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 data-sets, 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
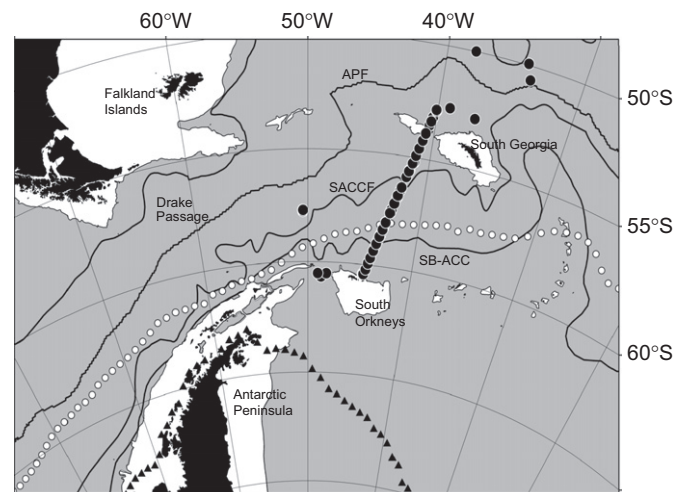

Fig. 1. The Scotia Sea showing the position of the transect along which the majority of stations were sampled during Oct–Nov 2006, Jan–Feb 2008 and March–April 2009. Also shown are mean positions of frontal zones, from north to south APF=Antarctic Polar front, SACCF=Southern Antarctic Circumpolar Current 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 m^2 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 m^2) 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 Echoview^{TM} 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 Matlab^{TM} 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 ($S_{v120\ kHz}$) 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 $S_{v120\ kHz}$ 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; m^2 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)
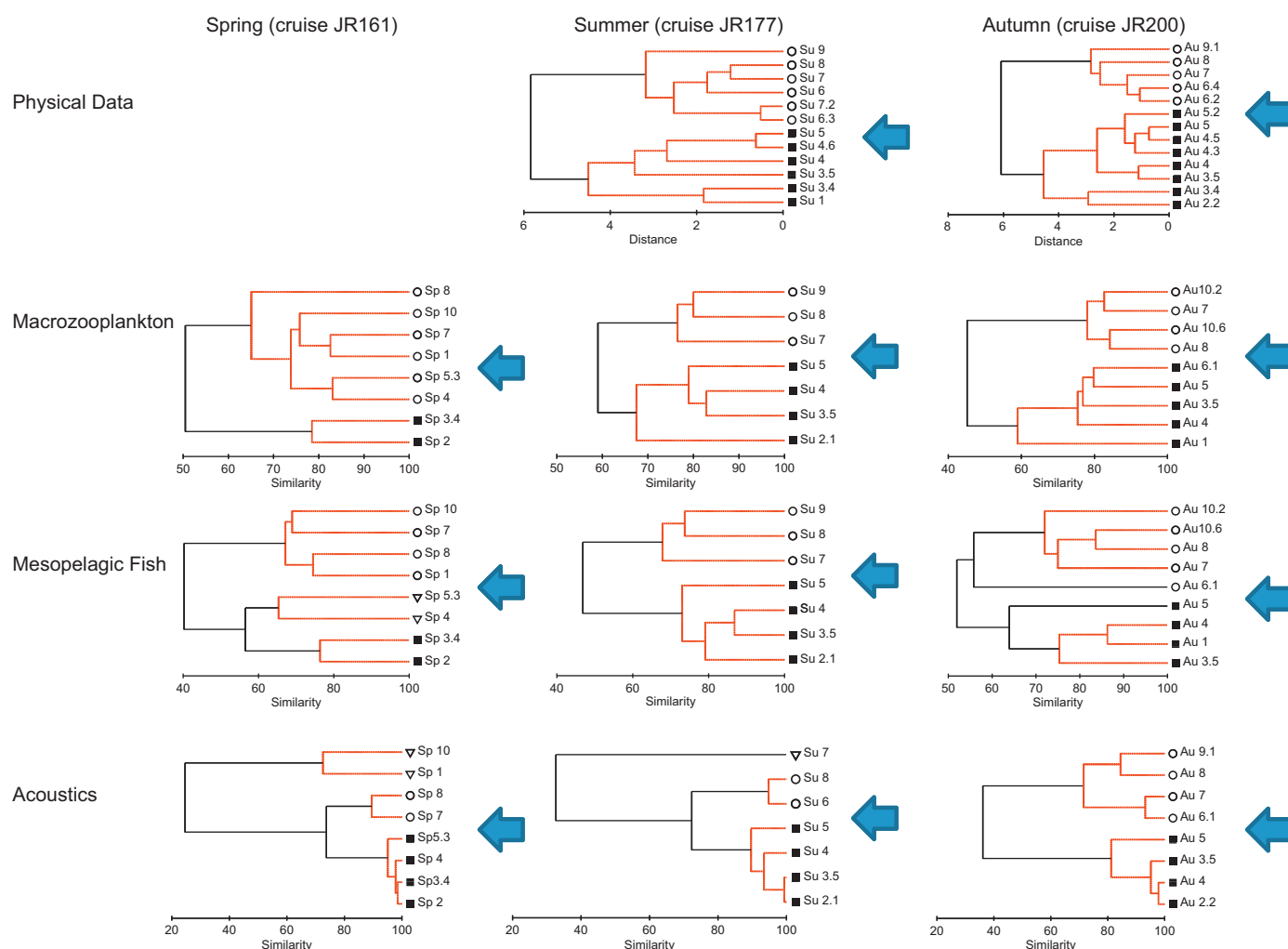
Fig. 2. Results of clustering analysis by season performed on Physical data (silicate and nitrate concentrations from the winter water level (200 m), SST and log water depth). Macrozooplankton data obtained with an RMT25 net from night-time stratified hauls to 1000 m. Mesopelagic fish data obtained with 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 *Calycopsis* 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
Salpa thompsoni	1	84.4	102.5	467.7	12629	75.4
E. superba	669	46	8891	77.4	22.2	8.1
E. triacantha	0	226	45.3	970	41	1653
Thysanoessa spp.	515	78	28.6	450	5.9	40
Euphausiids (other)	0	9.2	0.9	267	1.9	181
Themisto gaudichaudii	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 *Krefftichthys 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 macrozoooplankton 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) g m^{-2}) and summer (27.17 (21.14) g m^{-2}) but significantly lower (2.24 (1.35) g m^{-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
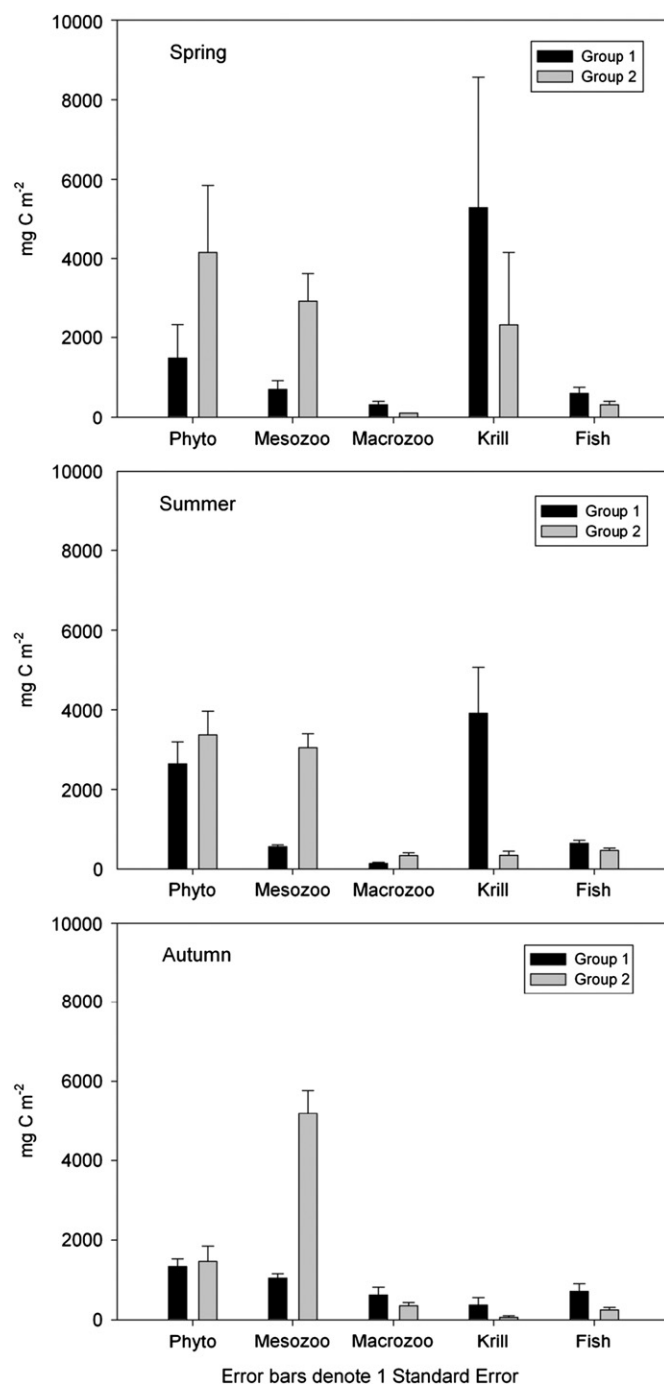

Fig. 3. Mean (SE) Carbon mass (mg C m^{-2}) within phytoplankton, mesozooplankton, macrozooplankton, krill and mesopelagic fish groupings with respect to season and station group. Phytoplankton was integrated over the euphotic zone (Korb et al., 2012), mesozooplankton (0–400 m), macrozooplankton (0–1000 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 m²) 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 disconti-nuities 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 con-tinent northwards is not uniform and the sharp changes in gradients that exist at some frontal zones often mark disconti-nuities 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 Conver-gence 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 else-where 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 corre-sponding changes in nutrient levels, particularly silicate, are apparent where there are strong currents but overall the sur-face/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
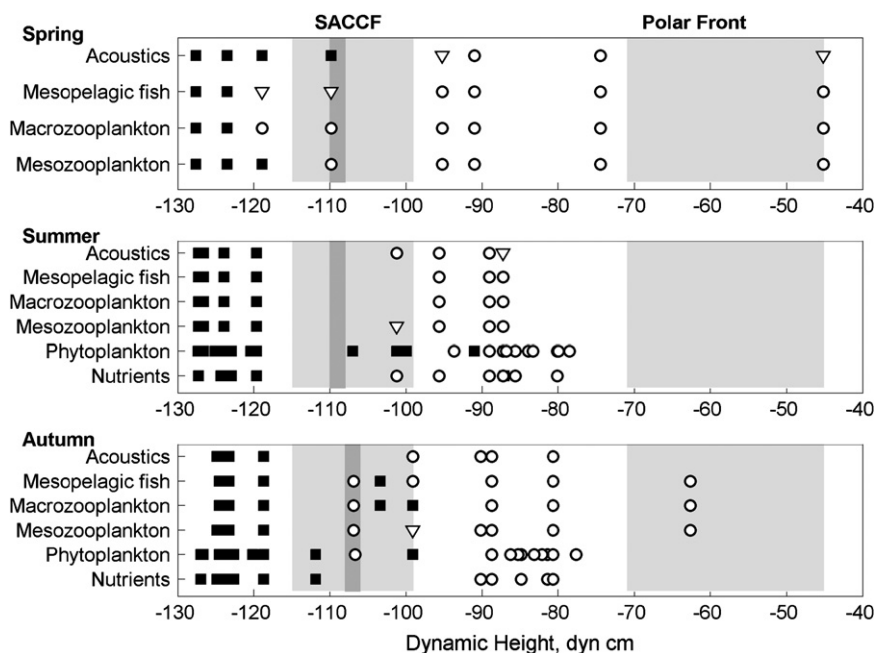

Fig. 4. Stations classified by station group as determined from cluster analyses performed on nutrients, phytoplankton, mesozooplankton, macrozooplankton, mesopelagic fish and acoustic datasets in relation to sea surface dynamic height measurements. The data are presented by cruise. Solid squares represent 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
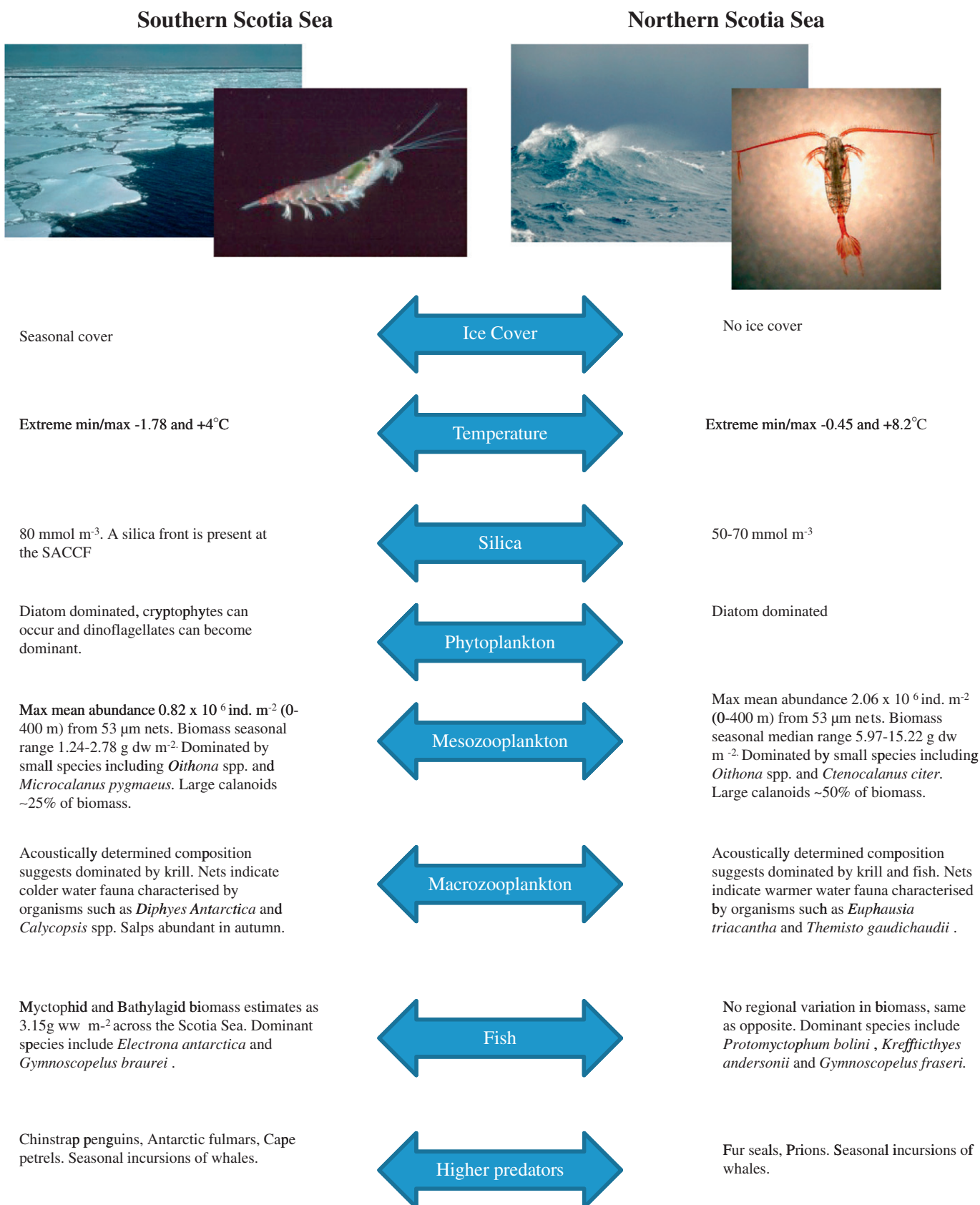
Southern Scotia Sea   ## Northern Scotia Sea

Ice Cover

Seasonal cover

No ice cover

Temperature

Extreme min/max -1.78 and +4°C

Extreme min/max -0.45 and +8.2°C

Silica

80 mmol m^{-3}. A silica front is present at the SACCF

50-70 mmol m^{-3}

Phytoplankton

Diatom dominated, cryptophytes can occur and dinoflagellates can become dominant.

Diatom dominated

Mesozooplankton

Max mean abundance 0.82 x 10 ^{6} ind. m^{-2} (0-400 m) from 53 µm nets. Biomass seasonal range 1.24-2.78 g dw m$^{-2.}$ Dominated by small species including *Oithona* spp. and *Microcalanus pygmaeus.* Large calanoids ~25% of biomass.

Max mean abundance 2.06 x 10 ^{6} ind. m^{-2} (0-400 m) from 53 µm nets. Biomass seasonal median range 5.97-15.22 g dw m $^{-2.}$ Dominated by small species including *Oithona* spp. and *Ctenocalanus citer.* Large calanoids ~50% of biomass.

Macrozooplankton

Acoustically determined composition suggests dominated by krill. Nets indicate colder water fauna characterised by organisms such as *Diphyes Antarctica* and *Calycopsis* spp. Salps abundant in autumn.

Acoustically determined composition suggests dominated by krill and fish. Nets indicate warmer water fauna characterised by organisms such as *Euphausia triacantha* and *Themisto gaudichaudii* .

Fish

Myctophid and Bathylagid biomass estimates as 3.15g ww m^{-2} across the Scotia Sea. Dominant species include *Electrona antarctica* and *Gymnoscopelus braurei* .

No regional variation in biomass, same as opposite. Dominant species include *Protomyctophum bolini* , *Kreffticthyes andersonii* and *Gymnoscopelus fraseri.*

Higher predators

Chinstrap penguins, Antarctic fulmars, Cape petrels. Seasonal incursions of whales.

Fur seals, Prions. Seasonal incursions of whales.

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 cross 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.

Acknowledgments

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