harder to establish, in part because of a lack of extensive time-series measurements. Changing patterns of atmospheric variability such as the Southern Annular Mode (SAM) which has an important influence on zonal winds (Sen Gupta and McNeil 2012) and the Southern Oscillation Index (SOI) have been linked to changes in plankton abundance. For example, near Elephant Island, Loeb et al. (2009, 2010) found significant correlations between the abundance and concentration of phytoplankton, zooplankton and krill with the SOI which

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exhibited 3–5 year frequencies characteristic of El Niño–Southern Oscillation (ENSO) variability. They found that abundances of *Calanoides acutus*, and *Rhincalanus gigas*, characteristic of the Antarctic Circumpolar Current (ACC), were positively correlated with chlorophyll *a* (Chl *a*) and the SOI. These changes appeared related to the influence of the SOI on water mass movements, with high copepod abundances associated with a southwards movement of ACC waters into the coastal regions off the northern–Antarctic Peninsula. Conversely, during periods when the sign of the SOI was negative, salps tended to become dominant. However, at South Georgia, abundances of krill and copepods were found to be negatively related across a range of scales suggesting direct interactions either as competitor or predator (Atkinson et al. 2001), rather than being solely mediated by ocean–atmosphere coupling. Thus, the balance of zooplankton composition represents a complex of oceanic–atmospheric—sea-ice and competitive interactions which are only just beginning to be teased apart.

Over a longer timescale, Tarling et al. (2018) compared copepod distributions in the Scotia Sea from *Discovery Investigations* (1920s–1930s) and contemporary times (1996–2013) and showed that, over intervening years, populations have essentially remained in the same geographical location despite ocean warming. Had they occupied the same thermal envelope which they inhabited in the 1930s, current distributions would be up to 500 km further south (see also Mackey et al. 2012). Reasons for maintenance of their historical distributions were attributed to food availability and the properties of the underlying water masses where a number of the species over-winter. It was also found that there had been a negligible difference in the rank order of abundance of dominant copepod species sampled over 70 years apart. However, ranked abundance can mask numerical changes, particularly if some species/taxa are extremely abundant and others less so. In this paper, we explore this further and have focussed on the commonly occurring biomass-dominant large calanoid copepods (*C. acutus*, *R. gigas*, *Calanus simillimus* and *Calanus propinquus*). We wished to establish whether abundances were the same between eras and, if not, to seek to understand what factors may lie behind any changes.

Methods

Copepod net sampling and abundance

Net sample stations

We analysed net samples from stations south of the Polar Front in the southwest Atlantic sector of the Southern Ocean, collected as part of the *Discovery Investigations*

(1926–1938) and during contemporary cruises (1996–2013). Our analysis was confined to samples taken in the austral summer months of December–February, between the latitudes of 52–66°S.

The species under consideration have broad and overlapping distributions within the ACC although repeated sampling has shown that *C. simillimus* and *R. gigas* have more northerly distributions compared to *C. acutus* and *C. propinquus* which tend to inhabit colder waters to the south (Atkinson 1998; Schnack-Schiel 2001). The timing of their lifecycles and the presence of populations in near-surface waters vary according to latitudinal progression of the seasons (earlier in the north) with recruitment occurring up to 3 months earlier in some years in the northern parts of the ACC compared to the south (Ward et al. 2006, 2012a). In comparing between the two eras, we have assumed that any changes in the timing of the annual pattern of occurrence of species stages has been captured within the 3 summer months (December, January and February) on which the analysis focussed.

Stations were determined to be south of the Polar Front from the vertical temperature profile recorded at each station (Gordon et al. 1977; Tarling et al. 2018). The *Discovery* sample set accordingly comprised 53 N70V vertical closing net stations supplemented with an additional 10 N70V stations sampled during December 1926 and January 1927, for which catch data were extracted from *Discovery Report 11* (appendix of Hardy and Gunther 1935). The contemporary dataset comprised catches made with a paired Bongo net at 147 stations (Fig. 1).

Net sample analysis

During sample analysis, the copepodite stages and adults of large calanoid copepod species were either enumerated from complete samples, or the whole sample placed in a Folsom plankton splitter and fractionated into replicate aliquots until countable numbers (~200 individuals) were estimated to be present. Abundances of taxa were standardised to numbers per net sample and the amount of water each net filtered was estimated based on mouth area and distance towed, to derive individual species concentrations (ind. m⁻³). Of the large calanoid species, four were consistently present across the majority of samples and became the focus of subsequent numerical analyses, those species being *R. gigas*, *C. acutus*, *C. simillimus* and *C. propinquus*.

Data preparation

Accounting for different integrated depths

At each *Discovery* station samples were collected from three depth horizons (50–0, 100–50 and 250–100 m) and

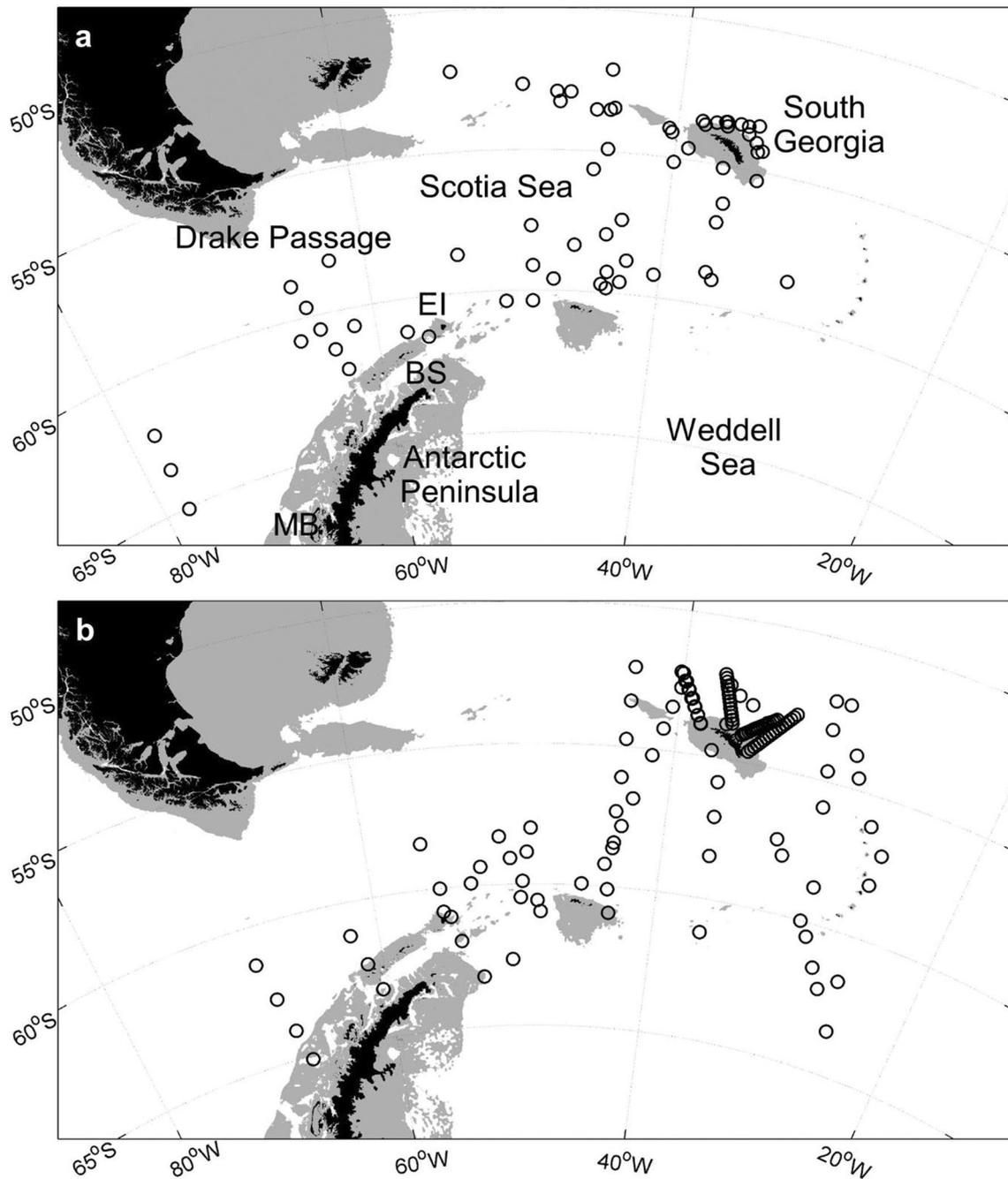


Fig. 1 Zooplankton sample distribution. **a** *Discovery Investigations* (1926–1938). **b** Contemporary era (1996–2013). Bathymetry shallower than 500 m is shaded grey. Place name abbreviations on (a) are Bransfield Strait (BS), Elephant Island (EI), Marguerite Bay (MB)

abundances integrated from 250 to 0 m. Contemporary samples were collected between 200 and 0 m. Copepod abundances were determined in terms of concentrations as individuals per cubic metre (ind m^{-3}) for both sets of samples. However, the majority of copepods reside in the top 200 m at this time of year (Atkinson 1991; Atkinson and Sinclair 2000) which potentially reduces concentrations in

the *Discovery* samples relative to the contemporary samples because of the extra 50 m depth contributing to overall sample volume. Therefore, we multiplied *Discovery* abundances by 1.25 to account for this potential bias. Both sets of samples were subsequently multiplied by 200 m to derive a depth integrated abundance value for the 0–200 m surface layer (ind. m^{-2}).

Accounting for net type bias

Different net types were used in the two eras of sampling. The *Discovery Investigations* collected N70V samples from nets deployed vertically between the 3 horizons (see above) within the surface 250 m (Kemp et al. 1929). Mesh sizes in this net decrease in stages from 5 mm in the upper part, to 440 μm and then 195 μm in the mid and lower parts respectively (measurements are metric equivalents of the original imperial units; see Kemp et al. 1929). In contrast, the contemporary samples were collected from Bongo net deployments (net dia. 0.61 m, 200 μm mesh net) fished vertically from 200 to 0 m.

To enable a comparison between the two net types, an N70V net was reconstructed using nylon mesh of the nearest metric equivalent to the imperial measurements of the bolting silks originally specified in Kemp et al. (1929). The nets were fished alongside each other at a series of stations in Marguerite Bay on the Antarctic Peninsula and across the Scotia Sea to determine a broad spectrum calibration factor (Ward et al. 2012b). For the present study, we re-analysed these data to establish species-specific inter-calibration factors for the four principal calanoid species under consideration.

One particular issue was to take into account the different developmental stages (CI to adult) of the sampled copepods, since the changes of size may alter respective catchabilities and retentions by the two different nets. We therefore compared the abundances of each individual developmental stage of each of the 4 species in every calibration station of Ward et al. (2012b) to determine the average residual difference (Res), as follows:

$$Res_{s,d} = \frac{\sum_{station=1}^n (N_{B,s,d} - N_{N70,s,d})}{n} \quad (1)$$

where N is abundance (ind. m^{-2}) of either the calibration Bongo net, B , or the calibration N70V net, $N70$, s is species and d is developmental stage from CI to adult (male and female).

It was also necessary to take into account the relative contribution of each of these developmental stages to total species abundance. In certain *Discovery* samples, some individuals had previously been removed and although numbers taken were specified on sample labels, stage distributions were not. Data taken from Hardy and Gunther (1935) were also simply reported as species numbers rather than by stage. Therefore, it was necessary to infer typical proportional stage distributions from the contemporary samples. Hence, $Res_{s,d}$ was multiplied by the relative proportion of stages within species in the contemporary samples ($Pr_{s,d}$), so that a standardised residual difference, $SRes_{s,d}$, could be determined as follows:

$$SRes_{s,d} = Res_{s,d} \times Pr_{s,d} \quad (2)$$

$SRes_{s,d}$ was divided by the average abundance of the N70V calibration hauls to produce a normalised developmental stage specific calibration factor ($Cal_{s,d}$) which was then summed across all stages to produce a species-specific calibration factor (Cal_s):

$$Cal_{s,d} = \frac{SRes_{s,d}}{(\sum_{station=1}^n N_{N70,s})/n} \quad (3)$$

$$Cal_s = \sum_{d=d_1}^{d=d_t} Cal_{s,d} \quad (4)$$

where d_j is development stage 1 (CI), d_t is final adult stage (male and female).

Discovery sample abundances ($N_{DI,s}$) were then multiplied by $1 + Cal_s$ to determine a calibrated abundance ($N_{Dical,s}$) with which to compare against contemporary abundances ($N_{C,s}$):

$$N_{Dical,s} = N_{DI,s} \times (1 + Cal_s). \quad (5)$$

Accounting for seasonal bias

Further data analyses revealed a seasonal trend in datasets whereby there was a substantial increase in abundances in January compared to December and February in both the *Discovery Investigations* and contemporary sample sets. However, sampling effort varied between the two eras, with there being a proportionally greater sampling effort in January in the contemporary dataset compared to the *Discovery* dataset. To account for this potential bias, we resampled the two datasets so that there was even selection of datapoints across the 3 months. For both the *Discovery* and contemporary datasets ($N_{Dical,s}$ and $N_{C,s}$), 10 datapoints were selected at random (with replacement) from each of the 3 months and combined to make a new resampled dataset of 30 datapoints, for which an average was determined. The process was repeated 100 times for each species, to which statistical tests were then applied (see below).

Sensitivity analyses

To determine the sensitivity of the inter-era comparison of species abundance to the various stages in data preparation, a series of sensitivity analyses were run. The two main treatments to the original datasets were the inter-calibration of abundances caught by the two different nets and the resampling to account for seasonal sampling bias, so the objective of the sensitivity analysis was to determine whether species-specific abundances remained significantly different between eras when treatments were altered. For the calibration factor

sensitivity tests, the factors were increased by 25, 50 and 100% or removed completely. Multiplying the calibration factor by percentages below 0 was not considered given that this would always act to increase the level of difference between the two eras. For the seasonality sensitivity tests, runs were carried out to determine the effect of removing the resampling process. The 1.25 multiplication factor to the *Discovery* nets was also removed in a further test to determine its implications.

Statistical tests

Comparisons of abundances between eras were tested either using an unpaired *t* test or a Mann–Whitney Rank Sum test (*U* test), the latter being used in instances where the datasets failed a priori tests for normality (Shapiro–Wilk test) or equal variance. A Kruskal–Wallis 1-way ANOVA on ranks test was applied to differences between months. Tests producing significant differences were further tested using a Dunn's Method all Pair-wise Multiple Comparison Procedure.

Results

Calibration

To determine the calibration factor, it was necessary to consider the relative proportion of stages within species in the contemporary samples (Fig. 2). Although there was interspecific variation in the relative abundance of developmental stages, the CIII and CIV stages were generally among the most frequent (Fig. 2). For instance, CIII was the most frequent stage in *R. gigas*, with stages CII and CI also being relatively abundant. A similar pattern was apparent in *C. propinquus* although stage CI was comparatively low in abundance while CIV had a similarly high frequency to stage CII. In *C. acutus* and *C. simillimus*, the later developmental stages (CIV and CV) had higher frequencies than the earlier developmental stages. Adult females were more abundant than males in all species, although both were relatively infrequent compared to the earlier developmental stages.

The calibration factor also required the residual difference in species and stage specific abundances to be determined in matched Bongo and N70 hauls. In these hauls, it was found

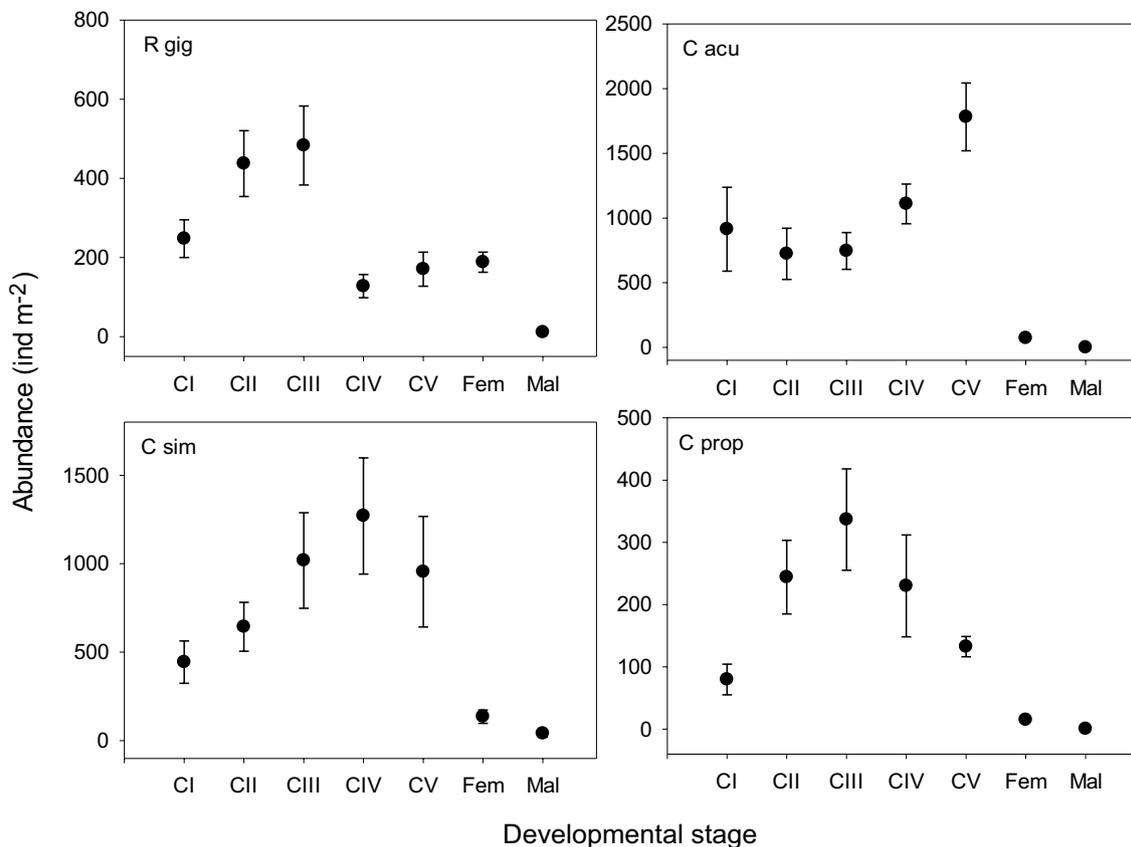


Fig. 2 Development stage abundance (contemporary data only): Average (SE) depth integrated abundance (ind m⁻²) of developmental stages of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* from Bongo net samples in the contemporary era

that more individual copepods were captured by Bongo nets than N70V nets, with the majority of residual differences (i.e. Bongo minus N70V, $Res_{s,d}$) being positive (Fig. 3). The residual differences were much greater in *C. acutus* and *C. simillimus* than they were in *R. gigas* and *C. propinquus*. In *C. acutus*, some of the greatest differences were observed in the early developmental stages, although CIV also exhibited a high value for $Res_{s,d}$. Only CI and CII showed notably high values for $Res_{s,d}$ in *C. simillimus* with a further minor peak in the females. *R. gigas* exhibited a similar peak in $Res_{s,d}$, but there was little pattern in the low values of $Res_{s,d}$ in *C. propinquus*.

The calibration factor ($1 + Cal_s$) is a function of both the residual difference between calibration hauls and relative proportion of stages within species (Table 1). The highest calibration factors were observed in *C. acutus* and *C. simillimus*, for which the highest values for $Res_{s,d}$ were observed. However, the corresponding stage distribution downweighs the calibration factor in *C. acutus* in relation to *C. simillimus*. The calibration factors for *R. gigas* and *C. propinquus* were low since both have comparatively low species abundances and low residual differences.

Comparison of abundances between eras

There were substantial differences in species abundances between the three summer months included in the analysis, with abundance levels in January being almost double those of December and February in both the *Discovery Investigations* and contemporary samples (Fig. 4). The difference between months was significant in both eras (*Discovery Investigations*, Kruskal-Wallis test, $H=7.328$, 2 df, $p=0.026$; Contemporary, $H=7.475$, 2 df, $p=0.024$).

There was a difference in sampling effort between the respective months, with January containing the highest sampling effort in the contemporary dataset and the lowest in the *Discovery Investigations* dataset (Fig. 4). This necessitated data resampling in order to dampen any temporal bias in the comparison of abundances between the two datasets (see "Methods").

The calibrated abundances of *R. gigas*, *C. acutus* and *C. simillimus* in the *Discovery* samples were considerably and significantly lower than those in the contemporary samples (Fig. 5) (*Discovery* vs Contemporary; *R. gigas*: Mann-Whitney *U* Test, $T = 6590.000$ $n(\text{small}) = 100$ $n(\text{big}) = 100$,

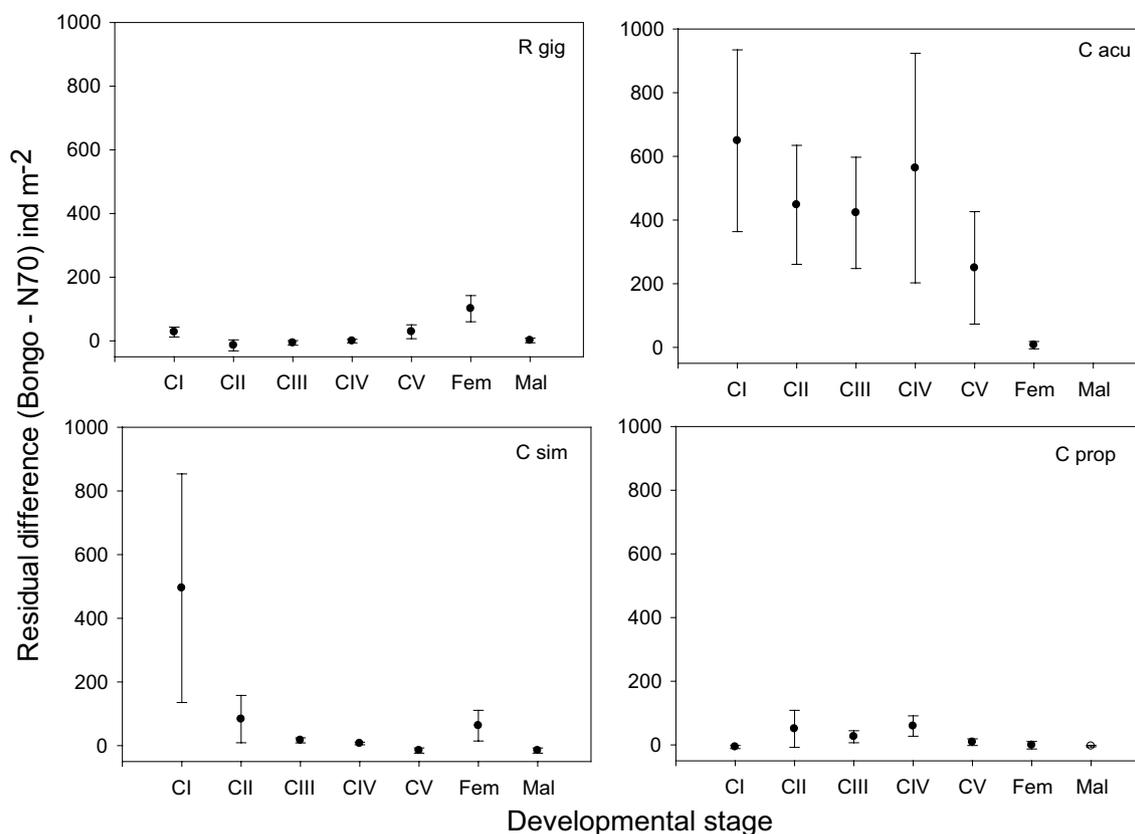


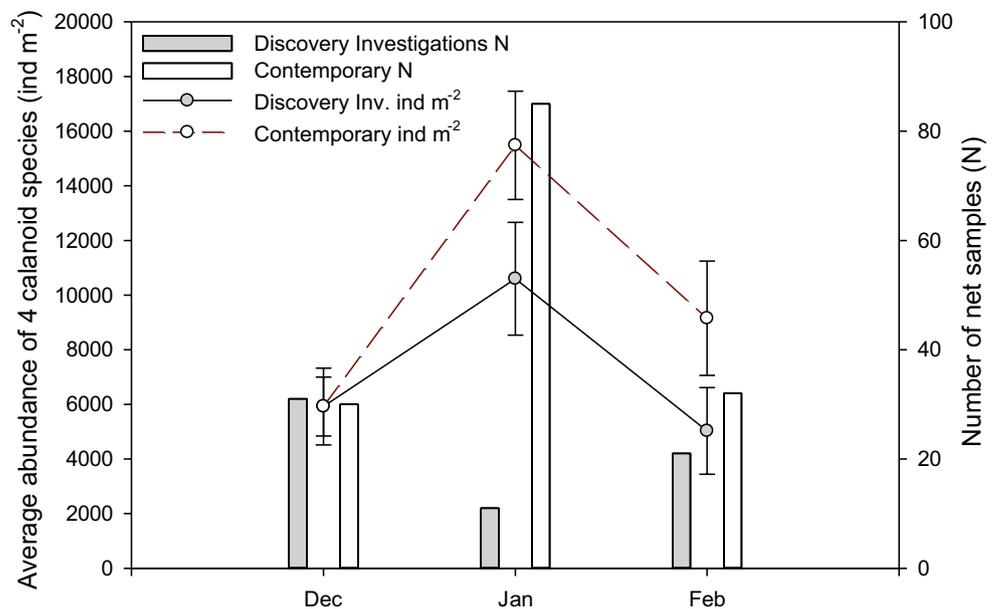
Fig. 3 Residual difference species stage: Residual difference ($Res_{s,d}$ ind m^{-2}) between abundances of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* individual

developmental stages estimated by Bongo nets and N70V nets in simultaneous calibration hauls

Table 1 Calibration factor: Parameters derived in order to determine a Calibration factor (Cal_s) for *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* to standardise abundance estimates of N70V catches during the *Discovery Investigations* against contemporary Bongo catches

	Mal	Fem	CV	CIV	CIII	CII	CI	Calibration factor ($1 + Cal_s$)
<i>R. gigas</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})	1.609	101.527	28.931	-0.420	-6.327	-13.995	28.051	
Stage proportions ($Pr_{s,d}$)	0.013	0.211	0.137	0.064	0.213	0.235	0.127	
Normalised proportional difference ($Cal_{s,d}$)	0.000	0.193	0.036	0.000	-0.012	-0.030	0.032	1.219
<i>C. acutus</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})		7.413	249.952	563.340	422.820	447.800	649.381	
Stage proportions ($Pr_{s,d}$)		0.060	0.393	0.255	0.116	0.077	0.100	
Normalised proportional difference ($Cal_{s,d}$)		0.000	0.090	0.132	0.045	0.032	0.060	1.359
<i>C. simillimus</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})	-15.543	62.503	-15.543	6.633	16.450	83.075	494.562	
Stage proportions ($Pr_{s,d}$)	0.016	0.145	0.116	0.184	0.235	0.192	0.112	
Normalised proportional difference ($Cal_{s,d}$)	-0.002	0.062	-0.012	0.008	0.026	0.109	0.379	1.571
<i>C. propinquus</i>								
Residual difference ($Res_{s,s}$ ind m^{-2})	-3.855	-1.188	8.542	59.011	25.490	50.165	-6.674	
Stage proportions ($Pr_{s,d}$)	0.001	0.073	0.227	0.256	0.245	0.149	0.049	
Normalised proportional difference ($Cal_{s,d}$)	0.000	-0.001	0.018	0.144	0.059	0.071	-0.003	1.289

Fig. 4 Seasonality: Average (SE) abundance (ind m^{-2}) and number of net-catches (N) in individual summer months in *Discovery Investigations* and contemporary sample sets

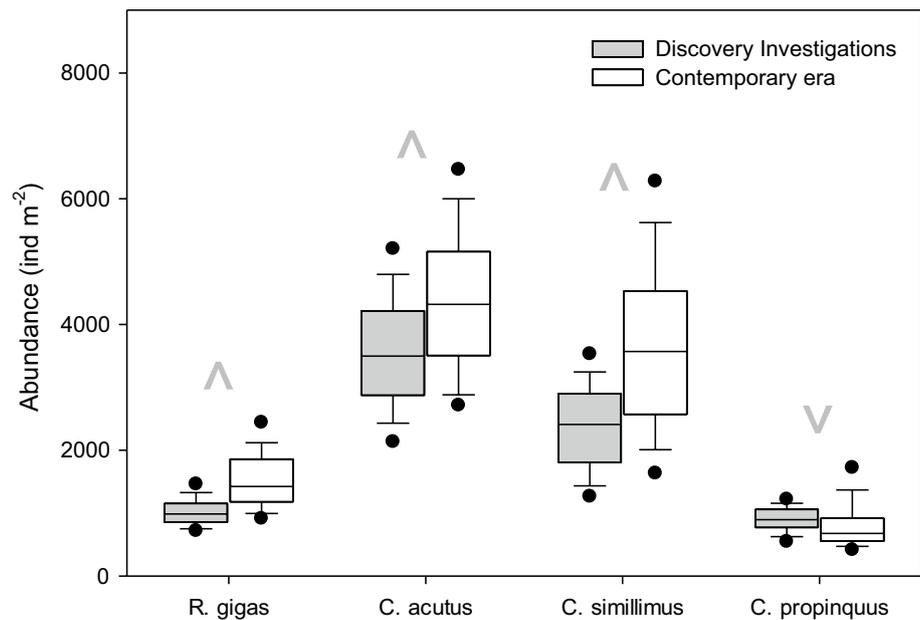


$p < 0.001$, *C. acutus*: $T = 7590$, $n(\text{small}) = 100$ $n(\text{big}) = 100$, $p < 0.001$; *C. simillimus*: $T = 7053.000$ $n(\text{small}) = 100$ $n(\text{big}) = 100$, $p < 0.001$). In the case of *C. acutus*, calibrated abundances were around 80% of the values observed in contemporary times (mean \pm SE of 3553 ± 101 and 4374 ± 116 ind m^{-2} respectively) while, in *R. gigas* and *C. simillimus*, *Discovery* samples were between 65 and 70% of contemporary values (respective mean \pm SE of 1020 ± 22 and 1525 ± 47 ind m^{-2} for *R. gigas* and 2377 ± 70 and 3711 ± 139

ind m^{-2} for *C. simillimus*). However, in *C. propinquus*, the opposite trend was observed, with values being significantly higher in the *Discovery* era (mean \pm SE of 903 ± 21 ind m^{-2} vs 812 ± 41 ind m^{-2} for contemporary era), although the absolute or proportional differences (91 ind m^{-2} and 90% respectively) were not as substantial as for the other species.

Levels of significance in these results were relatively insensitive to the calibration factor (Table 2). When removing the calibration factor altogether or increasing its value

Fig. 5 *Discovery Investigations* versus Contemporary abundance Box plot of estimated abundance (ind m⁻²) of *Rhincalanus gigas*, *Calanoides acutus*, *Calanoides simillimus* and *Calanoides propinquus* during the *Discovery Investigations* and contemporary times. Horizontal line represents the median, limits of boxes, 25th and 75th percentiles, limits of whiskers, 10th and 90th percentiles, dots, 5th and 95th percentiles. ^ indicates abundances during contemporary era were significantly larger than those during the *Discovery Investigation* era, v, that *Discovery Investigation* era abundances were significantly larger than those in the contemporary era ($p < 0.001$)



by 25 or 50%, values in contemporary times were still significantly larger in *R. gigas*, *C. acutus* and *C. simillimus*. Only when the calibration factor was increased by 100% was there any change to this result, with *C. acutus* no longer

significantly more abundant in the contemporary era. Greater sensitivity was exhibited in relation to seasonality in abundance levels, with the removal of the resampling procedure to dampen the effect of different levels of sampling effort

Table 2 Sensitivity: Analyses to determine the sensitivity of *Discovery Investigations* and contemporary estimates of species-specific abundance to the parameters used in the inter-calibration of the respective nets and the standardisation of differences in sampling effort and sampling protocol

	<i>R. gigas</i>		<i>C. acutus</i>		<i>C. simillimus</i>		<i>C. propinquus</i>	
	Disc	Cont	Disc	Cont	Disc	Cont	Disc	Cont
Best run								
Av	1019.84	1525.19	3552.79	4374.24	2376.70	3710.72	902.70	811.96
SE	22.08	47.36	101.39	115.99	70.20	138.52	20.89	41.33
No calibration factor								
Av	733.27	1561.93	2337.57	4191.51	1393.69	3718.40	684.22	774.30
SE	17.99	44.55	61.06	115.45	44.49	160.35	16.64	40.09
Increase of calibration factor by 25%								
Av	934.01	1561.93	3386.55	4191.51	2388.43	3718.40	931.39	774.30
SE	22.92	44.55	88.46	115.45	76.24	160.35	22.64	40.09
Increase of calibration factor by 50%								
Av	974.15	1561.93	3596.35	4191.51	2587.38	3718.40	980.82	774.30
SE	23.90	44.55	93.94	115.45	82.59	160.35	23.85	40.09
Increase of calibration factor by 100%								
Av	1054.45	1561.93	4015.94	4191.51	2985.28	3718.40	1079.69	774.30
SE	25.87	44.55	104.90	115.45	95.29	160.35	26.25	40.09
No normalisation to accommodate seasonal bias in sampling effort								
Av	906.89	1703.46	3597.19	5505.49	1875.33	3610.87	717.53	1029.01
SE	20.41	48.70	107.11	172.16	75.17	150.64	24.11	51.32
Remove 1.25 multiplication factor to <i>Discovery Investigation</i> samples								
Av	653.46	1541.88	2542.84	4084.85	1088.00	3264.01	491.34	728.53
SE	28.29	72.58	148.09	248.98	117.63	219.71	35.96	67.58

Bold indicates where contemporary abundance is significantly greater than that of the *Discovery Investigations*, italics indicates where *Discovery Investigations* abundance is significantly greater than contemporary era abundance, standard text indicates that no significant differences in abundance exist

between months increasing the level of difference between eras, with even *C. propinquus* now exhibiting significantly greater abundances in contemporary times. Removal of the 1.25 multiplication factor to accommodate the different integrated depth intervals between the *Discovery* and contemporary nets had a similar effect, with abundances being significantly greater in contemporary times in all species.

Discussion

In this study we have demonstrated that three of the four species of large calanoids studied have increased in abundance within the Scotia Sea over the past 70 years. Over the same period the Southern Ocean has changed profoundly. There have been significant increases in temperature and, in some regions, reductions in sea-ice, alongside a decline in krill biomass (Atkinson et al. 2004). The commercial extinction of the great whales during the 20th century is also conjectured to have had significant impacts on the functioning of food-webs (Laws 1977, 1985; Willis 2007, 2014; Smetacek 2008; Nicol et al. 2010).

We can rule out methodological differences as the cause of the changes in abundance even though estimates of abundance from the different periods were derived from different nets. Our inter-net calibration determined size-related differences in catch efficiency and appropriate correction factors were applied to N70V catches.

A study carried out in the Weddell Sea comparing historical *Discovery* N70V (1929–1939) and contemporary WP-2 (1989–1993) net samples concluded that there had been marginally significant long-term changes among large calanoids but overall, no consistent trend was apparent (Vuorinen et al. 1997). However, and importantly, no inter-calibration of net performance was carried out.

Calibration factor

The survey data from which we generated the calibration factors were originally reported in Ward et al. (2012b). When considered across the entire catch, that study estimated that the Bongo net caught ~3 times as many individuals as the N70 net. This increased to ~4 times greater when limited only to copepod developmental stages or individuals that were <0.5 mm body length. However, between body lengths of 1 and 7 mm, the Bongo net caught between 1.5 and 2 times as many individuals as the N70 net. Given the large dependence of Bongo:N70 abundance ratio on body size, we considered it necessary to develop a specific calibration factor for each of our four chosen calanoid copepod species that took developmental stages into account. We could only examine developmental stage composition in the

contemporary samples, since specimens had been previously extracted from *Discovery Investigation* samples without any record of their respective developmental stages. The contemporary samples showed that mid developmental stages (CII–CIV) dominated the summertime populations of three of the four calanoid species, the exception being *C. acutus*, where the dominant stage was late development stage, CV. *Calanoides acutus* is the only one of the four calanoid species known to enter true diapause for a large part of the year (Drits et al. 1994). Tarling et al. (2004) showed that the population in the Scotia Sea consists of a mixture of 1- or 2-year life-cycle types, with CV being the dominant over-wintering stage. CV therefore dominate the summertime population of *C. acutus* since their abundance comprises both 1 and 2 year old individuals. The other calanoid species appear to have summertime populations that are dominated by newly recruiting individuals from that same season. Although we cannot be certain that summertime populations had the same structure during the *Discovery Investigations* era as during contemporary times, we deliberately designed our analysis to encompass all of the summer months so as to average over any minor variations in life-cycle phenology between the two eras.

Through combining developmental stage composition with the residual differences in abundance between Bongo and N70 samples for each developmental stage, we derived calibration factors between 1.2 and 1.7. This reflects the fact that even though relatively large residual differences were observed in the early developmental stages, these stages were not that common in the population during the summer. These calibration factors are somewhat lower than those originally proposed by Ward et al. (2012b). That study considered the entire copepod community, which was numerically dominated by smaller species such as *Oithona similis* and *Ctenocalanus citer*. The calanoid species we analyse here are comparatively larger in body size even during the earlier developmental stages and the residual differences between the Bongo and N70 nets were correspondingly smaller. Nevertheless, the sensitivity analyses showed that even increasing the value of the calibration factors by 50%, which would act to inflate abundances during the *Discovery* era, did not change the overall pattern of significantly greater abundances in the contemporary era in three out of the four calanoid species.

Climate variability

Recent investigations carried out around the western Antarctic Peninsula and Elephant Island are unanimous in finding links between decadal changes in abundance of plankton and the dominant modes of climate variability such as SAM and ENSO, which importantly influence sea-ice extent (Stammerjohn et al. 2008). It has been suggested that sea-ice

extent in the first part of the 20th century may have been greater than in recent times (de la Mare 1997; Cotté and Guinet 2007). However data derived from satellite measurements from 1979 to 2006 show a positive trend of around 1% per decade reaching a new record maximum for the satellite era in 2012 (Turner et al. 2009, 2014). If ice extent was greater over the Scotia Sea in the early part of the last century we might have expected changes in cycles of productivity and hence in the timing of appearance in surface waters of some species, particularly large calanoids that overwinter at depth and appear in the surface waters in spring. Such a phenological change is not borne out by the data (Fig. 4) which show similar trends in relative abundance by month.

Movements of frontal zones have also been recorded in response to atmospheric forcing. During El Niño events, north-west winds in the vicinity of Drake Passage decrease, allowing colder water from the Weddell Sea to flow north and penetrate into the Bransfield Strait. Increased winds and a southwards movement of the SACCF allows warmer water to mix with cold coastal waters during the La Niña phase (Loeb et al. 2009, 2010). This increased oceanic influence results in more Chl *a*, more copepods and better krill recruitment in the coastal area whereas, under the El Niño regime, salps dominate, Chl *a* is low and krill recruitment is poor. Aside from sea-ice reduction, climate variability also induces physical changes in the marine environment such as water column stability which influences primary productivity and links to species abundance in space and time (Saba et al. 2014; Steinberg et al. 2015). We have only incomplete data on prevailing atmospheric conditions and their impacts during the time of the *Discovery Investigations*. Our data are also insufficient to allow us to test for changes in regional abundance of species across the Scotia Sea which we acknowledge may be a possibility. However, averaged over the entire region, and across two decadal periods, differences in abundances are proportionately large and strongly suggest wider changes within the ecosystem, rather than local displacements of water masses and changes in nutrient supply.

Temperature and food availability

It is hard to see how the observed increases in temperature between eras would impact on population demography and account for the differences observed. The increases of ~1.5 °C are apparent only within the near-surface ocean, although lesser warming has been observed at depth (Gille 2002). We might in any case have expected species to respond differently to changing temperature since we considered species with both warm (*R. gigas* and *C. similimus*) and cold (*C. acutus* and *C. propinquus*) water preferences and yet, with the exception of *C. propinquus*, which showed a marginal decrease in contemporary times, all have

increased in overall abundance. In terms of food availability, there have been a number of studies suggesting both recent decreases and increases in primary production in the Southern Ocean during the satellite era. Gregg et al. (2003) found a 10% decline in productivity when comparing satellite mounted Coastal Zone Colour Scanner (CZCS) data for the period 1979–1986 compared to more recent SeaWiFS (Sea-viewing Wide Field-of-view Sensor) measurements (1997–2002). In contrast, Smith and Comiso (2008) found that productivity in the entire Southern Ocean showed a substantial and significant increase during their 9-year observation period (1997–2006), with much of this increase due to changes during the austral summer months. However, we have no direct way of knowing how present levels of phytoplankton compare to those found 70 years ago during the *Discovery Investigations*.

It is also important to consider how changes elsewhere in the ecosystem may have brought about increased abundances by virtue of trophic cascade effects. An increase in abundance could have arisen due to an increase in available food, a relaxation of predation pressure, or both. Antarctic krill (*Euphausia superba*) might provide a key to understanding some of the ecosystem interactions as it has been argued that krill occupy a position in the Southern Ocean food-web whereby they influence trophic levels above and below themselves, in a so called ‘wasp-waist’ ecosystem (Flores et al. 2012; Atkinson et al. 2014). For example, it has been demonstrated that intense krill grazing can alter phytoplankton species composition by preferentially grazing diatoms leading to a dominance of flagellates < 20 µm (Jacques and Panouse 1991; Kopczynska 1992; Granéli et al. 1993). Equally, through fluctuations in biomass, their availability to higher predators varies and can impact breeding success and population size (Trathan et al. 2007). It has been suggested that, historically, both whales and krill were able to act as ‘ecosystem engineers’ in the sense that by virtue of their great abundance they were, and are, important recyclers of nutrients essential for phytoplankton growth (Tovar-Sanchez et al. 2007; Willis 2007, 2014; Smetacek 2008; Nicol et al. 2010; Schmidt et al. 2011). In this way, increased phytoplankton production would have supported a greater krill population ultimately benefiting whales and perhaps placing greater pressure on copepods, both as competitors and as potential prey.

The degree of competition for food resources is likely to be highly variable in space and time reflecting plankton densities and distributions as well as conditions conducive to primary production. However, food limitation is commonly observed in the world ocean, particularly among large copepods (Saiz and Calbet 2011). In the Southern Ocean, egg production rates of *C. acutus* and *R. gigas* reach an asymptote at around 3 mg m⁻³ Chl *a* (Shreeve et al. 2002) which is a relatively high concentration for much of

the predominantly high nutrient low chlorophyll Southern Ocean. Longhurst (1998) notes that, within the southern part of the ACC, only 5% of underway-sampled chl-*a* concentration data exceeds 1 mg m^{-3} and most are a quarter of this (Tréguer and Jacques 1992). Not only copepod abundance but carbon mass and condition have also been found to be related closely to proxies of past production levels such as silicate levels and nutrient deficits (Shreeve et al. 2002; Ward et al. 2007), showing that bottom up control is important. Microphytoplankton ($> 20 \mu\text{m}$) has also been found to account for a large part of the variance in copepod abundance and carbon mass around South Georgia and elsewhere (Berggreen et al. 1988; Paffenhöfer 1988; Shreeve et al. 2002). Krill grazing may selectively remove microphytoplankton, thus disadvantaging large calanoid copepods which require blooms of large diatoms to optimise recruitment (Ward et al. 2005). However, of the 4 species, only *C. propinquus* showed a marginal but significant decrease in contemporary abundance, suggesting other factors may be paramount in this case. All species have broad and overlapping distributions within the ACC but life history traits are variable. For example, *C. acutus* is the most herbivorous and has a clear period of diapause in winter (Atkinson 1998), whereas *C. propinquus* has a closer association with ice-covered waters to the south of the Scotia Sea and, along with the northerly distributed *C. simillimus*, has extended periods of reproduction, with at least part of each population remaining active during winter (Bathmann et al. 1993; Atkinson 1998; Pasternak and Schnack-Schiel 2001). In contrast to *C. acutus* and *R. gigas*, in which wax esters are the main storage lipid, triacylglycerides dominate in both species of *Calanus*, suggesting more or less continuous feeding throughout the year (Hagen et al. 1993; Ward et al. 1996) and it has been found that microzooplankton can form a considerable part of the diet of both *Calanus* species (Hopkins et al. 1993; Atkinson 1995, 1996). The extent to which the diet of *C. propinquus* includes sea-ice algae is currently debateable. It has generally been found to be more abundant in open water than in the ice and marginal ice zones and was shown to have a higher proportion of empty guts when found under sea-ice (Burghart et al. 1999). However, recent data from the Scotia Sea show areas of recruitment for *C. propinquus* and, to an extent, *C. acutus*, which match surface concentrations of an isoprenoid ice-algae biomarker in the wake of the retreating ice edge (Schmidt et al. 2018). It is possible that a reduction in sea-ice means that under-ice productivity available to *C. propinquus* has declined or that any historical increase in chlorophyll available to copepods did not occur in the more southern parts of the Scotia Sea.

Krill may also directly prey on copepods (Atkinson and Snýder 1997; Atkinson et al. 1999; Cripps et al. 1999; Hernández-León et al. 2001), particularly at times of low phytoplankton production and biomass. Through either

preying directly upon or outcompeting copepods for food, krill may therefore, to a greater or lesser extent, control copepod population numbers. An overall increase in the number of large calanoids therefore suggests that control on this group has relaxed since the time of the *Discovery Investigations*. The reported decline of krill in the Atlantic sector of the Southern Ocean since the 1970s (Atkinson et al. 2004) could therefore be a mechanism by which competition and or predation has reduced, allowing copepod numbers to increase.

Ecosystem impacts

There is little doubt that a decreased abundance of krill will have had a significant impact on the amount of carbon passing through direct diatom-krill-higher predator food-chains. Copepod and krill food-webs have different characteristics in terms of carbon demand and fate depending on which is the dominant organism. Krill grazing can decrease phytoplankton standing stocks, particularly when swarms are present, although copepods rarely do, unless standing stocks are low (Atkinson 1996; Dubischar and Bathmann 1997). Within the Scotia Sea, krill and copepods are the dominant crustaceans, with krill tending to be more abundant in the southern part and copepods towards the north (Ward et al. 2012a). In a modelling study, Priddle et al. (2003) found that the biogeochemical consequences of grazing by krill and copepods were also different in terms of nutrient regeneration and resupply to primary producers. In a low krill-high copepod scenario, higher phytoplankton biomass and production, lower mixed layer ammonium, nitrate and silicate concentrations and higher detrital carbon were predicted than for a high krill low copepod scenario. Phytoplankton chlorophyll biomass was negatively related to krill biomass, and mixed layer nutrients were positively correlated with krill biomass in these data. Both observations and model results suggest that variation in biogeochemical carbon and nitrogen cycles in the South Georgia pelagic ecosystem is determined largely by changes in zooplankton community composition and its impact on phytoplankton dynamics. Contemporary estimates of krill and copepod biomass suggest that copepod standing stocks are at least equal to those of krill or indeed exceed them (Voronina 1998). Estimates of copepod vs krill production around South Georgia (where the biomass of both groups is generally high) suggest that the copepod community as a whole may be four times as productive as krill (Shreeve et al. 2005). Over the wider scale, Voronina (1998) estimates that 92% of annual zooplankton production in the Southern Ocean can be attributed to copepods whereas Conover and Huntley (1991) estimate productivity to be three times higher than krill-based estimates of ingestion and assimilation. Given that the biomass of baleen whales was so much higher in the past, it is axiomatic that krill biomass

must also have been higher than contemporary estimates to support this biomass (Willis 2007, 2014; Smetacek 2008). The balance of production would also have changed but, even with large calanoids being less abundant in the past, as shown by our study, copepods would still have contributed significantly to secondary production.

Our previous analysis has shown that over the last 70 years, despite warming, the geographical distribution of the plankton community of the Scotia Sea has not changed (Tarling et al. 2018). This study has shown that, despite the rank order of species abundance staying broadly the same, there have been changes in absolute abundance of biomass-dominant copepod species. The factors we consider responsible are linked through to changes occurring within the food chain brought about by decreasing krill abundance both as a result of warming induced habitat loss and also the commercial exploitation of whales.

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Compliance with ethical standards

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