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Comparison of the structure and function of Southern Ocean regional ecosystems: The Antarctic Peninsula and South Georgia

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ABSTRACT

The ocean ecosystems around the west Antarctic Peninsula and South Georgia are two of the best described regional ecosystems of the Southern Ocean. They therefore provide a useful basis for developing comparative analyses of ocean ecosystems around the Antarctic. There are clear and expected differences in seasonality and species composition between the two ecosystems, but these mask an underlying similarity in ecosystem structure and function. This similarity results from the two ecosystems being part of a continuum, from more ice covered regions in the south to open water regions in the north. Within this continuum the major factors affecting ecosystem structure and function are the sea ice, the biogeochemical conditions and the connectivity generated by the flow of the Antarctic Circumpolar Current. Antarctic krill are central to the food web in both ecosystems, but the other species of plankton and predators present are different. These different species provide alternative pathways of energy transfer from primary production to the highest trophic levels. The relative dominance of these species can provide indicators of change in ecosystem structure and function. Both ecosystems are changing as a result of physically and biologically driven processes, and the ecological responses being observed are complex and variable across different species and within the two regions. Species in parts of the northern Antarctic Peninsula are being replaced by species that currently dominate farther north in more oceanic areas such as at South Georgia. The similarity of structure and strong connectivity, mean that projections of future change will require generic models of these ecosystems that can encompass changes in structure and function within a connected continuum from ice covered to open water in winter.

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1. Introduction

Southern Ocean ecosystems are changing as a result of some of the most rapid regional warming that has been observed anywhere on the planet and further major physical and chemical changes are expected to occur in the coming decades (Costa et al., 2010; Meredith and King, 2005; Montes-Hugo et al., 2009; Schofield et al., 2010; Trivelpiece et al., 2011; Vaughan et al., 2003). These ecosystems are also of global importance in biogeochemical cycles, in contributing to food security through major fisheries and in maintaining unique biological diversity. Changes in their structure and function will, therefore, have consequences for human society, which makes the development of the basis for predicting the responses of these ecosystems to change an urgent requirement (Murphy et al., 2008).

Understanding the factors that generate differences in ecosystems that exist in different regions of the circumpolar Southern Ocean is crucial

for the development of models that provide useful projections of ecosystem level responses to the changes in physical processes (affecting ocean temperatures, circulation patterns and sea ice), chemical processes (affecting nutrients, carbon dioxide concentrations and pH) and direct human impacts (fisheries and tourism), which are expected to occur in the coming decades (Murphy et al., 2008; Trathan and Agnew, 2010; Trivelpiece et al., 2011; Turner et al., 2009). Recent development of a strategic basis for generating the models required to produce such predictions has emphasised the requirement for a range of ocean-scale models of Southern Ocean ecosystems (Murphy et al., *in press*). Generating these models, with the appropriate space and time scales and processes, requires knowledge of the controls on the structure and function of Southern Ocean ecosystems at regional scales. This in turn requires development of comparative views of how properties of ecosystems can be characterised so that differences or changes can be distinguished (Megrey et al., 2009b; Murawski et al., 2009; Sydeman and Bograd, 2009).

The western Antarctic Peninsula (wAP) and the northern Scotia Sea around South Georgia (Figs. 1 and 2; Ducklow et al., 2007; Murphy et al., 2007b; Hofmann et al., 2011) are the most studied regions of the

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Southern Ocean and sufficient information exists on ecosystem structure and function to allow comparative analysis of the two systems. Ecosystems around the wAP are undergoing major changes in ecological structure that reflect the rapid regional warming over the last 50 years (Clarke et al., 2007; Schofield et al., 2010; Trivelpiece et al., 2011). Around South Georgia major changes are also occurring, but although the region has warmed over the last century, the underlying causes and directions of ecological change are difficult to determine. This is partly because of the short length (<30 years) of most datasets, but also because it was historically the centre of exploitation of marine living resources in the Southern Ocean (Everson, 1977; Murphy et al., 2007b; Whitehouse et al., 2008b). Here our aim is to develop a comparative analysis of the wAP and South Georgia ecosystems by examining their major structural and functional features and dynamics (i.e. their operation), at regional scales (tens to hundreds of kilometres in extent) to consider the factors generating differences between these ecosystems and their responses to change. This comparison will also contribute to the process of developing regional models of Southern Ocean ecosystems and in assessing their utility in predicting structure and function.

Ecosystem comparisons require a clear definition of what is meant by “to compare ecosystems”. The value of using “ecosystem” to describe particular ecological systems has been debated for some time (e.g. O’Neill, 2001), and often centres on whether the system being described can be considered as a distinct biological entity (see also Salihoglu et al., *in press*), but there is now general acceptance that ecosystem is a useful term. The biological system is defined as an ecological system when organism interactions with their environments, including other organisms, are considered. Ecosystems therefore include the physical and chemical environments in which they occur and lead to our definition of an ecosystem as: “the abiotic and biotic components

interacting over a set of defined temporal and spatial scales”. This definition gives a perspective of a regional oceanic ecosystem with a spatial scale of 100 s km (the mesoscale). The abiotic system within the regional scale provides a dynamic physical and chemical process framework and biotic process interactions occur within this framework at different scales (Murphy et al., 1988, 2007b). The structure and function of the ecosystem are then emergent properties of the dynamic abiotic and biotic process interactions (Murphy et al., 1988, 2007b, *in press*). Comparison of ecosystems therefore requires an understanding of both the biologically-based interactions between species and the interactions with the physical and chemical environments in which they occur.

Comparative analyses of ecosystems requires definition of the properties of ecosystems that are consistent and comparable (Bailey et al., 2010; Hunt and Nettleship, 1988; Hunt and Megrey, 2005; Legendre and Niquil, 2013–this volume; Link, 2002; Link et al., 2010; Megrey et al., 2009b, 2009c; Murawski et al., 2009; Petchey et al., 2008; Sydeman and Bograd, 2009). Different comparison attempts have focused on particular aspects of ecosystems or their properties such as primary productivity, carbon budgets, food web structure or total fishery yield (Baird et al., 1991; Blanchard et al., 2010; Bundy et al., 2009; Carmack and Wassmann, 2006; Carmack et al., 2006; Drinkwater, 2009; Drinkwater et al., 2009; Gaichas et al., 2009; Johnson et al., 2011; Legendre and Niquil, 2013–this volume; Link et al., 2009; Megrey and Aydin, 2009; Megrey et al., 2009a). Recognition of the importance of understanding the interactive influence of processes at different trophic levels led to an emphasis on whole ecosystem analyses that consider the end-to-end operation of food webs. However, accounting for the complexity of all the potential species interactions at different trophic levels was difficult and resulted

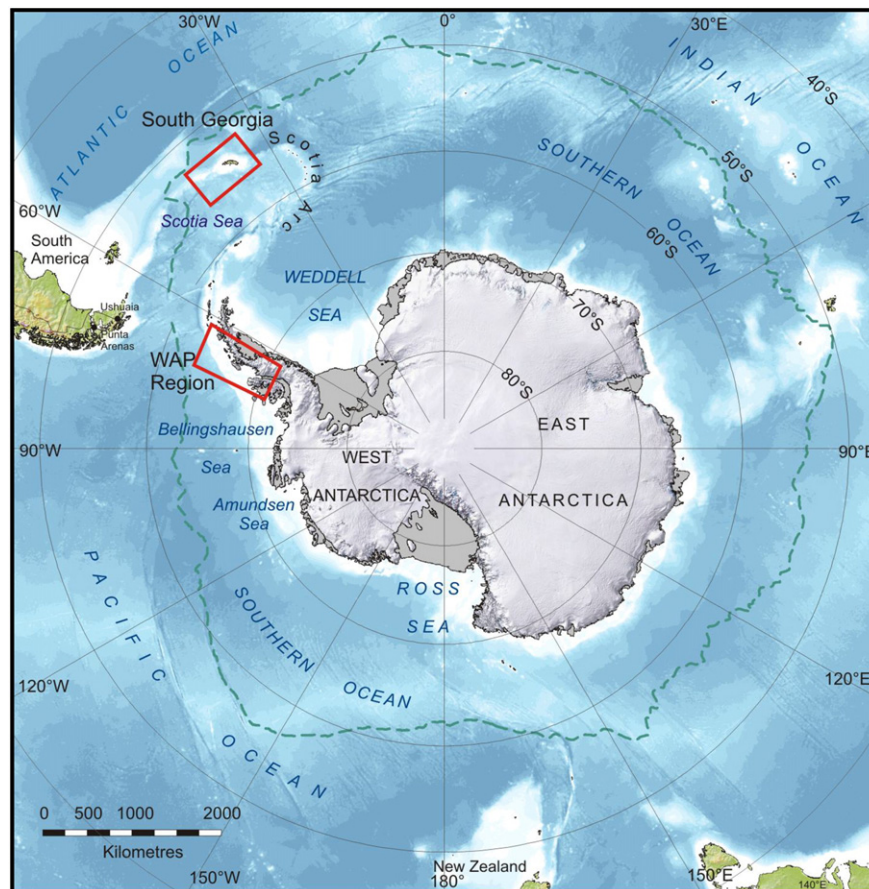


Fig. 1. Map of the Antarctic showing the location and extent of the western Antarctic Peninsula (wAP) and South Georgia regions (red boxes) considered in this paper. The general location of the Polar Front is shown by a dashed line.

in development of a range of approaches for aggregating ecosystem components by trophic levels, size or functional groups (Hannah et al., 2010; Hofmann, 2010; Murphy et al., in press). There remain however, major theoretical and practical challenges in developing analyses of whole ecosystems (Allen and Fulton, 2010; Hofmann, 2010), and there is no standard methodology currently available that can capture the complexity of natural systems and identify appropriate scales for comparison (Bailey et al., 2010; Legendre and Niquil, 2013–this volume; Link et al., 2009, 2010; Megrey et al., 2009b; Petchey et al., 2008). An additional aim of this study is, therefore, to consider how the methodological basis for comparisons of ecosystems can be developed to examine the importance of different biological and physical processes and interactions over different spatial and temporal scales.

This comparative study of the wAP and South Georgia ecosystems highlights the spatial and temporal variability of their structure and function, but also shows that these ecosystems are more similar than expected from simple views of species occurrence. Although different species do dominate in the two ecosystems, these replace similar species in groups that exist in both areas. In addition, the ecosystems are connected, and form part of a continuum from the more ice-covered regions in the south to the open water regions to the north. We develop a generic representation of food web structure for these two areas and suggest that a generic ecosystem model is a viable approach for analysing and modelling South Ocean ecosystems.

2. Structure and function of the wAP and South Georgia ecosystems

The dynamics of the wAP and South Georgia regional marine ecosystems have been the focus of sustained analyses over the last few decades. Extensive analyses and overviews of results from multidisciplinary studies undertaken along the wAP in the past two decades are available (Ducklow et al., 2007; Hofmann and Murphy, 2004; Hofmann et al., 2002, 2008, 2011), as is a perspective on recent

climate change impacts and consequences for the wAP marine food web (Clarke et al., 2007). Reviews of the South Georgia ecosystem and the wider Scotia Sea context are given in Atkinson et al. (2001) and Murphy et al. (2007b), respectively. The drivers of variability and change in the South Georgia and Scotia Sea region have been considered and analysed by Murphy (1995) and Murphy et al. (1995, 2007a, 2007b). Recent syntheses of detailed knowledge of the food web components and interactions at South Georgia is given in Hill et al. (2012), and for the wAP (Ballerini et al., submitted for publication).

The western region of the Antarctic Peninsula extends from about 61°S at the northern tip to about 75°S in the southern region. This region encompasses very different physical systems and habitats for which varying levels of biological data and knowledge are available. This analysis focuses on the Marguerite Bay region of the wAP (~62°S to 70°S, Figs. 1 and 2), which was the focus of the Southern Ocean GLOBEC and Palmer Long-Term Ecological Research (PAL LTER) Programmes (Ducklow et al., 2007; Hofmann et al., 2002, 2004, 2008, 2011). Around South Georgia, we consider both oceanic and shelf areas extending from ~53°S to 56°S and 34°W to 44°W (Figs. 1 and 2), which were encompassed by the British Antarctic Survey DYNAMOE and DISCOVERY 2010 Programmes (see Murphy et al., 2007b and Tarling et al., 2012). These studies provide the basis for describing the general physical features (Table 1) and biological operation of the two ecosystems, from microbes to higher trophic level predators, and their primary physical and biological controls. Species differences between the two regions are considered in the context of major life history traits of key species (Table 2).

Our comparative analysis begins with consideration of the Southern Ocean context of the wAP and South Georgia ecosystems. The major features of the two regional ecosystems are then compared based on physical characteristics, primary producers and links to secondary producers, secondary and tertiary producers, and the spatial variability and connectivity of the two regional systems.

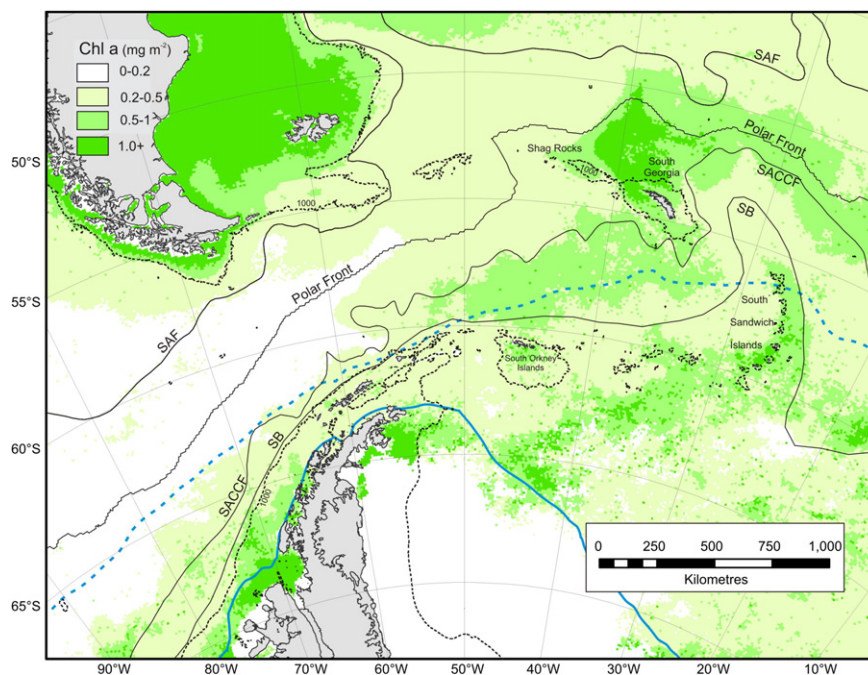


Fig. 2. Map encompassing the western Antarctic Peninsula and South Georgia regions. The 1000 m isobaths (black dashed lines) and mean positions of the Sub-Antarctic Front (SAF), Polar Front, Southern ACC Front (SAACF), and Southern Boundary of ACC (SB) are shown. Also shown are the mean winter (dashed blue line) and summer (solid blue line) sea ice extent (15% concentration) and the mean surface chlorophyll a concentration (mg m^{-3}) between September and March (SeaWiFS derived satellite data, NASA, means calculated only for cells where 10 values were obtained within a year). The white areas include cells where no data are available.

Table 1

Comparison of the ocean, sea ice, and environmental characteristics of the western Antarctic Peninsula (wAP) and South Georgia ecosystems. Water masses are abbreviated as: AASW—Antarctic Surface Water; WW—Winter Water; CDW—Circumpolar Deep Water.

Physical environmental characteristics	Western Antarctic Peninsula	South Georgia
Main water masses and circulation features	AASW, WW and CDW South of SACCF, which runs along the outer shelf No slope or shelf-slope front Gyres (100 km's) over the shelf Connection to offshore oceanic system via deep troughs and deep shelf	AASW, WW and CDW Between SACCF and PF SACCF steered along southern shelf to the east and retroflects around the north of the island Main area of deep water connection appears to be in the south western shelf in an area of an extensive ~400-m plateau Main area of surface water entrainment is in the east, although may also occur along north coast
Ice presence Means and variability	Seasonal advance and retreat, forms in May–June, retreats October Minimum (~10% but can be >25%) in ~March Concentration peaks (75–100%) in September Variability (~90%) greatest in spring (November to December) and in autumn (June)	No ice—has been on edge of northern extent of ice 1 year in last 30
Seasonality and daylength variation	Shortest days—0 (southern wAP) to 1–2 h Longest days—just less than 24 h Total annual daylight days—188 Maximum daylength at 64°S, 64°W >20 h Minimum daylength at 64°S, 64°W >3 h	Shortest days—7 h Longest days—17 h Total annual daylight days—183
Temperature (°C) ranges and variability	Summer mean maximum: February –0.97 Winter mean minimum: September – –1.65 Month of maximum: February 2.56 Month of minimum: June–December – 1.79 to –1.80 Month of maximum variation January standard deviation = 0.82, range 4.09 Month of minimum variation September standard deviation = 0.14, range 0.79	Summer mean maximum: February/March –3.55/3.48 Winter mean minimum: September –0.22 Month of maximum: February 5.40 Month of minimum: September –0.86 Month of maximum variation January standard deviation 0.68, range (January) 4.28 Month of minimum variation September standard deviation = 0.43, range (October) 2.16

2.1. The Southern Ocean context of the wAP and South Georgia ecosystems

The Antarctic Peninsula is connected to the South American continent by the Scotia Arc, which is a mainly submarine feature forming the southern, eastern and northern boundaries of the Scotia Sea with the Weddell Sea to the south and the South Atlantic to the north (Figs. 1 and 2). Along the Scotia Arc, a series of mountainous island groups extend above the ocean surface including Shag Rocks and South Georgia in the north, the South Sandwich Islands in the east and the South Orkney Islands to the south. From the Amundsen and Bellingshausen Seas to the west in the South Pacific region, the easterly-flowing Antarctic Circumpolar Current (ACC) moves poleward and flows along the outer portion of the Antarctic continental shelf. After passing the tip of the Antarctic Peninsula and exiting Drake Passage, the ACC follows a mostly eastward zonal path across the Scotia Sea. Along the eastern extent of the Scotia Arc, the ACC is deflected northwards. A part of the ACC flows north of South Georgia and part flows south forming a reflection region on the eastern side of South Georgia. Downstream of South Georgia, the ACC shifts southward and continues its zonal flow across the South Atlantic.

The ACC encompasses a series of circumpolar fronts that are separated by zones with distinct thermohaline properties (see Orsi et al., 1995 and references cited within). The sub-Antarctic Front (SAF), Polar Front (PF) and Southern ACC Front (SACCF) (Fig. 4a) carry most of the transport of the ACC (Orsi et al., 1995) and are highly dynamic and variable in location and latitudinal extent (Dong et al., 2006; Sokolov and Rintoul, 2009a, 2009b; Thorpe et al., 2002, 2005). The Southern Boundary of the ACC (SBACC) is marked by the poleward edge of Upper Circumpolar Deep Water (UCDW; Orsi et al., 1995), which is the upper level of Circumpolar Deep water (CDW); the lower level is Lower Circumpolar Deep Water (LCDW). UCDW is distinguished by temperature and salinity maxima (2 °C, 34.72) that shoal from about 1200 m to 200 m along the wAP shelf edge (e.g. Orsi et al., 1995; Sievers and Nowlin, 1988). The flow of the ACC is strongly topographically steered and in many regions this generates intense interactions of the fronts with regions of the shelf slope of the

continent and around the Scotia Arc (Orsi et al., 1995). Along the wAP, interactions of the ACC with the bathymetry along the outer continental shelf produce intrusions of UCDW that flood the shelf below the permanent pycnocline (Dinniman and Klinck, 2004; Klinck, 1998; Klinck et al., 2004; Smith et al., 1999). The northward deflection of the ACC by the Scotia Arc generates mesoscale eddies and upwelling, and disperses material northwards, which affects physical, chemical and biological processes across the Scotia Sea (Meredith et al., 2003; Murphy et al., 2004, 2007a, 2007b; Veit and Hunt, 1992; Ward et al., 2003).

The wAP and Scotia Sea regions are areas of enhanced chlorophyll *a* and primary production (Fig. 2, Atkinson et al., 2004; Arrigo et al., 2008). This primary productivity forms the basis for the classical view of the Southern Ocean food web of high production and short food chains dominated by Antarctic krill (*Euphausia superba*), a view that has historically come from the predominance of studies that focused in these regions (Everson, 1977; Laws, 1983). This region, including the South Atlantic sector, supports over 50% of the circumpolar krill population in terms of numbers (Atkinson et al., 2004), which in turn supports large seabird and marine mammal colonies and large numbers of pack-ice seals. The Scotia Sea region was also the historical centre for whaling and sealing operations of the 19th and 20th centuries and is now where more recent fishing operations on Antarctic krill have developed (Everson, 2000; Nicol et al., 2011).

2.2. The physical basis of wAP and South Georgia ecosystems

2.2.1. Oceanographic conditions

The large scale physical structure of the Southern Ocean generates major physical differences between the wAP and South Georgia regions. The latitude difference produces marked differences in seasonality of the environments. The mean seasonal pattern of sea surface temperature (SST) variation at the wAP (Fig. 3a) shows temperatures are usually above 0 °C between January and March with a peak in February at ~1 °C (range ~–1.5 to 2.5 °C). During the late autumn and winter when the region is ice covered (usually June to November), the temperatures are

Table 2
 Characteristics of feeding and breeding biology of key species found in their predominant habitats within the western Antarctic Peninsula and South Georgia ecosystems.

Species	Characteristics of diet and breeding	
	Western Antarctic Peninsula	South Georgia
Antarctic krill <i>Euphausia superba</i>	Require sea ice in winter for larval feeding Shelf-oceanic connections High localised retention and recruitment Influx from areas to west	No local recruitment – influx recruitment No winter sea ice for larval krill High temperatures and food Benthic feeding
Antarctic silverfish <i>Pleurogramma antarcticum</i>	Found in ice covered regions Eggs and larvae develop in association with sea ice	
Mackerel icefish <i>Champscephalus gunnari</i>		Primarily located in island shelf areas Larvae develop inshore Are found further south
Myctophid species including <i>Electrona antarctica</i>		Oceanic species that penetrates onto shelf areas north and south Abundance higher in northern areas
Gentoo penguin <i>Pygoscelis papua</i>		Flexible in nesting habitats (tussock and rock/gravel areas) and in breeding timing Adults may delay breeding if poor conditions and/or re-nest if eggs lost early Feed on fish and krill
Chinstrap penguin <i>Pygoscelis antarcticus</i>		Populations that forage locally and are found in both regions Tendency for breeding on slopes and have flexible breeding timing Forage locally and are found in both regions, but smaller numbers at South Georgia Widely dispersed north of sea ice edge in winter
Macaroni penguin <i>Eudyptes chrysolophus</i>		Nest on scree/cliff areas that are ice free Cannot use sea ice environments and have early inflexible breeding period Mainly krill feeders, but also feed on fish Are found further south but in small numbers
Adélie penguin <i>Pygoscelis adeliae</i>	Use pack ice for feeding Mainly krill feeders, but also fish (silverfish) Inflexible breeding period	
King penguin <i>Aptenodytes patagonicus</i>		Feeding in areas of Polar Front on fish and squid and also in SACC Uses open beach areas for breeding, often near glaciers
Emperor penguin <i>Aptenodytes forsteri</i>	Feeding in and around the pack ice edge or in polynyas on fish (silverfish), squid and krill depending on proximity to shelf regions Require fast ice for breeding and consolidated pack ice for moulting	
Antarctic Fur seal <i>Arctocephalus gazella</i>		Widely dispersed over the area Need open sheltered ice free beaches for breeding Cannot deal with consolidated pack ice conditions, but do disperse to marginal ice zone in winter Mainly krill feeders but also feed on fish (icefish and myctophids). Also occur further south around northern Antarctic Peninsula
Crabeater seal <i>Lobodon carcinophagus</i>	Ice obligate Need to feed in pack ice areas and haul out onto ice for resting and breeding Feed mainly on krill and fish	
Weddell seal <i>Leptonychotes weddellii</i>	Ice obligate Need to feed in pack ice areas and haul out onto ice for resting and breeding Feed mainly on fish, squid and krill	
Southern Elephant seals <i>Mirounga leonina</i>		Occur in both regions but more in the north at South Georgia Require open beaches for harems during breeding season. Feed on fish and squid

generally < -1 °C (range ~ -1.8 to -0.5 °C) (Fig. 3a). At South Georgia the observed monthly minimum mean winter SST is 0.2 °C (September) and the maximum in summer is 3.5 °C (February) (Fig. 3a). The winter range of ~ 2 °C is much larger than at the wAP, but the summer range for January is similar at over 4 °C.

Sea ice is a major distinguishing feature between the two ecosystems. At the wAP, sea ice concentration is at a minimum in about March when the mean ice cover is less than 10% over most of the region, although it can remain at concentrations of $\sim 25\%$ (Fig. 3b). The sea ice concentration peaks in September at between ~ 75 and 100%. Variability in sea ice concentration is greatest in spring (November to December, range $\sim 90\%$) and in autumn (June, range $\sim 90\%$). The concentration of sea ice can remain at $> 90\%$ from June to December and can be almost negligible from December to June. In contrast to the wAP, South Georgia lies just north of

the extreme limit of the sea ice zone and does not have a seasonal advance and retreat of sea ice. However, South Georgia is still south of the Polar Front and is strongly influenced by waters from farther south.

Irradiance levels are also a key driver of the marked seasonal blooms in Southern Ocean systems and the seasonal irradiance profiles between the two areas differ. The southern wAP region has ~ 60 days of 24-hour daylight and about 48 days of almost no sunlight. At South Georgia the maximum is ~ 17 h with a minimum of ~ 7.5 h. Total annual daylight hours are similar in both regions (~ 180 – 190 days). However, differences in declination affect penetration of different wavelengths into the water, and along with differences in cloud cover, affect regional radiation budgets.

The ACC flows parallel to the shelf break at the wAP, while South Georgia lies across the flow (Fig. 4). The island is also located further

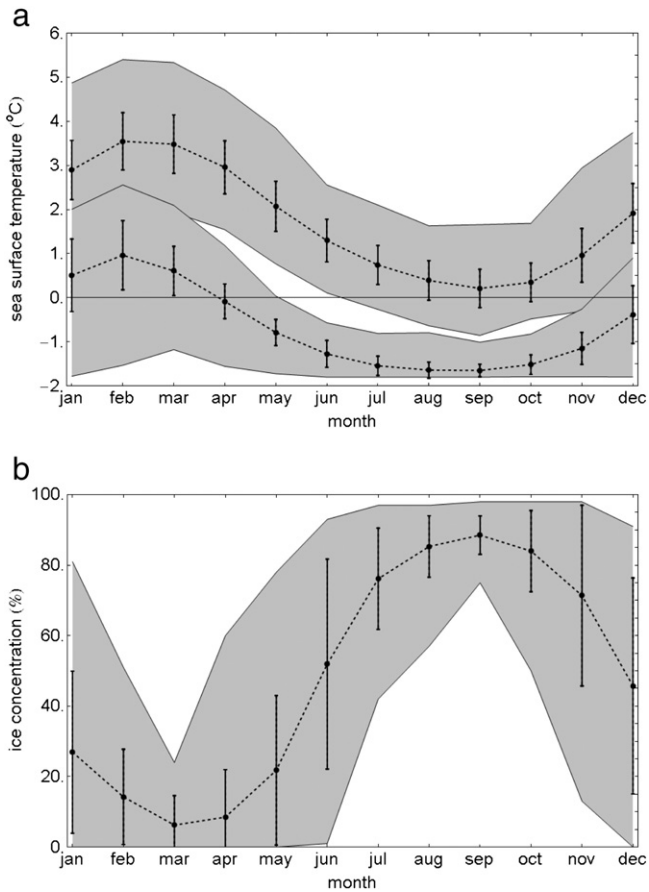


Fig. 3. Seasonal change in monthly mean (filled circles) and standard error (vertical lines) for (a) sea-surface temperature (SST) at the wAP (lower curve) and South Georgia (upper curve) and (b) sea ice concentration (% cover) at the wAP. The monthly variability in the minimum–maximum range (shaded area) is also shown for SST and sea ice. The SST and sea ice time series were obtained from a gridded climatology developed by Reynolds et al. (2002) that is based on satellite and in situ data collected from November 1981 to April 2011. The wAP region used for the time series extended from 69.5°W to 72.5°W and 66.5°S to 68.5°S (12 grid cells each month over 29 or 30 years). That for South Georgia extended from 34.5°W to 39.5°W and 52.5°S to 55.5°S (24 grid cells each month over 29 or 30 years).

north in the ACC system, being north of the SACCF compared to the wAP, which is south of the SACCF and SBACC (Figs. 2 and 4). The wAP shelf area is more extensive (greater than twice the area at depths <400 m), and is also generally deeper than at South Georgia, mainly as a result of deep troughs between 500 and 1200 m in depth that connect inshore to offshore regions. The largest of these, Marguerite Trough, connects Marguerite Bay to the oceanic waters along the outer shelf. Several islands occur along the inner shelf of the wAP, which restrict exchange between nearshore and offshore regions. Throughout the shelf at South Georgia there are shallow plateaus (minimum depth about 200–300 m) and deep depressions (~400 m).

Along the wAP and around South Georgia intense ocean–shelf water interactions occur as the ACC interacts with the shelf regions. This generates complex cross shelf exchange processes, which are variable depending on the bathymetry and the flow structure (Dinniman and Klinck, 2004; Dinniman et al., 2011; Meredith et al., 2008; Piñones et al., 2011; Young et al., 2011). In both regions Antarctic Surface Water (AASW), and below it Winter Water (WW), dominate surface and shelf waters. The most prominent water mass on the wAP continental shelf derives from UCDW, which covers the mid-portion of the wAP shelf and extends into the inner shelf in some areas. The influence of UCDW on wAP ecosystem structure is well characterised (Fig. 4a; Dinniman and Klinck, 2004; Klinck, 1998; Klinck et al., 2004; Smith et al., 1999; Smith and Klinck, 2002). CDW

also occurs throughout the ocean around South Georgia. Along the southwestern shelf of South Georgia in the divergence zone (SGDZ; Fig. 4 b), where a part of the ACC flows west along the shelf towards Shag Rocks Passage (with the shelf on the northern side), warmer more saline waters penetrate onto the shelf (Whitehouse et al., 2008a). This suggests that South Georgia shelf regions are influenced by upwelling or shelf flooding of deeper offshore waters (UCDW) in regions of complex bathymetric–circulation interaction (Fig. 4b). However, the influence of this upwelled water on surface production and shelf waters has not been fully evaluated (Whitehouse et al., 2008a). In both shelf areas, there are also finer scale interactions of current flows and bottom topography that can generate small scale structure (<10 km) and result in retention of biological material (Beardsley et al., 2004; Klinck et al., 2004; Meredith et al., 2008; Smith et al., 1999).

2.2.2. Coastal habitats

The coastal regions are crucial habitats for many land-based breeding predators. Around the wAP the sea ice is a major habitat for a wide range of species and the coastal regions of the southern and central wAP are affected by ice and snow accumulation during spring (Ducklow et al., 2007). The southern side of South Georgia has extensive high cliff regions rising steeply to ~1000 m with few embayments that are dominated by glaciers with little vegetation during summer. The northern coast of South Georgia consists of widespread embayments with adjacent open regions of vegetation during summer and extensive and open beaches. At the extreme western point lies Bird Island with large open beaches and hillsides, which provide suitable areas for seal haul out and seabird nesting sites.

2.3. Primary producers and links to secondary producers

Extensive spring and summer phytoplankton blooms in both regions are dominated by diatoms, but these blooms are variable in timing and magnitude within and between years (Garibotti et al., 2003; Korb and Whitehouse, 2004; Korb et al., 2010; Park et al., 2010; Smith et al., 1998; Whitehouse et al., 1996a, 1996b, 1999, 2000). Ice cover or mixing associated with storminess and low light levels generate reduced productivity in both ecosystems during winter, which can last 2–3 months longer at the wAP than South Georgia (Atkinson et al., 2001; Stammerjohn et al., 2008a). There is clear seasonal succession in community assemblages, particularly around the wAP, with shifts from diatoms to cryptomonads and flagellates during the period of the bloom (Ducklow et al., 2007; Garibotti et al., 2003; Korb et al., 2010). Within both regions there is spatial variability, with an onshelf–offshelf gradient of higher chlorophyll *a* concentrations in shelf areas apparent at times around the wAP, while at South Georgia there is a marked east–west split (Fig. 2; Ducklow et al., 2007; Garibotti et al., 2003; Korb et al., 2004, 2008; Prézélin et al., 2000, 2004). In the western and northern areas around South Georgia there are generally higher chlorophyll *a* concentrations associated with blooms of large diatoms and higher productivity. In areas to the east of the island chlorophyll *a* concentrations are generally lower, smaller autotrophs tend to dominate, and production is lower (Korb et al., 2004; 2008). There is also fine scale variation (<10 km) in the chlorophyll *a* distribution and production in both regions associated with mesoscale features generated by local interactions between the currents and the bottom topography (Korb and Whitehouse, 2004; Korb et al., 2008; Prézélin et al., 2000, 2004). Sub-surface chlorophyll maxima also occur in both areas, and these have been associated with upwelling of CDW (Korb et al., 2008; Prézélin et al., 2000, 2004; Whitehouse et al., 2008a). The phytoplankton bloom that extends from South Georgia downstream to the north and east can last for 4–5 months (Fig. 2; Korb et al., 2004, 2005, 2008). An equivalent feature is not observed in the wAP, although there are localised areas of enhanced surface chlorophyll concentration along portions of the shelf (Fig. 2 and see Fig. 1 in Holm-Hansen et al., 2004).

The physical, chemical and biological processes underpinning primary production are similar in the two ecosystems. In both areas, the oceanic circulation is in direct contact with the shelf regions facilitating upwelling and cross shelf exchanges that maintain enhanced macronutrient levels and affect micronutrient budgets (Prézelin et al., 2004; Whitehouse et al., 2009). Iron is a critical micronutrient for phytoplankton growth and is limiting over much of the Southern Ocean (Boyd and Ellwood, 2010). Natural iron fertilisation occurs in coastal areas around the Antarctic continent, in seasonally sea ice influenced regions and around island areas, where it allows the development of large phytoplankton blooms (Ardelan et al., 2010; Chever et al., 2010; Morris and Sanders, 2011). This injection of iron into surface waters can result from oceanic processes (e.g. deep water upwelling or shelf flooding), ocean–sediment interactions, sea ice melting, and iceshelf or glacial melt water input. This increase in iron concentrations generates iron-replete conditions that favour the growth of large silicified diatoms (Prézelin et al., 2000, 2004;

Whitehouse et al., 2008a). Natural iron fertilisation is a well characterised feature of the South Georgia ecosystem and is probably also important in the development of blooms at the wAP, but the evidence for this is less direct and extensive (Ardelan et al., 2010; Prézelin et al., 2004). In both regions light, mixed layer depth and temperature can be locally important but are not primary limiting factors for summer primary production (Prézelin et al., 2004; Smith et al., 1998; Whitehouse et al., 2009). Although the mechanisms involved are not fully understood, the biogeochemical conditions in both regions favour the development of large and extended blooms of large species of diatoms (Atkinson et al., 2001; Ducklow et al., 2007; Korb et al., 2010).

Overall there appears to be little difference in daily rates of productivity, although there is spatial variability in these rates in both areas at scales of <10 km to regional scales. This variability in primary production results from interactions between physical (e.g. local circulation features, upwelling) and chemical factors (e.g. nitrate,

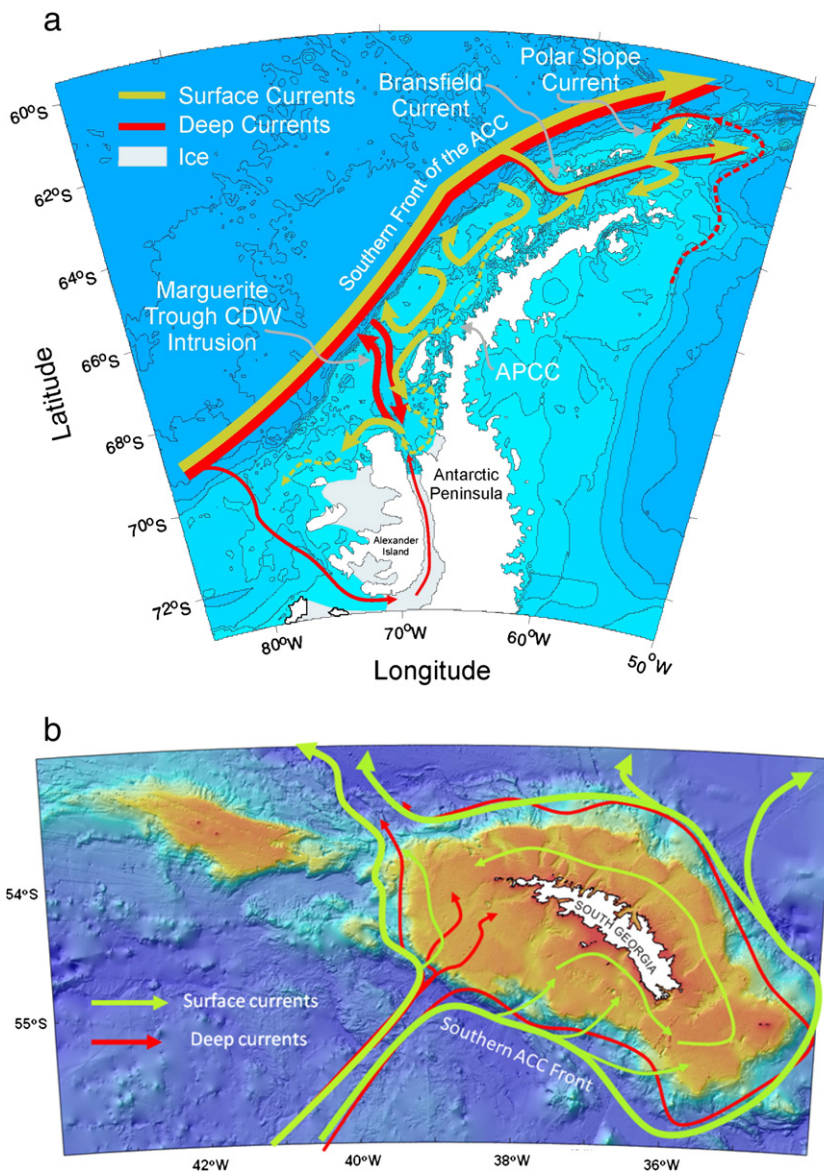


Fig. 4. Schematic illustration of (a) the main surface (green lines) and deep water (red lines) current flows along the western Antarctic Peninsula (adapted from Beardsley et al. (2007) using Moffat et al. (2008)) and (b) the surface (green lines, <100 m) and deep current (red lines, >200 m) flows around South Georgia highlighting regions of cross shelf exchange. The position of the major ice shelves along the western Antarctic Peninsula is shown (light grey shading) and abbreviations are: CDW—Circumpolar Deep Water, APCC—Antarctic Peninsula Coastal Current, ACC—Antarctic Circumpolar Current.

ammonium and iron), and generates spatial and temporal shifts in microplankton community composition and dynamics (Atkinson and Whitehouse, 2000, 2001; Korb et al., 2008, 2010; Prézélin et al., 2004; Smith et al., 1998; Whitehouse et al., 2009). For example, macronutrient concentrations are generally high around South Georgia, but at times concentrations of silicic acid ($\text{Si}(\text{OH})_4$) can be at limiting levels in bloom areas to the west (Korb et al., 2008). The effects of this macronutrient limitation are also modified by variation in the concentrations of iron (Korb et al., 2008). Such interactive effects also involve food web interactions, and a range of studies have noted the spatial and temporal variability of plankton dynamics around South Georgia (Atkinson et al., 2001; Murphy et al., 2007b; Shreeve et al., 2005; Whitehouse et al., 2009). In both areas significant microbial activity occurs during winter associated with benthic communities, while in the wAP region there is also microbial activity and production associated with the sea ice. Both the benthic and ice associated microbial systems provide alternative energy sources to intermediate trophic level species (zooplankton) during periods of low pelagic primary production.

2.4. Secondary producers: zooplankton and krill

Copepods are the main consumers of primary production around South Georgia (Shreeve et al., 2005). However, in areas of high krill abundance, grazing by krill can dominate the zooplankton community demand for food and can therefore consume a significant proportion of the primary production, especially in areas of low production (Whitehouse et al., 2009, 2011). The impacts on the plankton dynamics and biogeochemical cycles of such food web interactions go beyond the top-down grazing impacts that can limit the development of phytoplankton blooms, and include more direct effects on biogeochemical cycles. For example, in the western regions of the South Georgia shelf, there is a dominance of nitrate usage in iron-replete areas, whereas recycled nitrogen (NH_4) is more important in the east where iron levels are low. The ammonia generated by zooplankton excretion, probably mainly by krill which can graze on phytoplankton, can fertilise the region promoting enhanced production rates (Atkinson and Whitehouse, 2000, 2001; Whitehouse et al., 2009, 2011). It has also been suggested that krill have a role in controlling production in these areas by recycling iron within the upper ocean, and by transferring iron into surface waters by benthic feeding (Schmidt et al., 2011). These complex food web effects have only recently begun to be quantified, but such dynamic top-down impacts by mid-trophic level species on biogeochemical processes will also occur along the wAP region, where the krill are abundant and there is significant variation and spatial transfers. Other benthic–pelagic interactions also occur in these neritic systems through epibenthic and semi-demersal plankton and fish species moving into pelagic systems and zooplankton and pelagic species consuming benthic production (Ducklow et al., 2007; Murphy et al., 2007b).

A major determinant of zooplankton community structure across the wAP/Scotia Sea region is the seasonality and its consequent impacts on the phenological development of different species (Ward et al., 2004, 2006). In areas further south, primary and secondary production occurs later resulting in the later development of particular species, and hence later peaks in their abundance. Throughout the region the oceanic zooplankton community structure is generally similar in terms of the species composition, but varies in the relative abundance and development state of different species (Ward et al., 2004, 2006, 2008). In both areas, there are more neritic species in shelf areas, but the same species are also found in offshore regions in lower numbers (Ashjian et al., 2008; Atkinson et al., 2001; Parker et al., 2011; Ross et al., 2008; Ward et al., 2004, 2007, 2008). The exceptions to this are the more ice associated species, such as ice krill, *Euphausia crystallorophias* (Parker et al., 2011; Ross et al., 2008), found in the southern wAP.

The zooplankton community assemblages also vary within the regions. Antarctic krill tends to be the primary member of the

zooplankton assemblage, but salps (*Salpa thompsoni*) can be more prevalent in the northern regions of the wAP and copepods dominate in the western regions around South Georgia (Ashjian et al., 2008; Atkinson et al., 2001; Parker et al., 2011; Ross et al., 2008; Ward et al., 2004, 2005, 2007, 2008). Copepod production at South Georgia can be high relative to krill production, and involves a range of oceanic and neritic species (Shreeve et al., 2005). The importance of other zooplankton is highly variable within and between regions, and includes other species of euphausiid, amphipods (*Themisto gaudichaudi*), ctenophores (*Callianira antarctica*), salps (*S. thompsoni*), mysids (*Antarctomysis ohlinii*) and pteropods (*Limicina helicina*) (Atkinson et al., 2001; Lancraft et al., 2004; Pakhomov and Perissinotto, 1996; Parker et al., 2011; Scolardi et al., 2006). These variations in zooplankton community structure are associated with differences in patterns of production, sea ice conditions, temperature and advection and influx, highlighting the spatially and temporally variable nature of the secondary production in both areas. Advective transport of zooplankton occurs into both regions from areas farther west and south, but this also varies between years, with variation in sea ice and ocean circulation conditions, which influence zooplankton development and dispersal (Marrari et al., 2008; Murphy et al., 1995, 1998, 2004, 2007a, 2007b; Piñones et al., 2011; Ward et al., 2002).

As a result of its abundance and size, Antarctic krill is the central species in the food webs in these two ecosystems. Along the wAP shelf, including Marguerite Bay, and adjacent off shelf regions, are areas where the krill can complete their life-cycle, with subsequent local spawning, recruitment, growth and maturation indicating a self sustaining krill population (Fraser and Hofmann, 2003; Hofmann and Husrevoglu, 2003; Piñones, 2011; Piñones et al., 2011). However, the degree to which the wAP krill population is supported by local versus remote input varies with time and with location along and across the continental shelf (Daly, 2004; Piñones, 2011; Piñones et al., 2011; Wiebe et al., 2011). The net result is that the populations along the Peninsula are connected to upstream regions in the Amundsen and Bellingshausen Seas, and coastal circulation patterns also connect the wAP to the Weddell Sea, generating complex and variable population mixing over a large area. This connected and mixed population provides the basis for the regional spawning and recruitment in the southern Scotia Sea that is dispersed northwards, connecting across the Scotia Sea to South Georgia (Fach et al., 2002, 2006; Murphy et al., 2007a, 2007b). This dispersal process involves overwintering of juveniles and adults in ice covered areas that further enhances mixing and affects dispersal routes (Fach et al., 2006; Murphy et al., 2007a, 2007b; Thorpe et al., 2007). The patterns of seasonal on–offshelf movement associated with krill maturation and spawning (Siegel, 1988; 2005) provide the basis for additional variability in the transport pathways for return of larvae and juveniles to the wAP shelf, and for export to downstream regions (Piñones, 2011; Piñones et al., 2011).

In contrast, the krill population at South Georgia is not thought to be self sustaining, as recruitment of larvae and the youngest age groups do not appear to occur on the shelf (Tarling et al., 2007). There is recruitment of larger individuals (generally >35 mm, although on occasion 20–25 mm animals dominate length frequencies) into the population, but it is unclear if this reflects a localised shelf based population or the wider Scotia Sea population structure (Murphy et al., 2007b). There is retention on the shelf, and the krill are moved north around the eastern end of the island in the direction of the general shelf flows. This produces enhanced concentrations in areas associated with shallow banks on the north coast, where much of the krill fishery has historically occurred (Murphy et al., 2007b). The general flow tends to move these krill into the most western areas close to Bird Island, where they are exploited by large numbers of predators that target these enhanced prey concentrations during summer (Murphy et al., 2007b). The krill population around South Georgia and the northern Scotia Sea is, therefore, part of the larger population that occurs across the

southern Scotia Sea and around the Antarctic Peninsula (Murphy et al., 2007a, 2007b).

Overwintering of krill across such a range of habitats is critical to their role in regional food webs. Sea ice is a vital habitat for overwintering of larval krill, where they have access to microbial production during periods when the water column is mixed to depths of greater than 100 m and plankton concentrations are very low. However, winter observations from the Marguerite Bay region of the WAP shelf showed that larval and adult krill are not always found in the upper water column, but can be distributed throughout the water column and aggregate in deeper areas below 100 m (Lawson et al., 2008a; Wiebe et al., 2011). As noted above, recent observations have emphasised the importance of benthic feeding of krill (Schmidt et al., 2011), and suggests that the sea-bed is also a key overwintering habitat in both ecosystems. Benthic feeding is probably a similar process to feeding on the undersurface of ice, acting as another substrate interaction for krill. The ability of krill to exploit sea ice or benthic habitats as alternative areas of food availability highlights the importance of vertical migrations in maintaining the food web.

The large scale over which the dynamics of krill populations operate mean they connect food webs, linking areas of production and recruitment in the south around the Antarctic Peninsula, southern Scotia Sea and northern Weddell Sea with areas further north across the Scotia Sea, where they are prey for higher predators (Murphy et al., 2004, 2007a, 2007b). However, krill also affect the structure and function of the whole food web. For example, the occurrence of krill at high densities in cooler eastern waters at South Georgia, where production is reduced, appears to uncouple the krill from the high-production (probably high-iron), large-diatom, dominated ecosystem in which they are produced. This disconnect results from the advective transport of krill generating connected food webs, rather than indicating a distinctly different food web structure. The local food web in the eastern areas of South Georgia is probably not self supporting, but is dynamically maintained through advection, dispersal and vertical biological interactions with benthic and mesopelagic groups. In these areas, krill can reduce phytoplankton concentrations, as well as out-compete and even suppress copepod concentrations through predation (Whitehouse et al., 2009). In the west, the planktonic community is generally dominated by copepods, possibly through rapid early seasonal population development in the comparatively warmer conditions (Shreeve et al., 2005). As noted above, krill are moved into these western areas through the westward circulation along the north coast on the shelf and in off shelf areas (Fig. 4b). However, the oceanography and circulation patterns around South Georgia are highly variable within and between years, generating very different interannual retention and dispersal dynamics, and hence food web structures.

Krill is, therefore, a key species in both of these regional ecosystems, and central to the main energy flow pathways and spatial connections (Murphy et al., 2007b). However, their role appears to go much further as major “ecosystem engineers” (Jordan, 2009), where feedback processes of grazing, predation and excretion can generate major changes in ecosystem structure and function. In consuming phytoplankton and other zooplankton, krill change the plankton dynamics, but they also provide recycled nitrogen and possibly iron (Schmidt et al., 2011) and consequently they can enhance local productivity, and affect regional biogeochemical cycles and carbon budgets. The patchiness in these interactions generates a dynamic mosaic of production and consumption that can affect overall production. The presence or absence of krill therefore reflects major structural changes associated with their role as grazers and predators in the system (Whitehouse et al., 2011).

A range of energy pathways, involving zooplankton species other than krill, maintain the overall ecosystem structure through seasonal and interannual variations at South Georgia and the WAP. These include various copepod, euphausiid and amphipod species. For example, around South Georgia, the amphipod, *T. gaudichaudi*, consumes other species including notably the pteropod *L. helicina*, and can dominate the

diet of pelagic and land-based predators during years of low krill abundance. *T. gaudichaudi* does occur around the WAP, but is less abundant than at South Georgia, perhaps indicating that it is not a viable alternative prey in the absence of krill in the WAP. These alternative pathways are poorly quantified because of the lack of general ecological knowledge of the role of many species (e.g. carnivorous zooplankton), which are present and consumed by a range of predators in both ecosystems (Lancraft et al., 2004; Ward et al., 2008). Along the northern WAP more oceanic waters influence the shelf areas and salps can dominate the zooplankton community when krill are largely absent (Loeb et al., 1997). This contrasts with the South Georgia ecosystem, where although salps do occur, copepods dominate the plankton community in years when krill are largely absent (Shreeve et al., 2002, 2005).

2.5. Tertiary producers: nekton and higher predators

Fish and cephalopods occur in both regions, but the species and the ecological niches they occupy change between the two areas (Collins and Rodhouse, 2006; Donnelly and Torres, 2008; Kock et al., 1994; Piatkowski et al., 1994). For example, semi-demersal species dominate the shelf fish communities at South Georgia and pelagic fish species are absent. Representative species include the mackerel icefish (*Champscephalus gunnari*) and various notothenoid species, and Patagonian toothfish (*Dissostichus eleginoides*) occur in deeper regions. Farther south around the WAP region, in coastal areas where sea ice occurs, the notothenoid Antarctic silverfish (*Pleuragramma antarcticum*), which is a primarily a pelagic species, dominates (Cullins et al., 2011). The life cycle of silverfish is closely linked to the sea ice, as it uses platelet ice as a brooding site for its eggs (Hubold, 1985; Kellerman, 1986). *P. antarcticum* also has antifreeze proteins in its body fluids, thus giving the silverfish a competitive advantage in ice covered regions (Cullins et al., 2011). The importance of the oceanic mesopelagic fish species, and especially myctophids, in both oceanic and neritic areas of these ecosystems, where they are major opportunistic feeders on mesozooplankton, has been known for some time (Ainley et al., 1992; Hopkins, 1985; Pakhomov et al., 1996; Smith et al., 2007). Only recently, however, has a more quantitative understanding of their role in these ecosystems begun to develop (Collins et al., 2008; Shreeve et al., 2009).

Of particular importance in these food webs is the myctophid species *Electrona antarctica*, which is the dominant fish of the circumpolar pelagic region of the Southern Ocean and the southernmost of the Myctophidae (Greely et al., 1999). *E. antarctica*, and also *E. carlsbergi* and *Protomyctophum choriodon* are important species around South Georgia, but it is *E. antarctica* that is the main prey item of some of the major air-breathing predators in both areas (Collins et al., 2008; Waluda et al., 2010). In addition, a number of other myctophid species are present around South Georgia, where they are both predators of zooplankton and prey in the diet of a range of higher predators (Olsson and North, 1997; Reid et al., 1997a; Shreeve et al., 2009; Waluda et al., 2010). Observations indicate that *E. antarctica* is increasing in abundance and becoming more important in foodwebs in areas of the northern WAP, where *P. antarcticum* is decreasing in abundance as the ice retreats (Ducklow et al., 2007). Although *E. antarctica* and *P. antarcticum* have very different life cycles they have a similar diet, consuming copepods during early stages of their life cycle, and krill as they get bigger, (Cullins et al., 2011). *E. antarctica* lives for 4 years and only reproduces during the last year, while *P. antarcticum* can live for 21 years and matures at about 9 years (Cullins et al., 2011). *E. antarctica* is a more oceanic species, and its influence in shelf systems is limited by their pattern of diurnal migration to deeper waters, which is possible in only small regions of the shelf areas (Loots et al., 2007). The changing distributions and relative dominance of these two species in nektonic communities along the WAP are, therefore, the result of different evolved adaptations and life history constraints that produce different responses to the changing physical environments.

The major groups of higher predators that feed on the zooplankton and nekton are generally the same in the wAP and South Georgia regions, with representatives of seals, penguins, flying seabirds and whales. However, the species and their abundances vary between the two areas as a result of differences in their evolved adaptations and life-history traits, and the habitats. Some of these species feed mainly on zooplankton, or a combination of zooplankton or fish, while the highest predators (e.g. leopard seals and killer whales) target penguins or seals. There are very large concentrated colonies of seals and flying seabirds at South Georgia, whereas along the wAP, although the penguins are concentrated, the seals and seabirds are generally more dispersed on the ice. At South Georgia, macaroni (*Eudyptes chrysolophus*) and gentoo (*Pygoscelis papua*) are the primary penguin species, both of which are mainly krill eaters that also consume fish (Waluda et al., 2010; Williams, 1995). Macaroni penguins breed in habitats north of the pack ice area, on rock slopes and on open rock on level ground in areas with little vegetation (Williams, 1995). Farther south, in the wAP area, the dominant Adélie penguins (*P. adeliae*) depend mainly on Antarctic krill, but can also exploit other prey such as Antarctic silverfish (Ducklow et al., 2007). Adélie penguins breed on rocky areas with cold dry conditions within the pack ice influenced zone (Ducklow et al., 2007; Fraser and Trivelpiece, 1996; Williams, 1995). The gentoo and chinstrap penguins (*P. antarcticus*) occur in both the open water areas around South Georgia and the more ice influenced regions of the northern and central wAP.

The differential affinity of evolved life-histories of species of pinnipeds and cetaceans with sea ice has been previously highlighted (Costa and Crocker, 1996; Ducklow et al., 2007). For example, Antarctic fur seals (*Arctocephalus gazella*) at South Georgia tend to utilise open ice-free beach areas to establish territories and gather harems, and these need to be relatively sheltered. They also forage and over-winter in open water and the marginal ice zone, and are not found in dense areas of pack. The ice-obligate seal species, the crabeater (*Lobodon carcinophagus*) and Weddell seals (*Leptonychotes weddellii*), are most numerous in ice covered areas and use the sea ice as a major habitat (Ducklow et al., 2007). These species need sea ice to occur during summer over shelf areas to allow them to haul out, rest and reproduce and for access to prey items at high densities in these areas (see Ducklow et al., 2007 and references therein).

There is a high degree of spatial, temporal and niche separation in breeding, foraging and feeding ecology of the seabird and marine mammals of the Southern Ocean that has been demonstrated in studies of the South Georgia ecosystem (Barlow et al., 2002; Boyd, 2002; Croxall et al., 1997; Gonzalez-Solis et al., 2000; Phillips et al., 2005, 2007b; Xavier et al., 2003). Knowledge of the impact of the very large populations of many species of flying seabirds (e.g. petrels) in the food webs remains limited, but they consume large numbers of copepods and other non-krill components of the plankton (e.g. Reid et al., 1997a, 1997b; Shreeve et al., 2005). There is also marked seasonality in the demand for prey as many of the predators leave the region during winter, dispersing across the Scotia Sea, into the seasonal pack ice zone or northwards across the Polar Front into areas near the Patagonian Shelf (e.g. fur seals) or around South Africa (Boyd et al., 1998; Croxall and Wood, 2002; Phillips et al., 2007a, 2007b, 2009). The resultant niche separation that these various foraging and breeding strategies represent is an important feature of both ecosystems, and generates differential species responses to food and environmental variability.

2.6. Spatial variability and connectivity

The wAP region has shelf and bay areas, such as Marguerite Bay, which have high retention as well as exchanges that are driven by the cross-shelf circulation processes (Piñones et al., 2011). Inflows from the Bellingshausen and Amundsen Sea areas occur, as does export from the wAP to the north, but these primarily affect the mid and outer shelves (Piñones, 2011). The inner shelf region tends to be

more retentive, except for those areas that are connected via troughs or other topographic depressions to the mid and outer shelf regions (Piñones, 2011). As a result, the production and consumption of organic carbon would be expected to vary across the wAP shelf.

Around South Georgia the system is more open, with the regional production dynamics more directly associated with flow of the ACC, which brings secondary production into the region, enhancing the capacity of the local food web to maintain higher trophic level species. The areas of enhanced retention in shelf and bay areas around South Georgia are less extensive compared to the wAP region. Many of the higher trophic level species at South Georgia forage over large distances, bringing back prey to feed young. The local system is, therefore, maintained by a combination of local and externally generated production (autochthonous and allochthonous) and local and externally dispersed consumption (Murphy et al., 2007b). Although the same occurs along the wAP, the importance of externally generated production is probably lower than around South Georgia (see Piñones et al., 2011). Within both regions there are also hotspots of predator foraging that are associated with local oceanographic and topographic conditions (Harrison et al., 1991; Hunt et al., 1992; Goss et al., 1997; Costa et al., 2007;), which will also be regions of high plankton production or aggregation (e.g. Piñones et al., 2011). The interactions emphasise that the spatial variability that exists within both of these ecosystems results from a range of physical and biological interactions at different scales.

The northeasterly to easterly flowing ACC provides connectivity between the wAP and South Georgia, and also makes these systems open and dependent on both local and larger-scale processes. In addition to the ocean circulation, other physical processes operating over larger scales (e.g. sea ice drift and atmospheric circulation) also affect regional habitat structure and properties (e.g. thermohaline, ice and nutrient properties). There are also biological processes (e.g. movement and migration) that operate over large scales (i.e. greater than the regional 100 km scale) that also affect regional scale biological processes (Fach et al., 2006; Murphy et al., 2004, 2007b; Thorpe et al., 2004, 2007). These processes result in high levels of openness of the regional ecosystems with significant physical and biological exchanges across regional boundaries (Fach et al., 2006; Hofmann and Murphy, 2004; Hofmann et al., 1998; Murphy et al., 1998, 2004, 2007a, 2007b). The ecosystems of the wAP, Scotia Sea and South Georgia are, therefore, connected at different scales and trophic levels, and are not isolated homogeneous ecological systems.

3. Generic representation of wAP and South Georgia food web structure

The more sub-Antarctic (South Georgia) and maritime to high Antarctic (wAP) environments have winter and summer seasons with different durations and characteristics. Although the overall seasonal phytoplankton production in the central areas of the two regions is similar, the production farther south is concentrated into a shorter period, which constrains the range of life-history strategies that will allow survival in the wAP (Table 2). Organisms in the wAP region are adapted for lower temperatures and sea ice cover, and also for more extended periods of low food availability (Clarke et al., 2007). Across a wide range of key species, operating at different trophic levels, the evolved species adaptations and life-history traits (Table 2) are crucial in determining their distribution and abundance, and also their relative success compared to similar competing species in these ecosystems (see Section 2). These life-history traits provide fundamental advantages and constraints on the capacity of particular species to exist and compete in particular habitats around the wAP and South Georgia. These advantages and constraints, and the niche separation they produce, are, therefore, crucial in determining the major components that compose the regional food webs. However, although many of the species differ between the two food webs, the biogeochemical conditions and the connectivity between the ecosystems

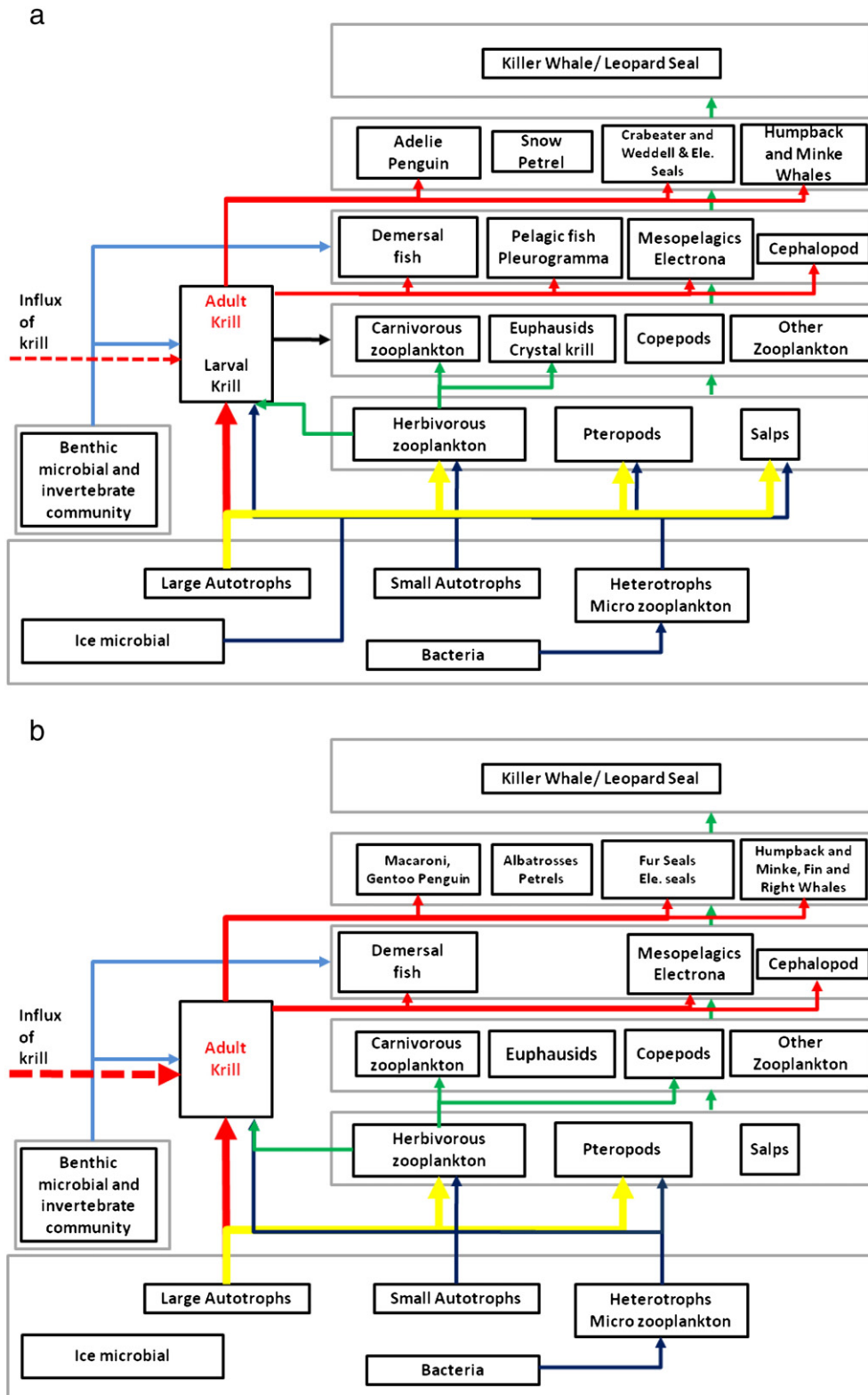


Fig. 5. Generic model of Southern Ocean food web structure applied to (a) the western Antarctic Peninsula and (b) South Georgia. This view of the food web is based mainly on knowledge of the summer food web operation and identifies the major known flows based on published assessments noted in the text. The generic food web includes a microbial group, with small and large autotrophs, an ice microbial component, a benthic component, zooplankton groups consisting of small herbivorous or omnivorous mesozooplankton and a group of larger both omnivorous and carnivorous macrozooplankton, a nektonic/semi-demersal predatory group involving fish and squid and a higher predator group that distinguishes different congener guilds, and finally the top predators. The main Antarctic krill trophic pathways (red arrows) and non-krill pathways involving the large autotrophs (yellow arrows) are shown. The main non-krill links associated flows from other components of the microbial system or larger planktonic systems (dark blue arrows) are indicated. Secondary and tertiary connections (green arrows) occur for the krill and non-krill pathways and benthic–pelagic/larger organism connections (lighter blue arrows) provide inputs to both. The influx of krill in current systems is indicated by the red dashed line. (Ele. seal = Elephant seal). Particularly important individual species at the WAP and noted separately are: Electrona = *E. antarctica* in the mesopelagic fish group; Pleurogramma = *P. antarcticum* in the pelagic fish group; Crystal krill = *Euphausia crystallorophias* in the euphausid group. At South Georgia Electrona is noted as a particularly important individual species in the mesopelagic fish group.

mitigates the major physical differences and suggests an underlying similarity in the structure and function of the wAP and South Georgia ecosystems.

To examine this suggestion, we develop qualitative model descriptions of the general (mean) food web structure for both areas that focuses on identification of major components, their links and the overall structure. The major species groupings of zooplankton, nekton and higher predators present in both ecosystems are similar (Section 2). Thus it is possible to identify a minimum set of categories of aggregated species/groups that can provide a consistent characterisation of the food webs, even if the exact species differ. The generic view of the food web structure for the two systems (Fig. 5) links a functional view of the lower trophic level plankton system with a congener-guild view of the higher trophic level community structure (Allen and Fulton, 2010; Hofmann, 2010). This model structure encompasses the main species found in the wAP and South Georgia ecosystems. Because of the importance of Antarctic krill as a single species in these ecosystems, it is included as an explicit separate element of the food web model. The higher trophic level groups include guilds of different predator congener species or types rather than distinct functional groups. For example, penguins or seals can both be mainly krill predators, but are distinguished by different life histories and foraging strategies. The benthic component includes the microbial and invertebrate communities. The structure of the model represents the major pathways of interaction that exist in both systems, but does not assume that all pathways are significant in both areas. The relative significance of the pathways will emerge from detailed quantification of the interactions and energy flows (e.g. Ballerini et al., submitted for publication; Hill et al., 2012).

Across the lower trophic levels, the wAP and South Georgia systems are generally similar in structure and operation (Fig. 5). In both areas, biogeochemical conditions allow large diatoms to dominate the microbial components of the summer ecosystem, although there are also areas and times where the smaller autotrophs and more complex interactions within the microbial community dominate the production dynamics. In both areas, there are interactions with the benthic ecosystems, but the ice cover in the wAP provides a further component of the ecosystem through much of the year that is not present at South Georgia. The benthic and ice-associated ecosystem elements provide mechanisms for production to be generated or stored. This energy is then available to intermediate trophic level groups of macrozooplankton and nektonic/demersal species of fish and squid during periods when there is little water column production, and when there are few smaller prey items available in the upper mixed layers. In both areas, krill are a major link in the transfer of energy from small to large predators (Fig. 5). However, at South Georgia, the influx of krill probably represents a more significant input of production into the regional ecosystem from outside that will have a strong seasonal signal and shows more marked interannual variability (Murphy et al., 2007a). At the wAP, the larval and juvenile krill will also be important in the food web, although there will be offshelf/onshelf differences in timing and hence interaction dynamics.

Differences in adaptations and hence life history traits (Table 2) result in dominance of different species within groups that occupy similar niches. For example, in the wAP zooplankton assemblage, ice krill/Antarctic krill/copepods/salps dominate, while Antarctic krill/copepods/amphipods dominate at South Georgia (Fig. 5). In the fish community, the silverfish (*P. antarcticum*) and *E. antarctica* are important in the wAP system, while at South Georgia it is *C. gunnari*, notothenioids and the myctophids (especially *E. antarctica* and *P. choriodon*). For the higher predators (air breathing and land breeding) the presence or absence of ice and snow, and associated processes, is the major factor that determines the species composition of the seals, penguins and other seabirds (Fig. 5 and Table 2). However, a range species are highly mobile and can occur in both regions and are not restricted by the particular regional conditions. This is especially true of some of the higher predators, including elephant seals, albatrosses, killer whales and leopard seals.

Energy flow pathways involving krill are important in both ecosystems in maintaining the high densities of the air-breathing predators. At South Georgia, copepods and other zooplankton can be at times the dominant consumers of primary production and the major determinants of its fate (Shreeve et al., 2005). At the wAP, the role of other zooplankton in the food web is less well understood, although the copepods and carnivorous zooplankton are abundant in the planktonic community (Ashjian et al., 2008). Krill are consumed by fish and squid, but estimates of stock sizes and consumption rates are highly uncertain, making it difficult to fully assess their importance in maintaining overall food web structure. These pathways are not as efficient in transferring energy to the highest trophic levels as those involving krill directly, but they are particularly crucial when krill are absent (Murphy et al., 2007a). For example, focusing on the trophic links of fur seals and macaroni penguins around South Georgia, when krill are abundant (Fig. 6a) and when they are not abundant (Fig. 6b, c) shows that the pathways are complex and interconnected. When few krill are available to fur seals during the breeding period they consume more fish, particularly the notothenid, *Lepidonotothen larseni*, and the myctophid, *P. choriodon* (Waluda et al., 2010; Fig. 6b). These in turn consume the smaller euphausiid species and copepods, but also the carnivorous amphipod *T. gaudichaudi*. In contrast the macaroni penguins feed more directly on the euphausiids and amphipods, but also take more of the myctophid, *E. antarctica*, which also feeds predominantly on the other euphausiids and amphipods (Fig. 6c). This highlights the different responses to change by the different krill predators and the different capacities and strategies for coping with reduced krill availability (Waluda et al., 2010).

In both systems there are a number of key species/groups in the plankton and nekton that characterise the alternative pathways of energy flow to higher trophic levels. In the southern ice covered shelf areas these include the ice krill (*E. crystallorophias*) and the silverfish (*P. antarcticum*); in the more seasonally ice-open water regions of the ACC, Antarctic krill and myctophids are characteristic components. In the northern open waters outside the sea ice influenced zone, the planktonic systems are characterised by copepods and mesopelagic fish in general (including a range of myctophid species). Each of these key species/groups is associated with particular habitats, but also with different primary production regimes and higher predator species. We suggest that these species/groups can be considered as indicators of ecosystem structure, because shifts in their dominance reflect major structural and functional changes.

Current views of these ecosystems are based mainly on analyses of summer observations. Neither the winter ecosystem dynamics nor the transitional spring and autumn dynamics are well understood or quantified, although it is clear that there are seasonal shifts in the dominance of the different pathways of energy flow and that similar processes will apply at South Georgia and along the wAP (Murphy et al., 2007b). However, significant latitudinal differences between the regions in seasonal dynamics (e.g. light) and sea ice presence (which affects production), mean that krill-alternative pathways involving species associated with the sea ice and benthic systems will be more favoured in the wAP ecosystem than at South Georgia. Instantaneous views of food web structure can also be misleading. The capacity of the species present to store energy and/or reduce metabolic rates (e.g. through diapause) during periods of low temperatures and low food availability mean that the structure of the food web at any particular time is dependent on both current and historical dynamics. In addition, many of the predator species present in the wAP food web either migrate from the region during winter or disperse with the autumn sea ice advance, moving farther north into areas where more daylight occurs and alternative food resources are available (e.g. through krill under ice or by access into shelf areas and the benthos in areas in the marginal ice zone). There are also strong seasonal spatial interactions; for example, the advance of sea ice across the Scotia Sea during winter allows predators from South Georgia to occupy an ice

habitat to the south of the island while, during summer, as the ice retreats, predators such as elephant seals travel to the WAP region to forage on fish and squid.

The above analyses indicate that the general food web structure of the WAP and South Georgia ecosystems is remarkably similar and can be represented with a generic view of the food web structure based on aggregated functional or congener groups. These food webs represent an integration of the spatial and temporal variability that occurs at different scales. The interannual variability and decadal and longer term changes are a fundamental aspect of the Southern Ocean with which the biological components interact and from which the food web structure emerges. To understand the controls on food web structure therefore requires quantification of not just the integrated trophic flows, but also the variability in food web operation.

4. Ecosystem structure and function: affects of variability and change

The WAP and South Georgia regions both experience marked interannual and sub-decadal variation associated with Southern Hemisphere scale processes such as the El Niño-Southern Oscillation (ENSO) and the changing strength of the westerly winds as indicated by the Southern Annular Mode (SAM) (Loeb et al., 2009; Meredith et al., 2004, 2005, 2008; Murphy et al., 2007a; Quetin et al., 2007; Smith and Stammerjohn, 2001; Stammerjohn et al., 2008a, 2008b; Trathan and Murphy, 2002). The underlying physical and oceanic processes involved in generating these variations also show marked decadal changes (Meredith et al., 2008; Quetin et al., 2007; Stammerjohn et al., 2008a, 2008b). These atmospheric changes have major impacts on

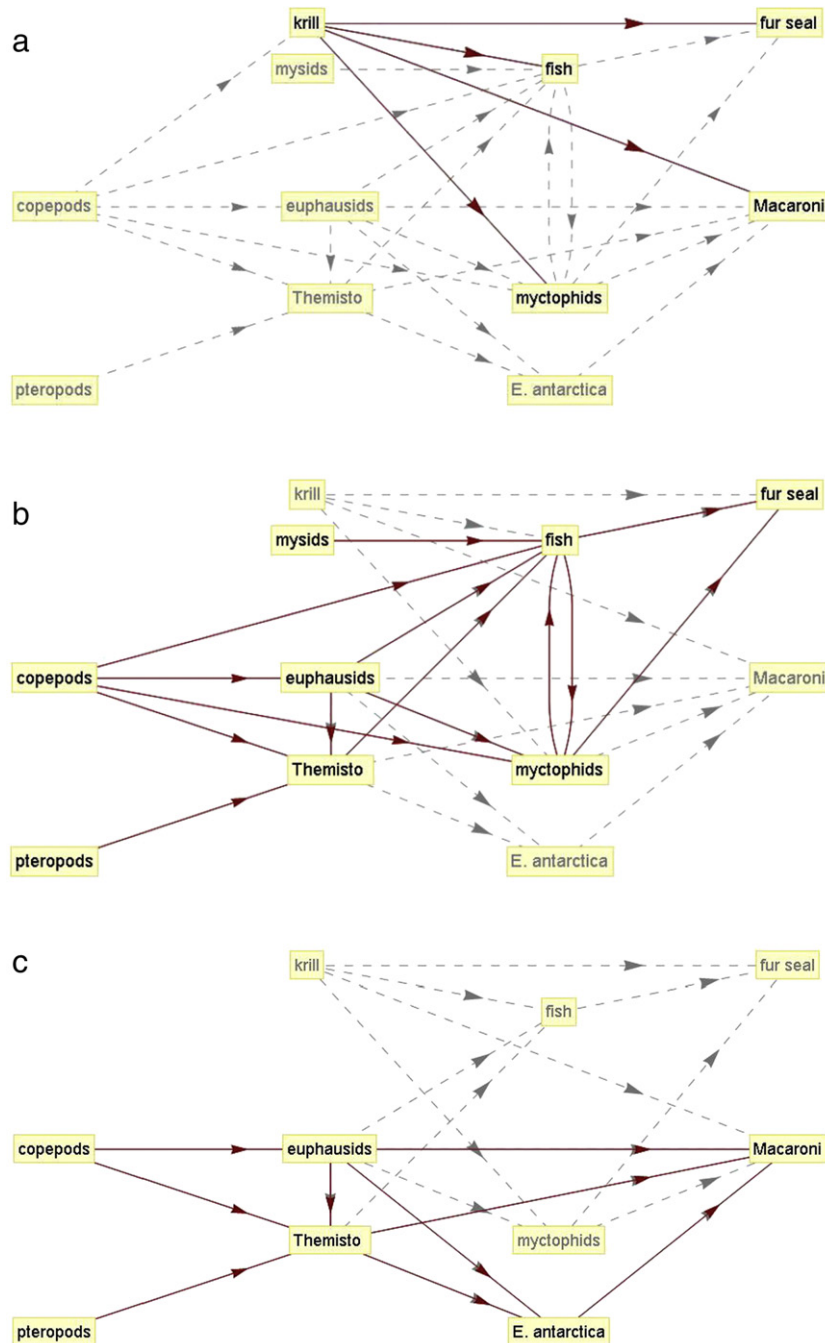


Fig. 6. Schematic of the major linkages in the South Georgia food web that support Antarctic fur seals and macaroni penguins showing the main: (a) Antarctic krill pathways, (b) non-krill pathways to Antarctic fur seals and (c) non-krill pathways to macaroni penguins (see text for details and references).

regional oceanic and sea ice processes, making interannual and decadal variations fundamental features of both ecosystems. However, the nature of the physical connections in the two areas is different, generating different responses to particular events.

Although the exact form of the physical variation differs between the two areas, the resident species have life history strategies to cope with the natural range of variation experienced (Forcada et al., 2008). For many species, extended life spans allow them to cope with periods of poor breeding success as long as there are not too many poor years before a strong cohort is generated (Fraser and Hofmann, 2003). For example, krill populations at the WAP and around South Georgia are maintained by strong recruitment events every few years (Murphy et al., 2007a, 2007b). The strength of recruitment into the local populations has been linked to regional oceanic and sea-ice conditions in both areas and results in changes in abundance and biomass of the krill (Murphy et al., 2007b; Quetin et al., 2007; Reid et al., 2010; Saunders et al., 2007). At South Georgia, changes in the overall zooplankton community structure occur in association with these changes in krill biomass and result in copepods dominating when conditions are warmer and krill when cooler (Atkinson et al., 2001; Shreeve et al., 2002, 2005; Ward et al., 2008). This fluctuating availability of krill and resultant changes in zooplankton community structure, result in shifts between years in the dietary composition of predators, such as fur seals, macaroni and gentoo penguins and black browed and grey headed albatrosses (Croxall et al., 1988; Forcada et al., 2005, 2008; Murphy et al., 1998, 2007b; Reid et al., 2007; Trathan et al., 2003, 2006, 2007). The strong environmental control of krill abundance at South Georgia (Murphy et al., 2007a) means that significant environment–predator performance (foraging and breeding) relationships emerge, with foraging and performance reduced in warmer periods when krill abundance is lower (Forcada et al., 2005, 2006, 2008; Trathan et al., 2006). The variability of krill abundance, biomass and availability to predators is greater at South Georgia than the WAP, generating greater changes in food web structure between years. This reflects the more variable underlying dynamics of the krill population at South Georgia, and its greater dependence on external recruitment than the population in the WAP region.

Both the WAP and South Georgia are regions where major physical changes have occurred over the last 50 years, and biological changes have been recorded across a range of trophic levels. There has been warming and reduction in sea ice along the WAP, which has modified freshwater input from ice melt and resulted in longer periods of open water. The corresponding strengthening of the winds has enhanced vertical mixing resulting in apparent reduction in water column stability (Montes-Hugo et al., 2009). In these areas the phytoplankton community composition appears to be shifting from dominance by diatoms to that of smaller autotrophs. At the same time there are suggestions that there is an along-shelf gradient in changes to the food web with salps occurring more frequently in the northern areas and displacing Antarctic krill (Ducklow et al., 2007). In areas where ice concentration has reduced, the more ice-dependent *E. crystallorophias* is being replaced by *E. superba* and *P. antarcticum* is being replaced by the oceanic mesopelagic fish species *E. antarctica* (Ducklow et al., 2007).

The penguin populations of the WAP have shown a clear change in community composition over the past three decades, with the ice-dependent Adélie numbers declining, while the more ice-intolerant gentoo (*P. papua*) numbers are reported to have increased (Ducklow et al., 2007), and chinstrap penguin (*P. antarcticus*) numbers are showing increases and decreases in different colonies (Croxall et al., 2002; Ducklow et al., 2007; Forcada and Trathan, 2009; Trivelpiece et al., 2011). These changes have been attributed to reduced winter sea ice concentrations (Ducklow et al., 2007; Fraser et al., 1992), increased snow precipitation (Thompson et al., 1994), which accumulates in the area of the breeding colonies (Chapman et al., 2011; Fraser and Patterson, 1997; Patterson et al., 2003) and changes in the abundance of their primary prey, Antarctic krill (Trivelpiece et al., 2011). Changing

physical aspects of the WAP habitat are likely to have been crucial in generating some of the observed changes in penguin species distribution and abundance. However, reductions in krill biomass, and other changes in prey availability, will be key factors in generating the changes being observed along the WAP and in the Scotia Sea (Trivelpiece et al., 2011). Overall in the northern regions of the WAP, reduced upper ocean stability and sea ice concentration, and possibly reduced micronutrient inputs from ice melt, are resulting in a shift away from a system dominated by large blooms of diatoms (Montes-Hugo et al., 2009), with resultant changes in the rest of the food web (Clarke et al., 2007; Ducklow et al., 2007).

At South Georgia the effects are less clear and are confounded by the historical changes generated by harvesting over more than two centuries. The impacts of harvesting of seals, great whales, finfish, and more recently, krill, are still ongoing (Everson, 1977; Murphy, 1995; Trathan and Agnew, 2010). For example, fur seals at South Georgia numbered less than few hundred during the middle of the last century, but have increased rapidly during the last 50 years, and now there are a few million animals present each summer and suggestions that numbers have now peaked. At the same time macaroni penguins numbers may be declining and regional whale populations are showing signs of recovery (Reid and Croxall, 2001; Trathan and Agnew, 2010). Such higher trophic level changes reflect the large perturbation of the ecosystem that the harvesting caused, which will have resulted in top-down impacts in the ecosystem. The changing population sizes will have generated competitive interactions for food and breeding space as the exploited populations of seabirds and marine mammals (including whales) have begun to recover (Murphy, 1995, 2007b; Trathan and Agnew, 2010), which will have resulted in cascading impacts on lower trophic level species. Major ecological changes are, therefore, an expected consequence of the harvesting that occurred in this ecosystem, which mean that any physical changes need to be assessed in this context.

South Georgia is on the northern edge of the polar waters, making the system particularly sensitive to the effects of warming and changes in patterns of ocean circulation. There has been summer and winter oceanic warming over the last century and glaciers are retreating (Cook et al., 2010; Whitehouse et al., 2008b), but the ecological impacts of these physical changes are not clear. We have noted that there is a strong physical influence on annual recruitment strength of krill, but there is no clear evidence at South Georgia that the reported long-term (~30 years) Scotia Sea wide decline in krill has affected the biomass and availability of krill around the island, or that there have been major shifts in zooplankton community structure (Atkinson et al., 2004; Ward et al., 2008). The dynamic and variable nature of the ecosystem, short duration of time series data and the patchy sample availability alongside the simultaneous changes in predator populations will all contribute to masking any long term trends in krill and zooplankton dynamics (Atkinson et al., 2004; Murphy, 1995; Murphy et al., 2007a, 2007b; Whitehouse et al., 2008b). The data required to be able to distinguish between these scenarios of bottom-up and top-down process driven change are not currently available, but both processes are probably occurring simultaneously at South Georgia and the WAP (Murphy et al., 2007b; Murphy et al., in press).

Physically driven changes due to warming at South Georgia are not necessarily a major problem for predator species that can move and establish colonies in similar habitats elsewhere. Fur seals and macaroni penguins are being found farther south and along the northern WAP, while gentoo penguins are also thought to be doing increasingly well in those areas (Ducklow et al., 2007; Trivelpiece et al., 2011). The capacity to move and establish colonies farther south as conditions warm and ice retreats suggests that, although there are discontinuities of land and ocean, the ecosystems from the Bellingshausen Sea to South Georgia might be usefully considered as a general continuum (Fig. 7). These two regional systems are parts within a broader ecosystem

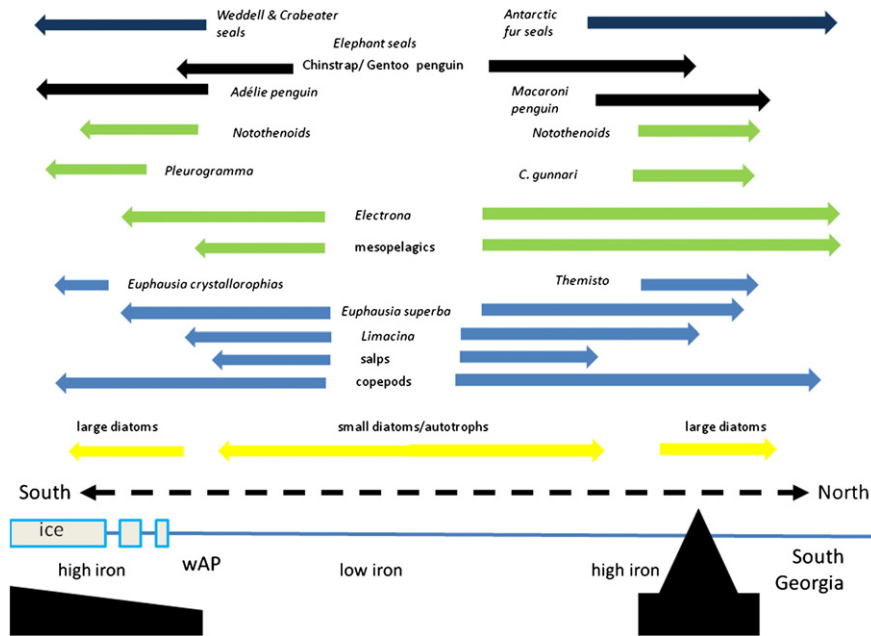


Fig. 7. Illustration of spatial distribution of key species/groups in food webs that extend from the western Antarctic Peninsula, across the Scotia Sea to South Georgia. Food web variability is dependent on position across the region and the combination of species/groups present. Black shapes indicate main continental shelf and island areas.

that forms a connected continuum, with further links into the southeast Pacific and South Atlantic sectors of the Southern Ocean, and indeed of the circumpolar Southern Ocean (Murphy et al., 2008; Murphy et al., in press). However, these regional ecosystems are not homogeneous, but are patchy at all scales, with areas of reduced iron and production, growth of smaller autotrophs and mixotrophic species, and complex zooplankton and nektonic community dynamics. The species assemblage present at any time is dependent on the local habitat conditions, seasonality and degree of connectivity, all of which contribute to limit the set of optimal life history characteristics of the species that are maintained in each area. Understanding the evolved adaptations and constraints on life-history strategies of Southern Ocean species will be an important step in developing understanding of the wider controls on ecosystem structure and function (Forcada et al., 2008; Suryan et al., 2009; Verity and Smetacek, 1996).

Consideration of overall food web structure (Section 3) and variability (Section 4), suggests that sea ice, biogeochemical conditions favourable to growth of large diatoms and connectivity are three main factors that determine the structure and function of ecosystems across the wAP–South Georgia continuum. Other environmental and biological factors modify and interact with these to determine the exact species present and the food web structure. The presence of ice, with the associated temperature regime and winter conditions, and the consequent seasonality, puts major physical and biological constraints on the survival of species, limiting the number of successful life history strategies in a given area. The biogeochemical conditions (probably associated with iron in both areas) provide the basis for production that sustains the food web and the large diatoms that are crucial for krill, and the food web interactions can in turn affect the fate of production and the biogeochemistry. The transport via the prevailing current systems and the highly mobile predators generates the connectivity that links the systems together, but are also crucial processes in determining the broader area ecosystem responses to variation and change. As a result the species assemblages and hence regional system structure can vary and change as conditions also vary and change. This view suggests that the current changes being observed in plankton, nekton and predators will continue as the regional warming continues and, over time, ecosystem structure and species composition in areas along the Peninsula could increasingly resemble the structure that currently exists at South Georgia. Macaroni penguins and fur seals that dominate

at South Georgia already occur in colonies in the northern regions of the Antarctic Peninsula, and their distributions may extend further south in the future. However, not all species are likely to be replaced by those at South Georgia. The importance of salps around the northern Peninsula but not at South Georgia highlights that there are also important life-history constraints and habitat differences that determine the exact species in each food web in these regions.

5. On the comparison of ecosystems—scale, structure, function and variability

The observation of the similarity of ecosystem operation between the wAP and South Georgia comes from both food web and wider ecosystem views. However, aspects of physical and chemical habitats as well as the biological characteristics combine to allow a particular form of an ecosystem to occur. Given this, what can be said about the effect of interaction of different physical, chemical and biological processes at different scales on wAP and South Georgia ecosystem structure and function? The major differences in these ecosystems relate to the driving influences of sea ice, biogeochemical conditions and connectivity and reflect the latitude and seasonality and the pervasive influence of the ACC. Within this broad framework, fundamentally similar physical and chemical processes operate over similar scales in the two regional ecosystems.

Both ecosystems are centred in seasonal shelf areas, which are strongly influenced by the ACC. In both regions, upwelling contributes to regional primary production dominated by diatoms presumably through introduction of micronutrients (iron). Within the regions there is also marked mesoscale and sub-mesoscale variability (10–100 km) arising from the shelf circulation that produce areas of low and high biological production (e.g. between east and west South Georgia and along the wAP shelf). Finer scale (<10 km) flow interactions with bottom topography generate hot-spots of enhanced production that become a focus of ecological interactions. Even finer scale (<km) biological–physical interactions generate patchiness in the plankton distributions that are a major feature of both systems, highlighted by the swarm basis for the distribution of krill. Cross shelf-exchanges of nutrients and biological material are key aspects of the ecosystem operation not only in maintaining primary production, but also in the advection of secondary production (particularly krill and mesopelagic

fish). Larger species are more mobile and forage over broad areas connecting different habitats and ecosystems. In both areas predators forage into oceanic regions and towards frontal zones well away from the shelf regions. Some of the large predators also disperse during the winter away from the main regional ecosystems centres. The wAP and South Georgia systems experience considerable within and between year variability, which favours species with life histories that can adapt to the variability and results in different species dominating in different years. Thus, descriptions of food web interactions need to account for this range of possible configurations.

Both ecosystems are part of a wider connected continuum, and with this wider perspective, the form of the ecosystem in terms of structure and function can be considered as a solution to the physical/chemical process operation at different scales. The exact species vary in relation to the major controls of sea ice, biogeochemical conditions and connectivity, but the basic form is maintained and therefore the overall ecosystem structure and function is similar at the wAP and South Georgia. This view of the similarity of the structure of the two ecosystems provides a focus for further analyses and modelling that encompass both systems in a single model structure that considers both food web and wider ecosystem processes.

The above comparative analysis allows three key conclusions that can inform the development of Southern Ocean ecosystem comparisons. The first is that differences in the food webs of the wAP and South Georgia ecosystems relate mainly to evolved adaptations and the resultant life-history constraints imposed on different species, rather than being the result of change in overall ecosystem structure and function. These constraints are the result of changes in the major controlling factors across the region: sea ice, biogeochemical conditions and connectivity.

The second conclusion is that within both regional ecosystems there is a high degree of spatial variability in ecosystem operation. The food webs of both regions are dominated by the classical diatom-krill-higher predator pathway, but this pathway is not isolated from the rest of the ecosystem. Important alternative pathways of energy flow involving copepods, carnivorous zooplankton (especially amphipods), pteropods or salps, generate complex pathways of energy flow through fish and cephalopods. These alternative pathways are part of the same ecosystems and represent changes in the magnitude of energy flows between particular species and in biogeochemical process interactions. These pathways also become more, or less, important in response to interannual variations and longer term change. These pathways are, therefore, key elements of the whole ecosystem, the structure of which is an emergent property of all of the weak and strong variable interactions and feedbacks, which are determined by processes at a range of space and time scales. This whole ecosystem perspective is important when comparing structure and function between ecosystems, because overall properties will be crucial in determining responses to change rather than just selected aspects of the ecosystem (Allen and Fulton, 2010; Hofmann, 2010).

The third conclusion is that the concept of a generic Southern Ocean food web model, based on functional/guild groups that can be applied to different ecosystems, is appropriate for the wAP and South Georgia regions and the wider connected-continuum in which they occur. Through the development of a generic model, driven by major habitat changes (sea ice, biogeochemical conditions and connectivity), it should be possible to capture much of the structural variation of food webs and element cycles in the different regions of the Southern Ocean. Such a model, in combination with models of life-history constraints, provides the prospect of ecosystem models that have as an emergent property the major group composition and structural interactions within the ecosystem. The concept of indicators of ecosystem structure that we have suggested can be extended beyond the regions associated with the wAP and South Georgia. For example, in the Ross Sea, where ice dominates for the much of the year, *E. crystallorophias* and *P. antarcticum* are key species in the ecosystem (Smith et al., 2007). In contrast, in the northern regions close to the Polar Front fish species, and particularly myctophids, are the

main prey items of many of the larger seabird and seal predators (Casper et al., 2010; Makhado et al., 2008). When Antarctic krill are present in areas further south, energy flow pathways are short and hence more efficient in transferring energy to higher trophic levels than when copepods dominate (Murphy et al., 2007b). In more southern regions, where ice dominates for much of the year, food chains can be short (Smith et al., 2007), but the lower overall primary production and the consequently low abundance of secondary producers (ice krill and silverfish) cannot maintain very large numbers of higher predators.

These conclusions can also inform the development of projections of ecosystem responses to change. Major changes in Antarctic systems associated with changing global atmospheric concentrations of CO₂ are expected to occur during the coming decades. These include further warming, sea ice reductions, changing patterns of ocean circulation and upwelling. These physical changes will also be associated with biogeochemically and ecologically important chemical changes, including changing carbonate chemistry and associated reductions in pH, which are expected to be manifest in the cold Southern Ocean more rapidly than elsewhere (McNeil and Matear, 2008). The major differences in ecosystem structure that are known to occur in the transition between an ice covered and a fully open water system (Fig. 8) emphasise the shift from high production, large diatom, krill dominated ecosystems of the high iron/cold ice influenced areas to low iron/warm smaller autotrophs and more complex interactions in the non ice system. However, ice to open water (Fig. 8) represents only one of the major factors in the interactive system. Developing a generic view of how the different factors and in particular, sea ice, biogeochemical conditions and connectivity, interactively impact both individual species and overall ecosystem structure will be crucial in developing projections of future states of Southern Ocean ecosystems.

Developing our understanding of the processes generating scale-based structure in these ecosystems will allow determination of the processes that generate differences between systems and between trophic levels within systems (Allen and Fulton, 2010; Hofmann, 2010). Different species interact on different scales and therefore integrate food web structures at different scales. The spatial and temporal variability at different scales generates complex ecosystem interactions that are difficult to characterise and quantify with reasonable certainty, and for which mean conditions will not provide a complete perspective. Forecasting responses to change will, therefore, need to account for the variability in ecosystem structure and for gaps in data and understanding so that bounds on uncertainty can be applied (e.g. Friedrichs et al., 2006). For example, general properties of ecosystems such as production, overall predator demand and general functional form may be forecast with some degree of skill, but prediction of exact species abundance in particular groups or the exact ecosystem structure may not be feasible. Therefore, comparative analyses of food web structures need to include the modifications to overall ecosystem structure and function that arise from the heterogeneity and variability, generating spatially and temporally distributed networks. This suggests that a network-based approach to modelling ecosystem structure that includes appropriate processes and trophic levels as nested structures operating over different scales with uncertainties, could be valuable in generating integrated analyses.

6. Summary

The obvious major differences between the wAP and South Georgia ecosystems are linked to latitude and hence seasonality and associated winter sea ice cover. These provide a major physical basis for differences in the species that can succeed in the two areas, but they do not generate major structural differences between the ecosystems. Both ecosystems are areas of intense production likely associated with natural iron fertilisation. The influence of deeper waters and particularly UCDW is more pervasive than has previously been realised and

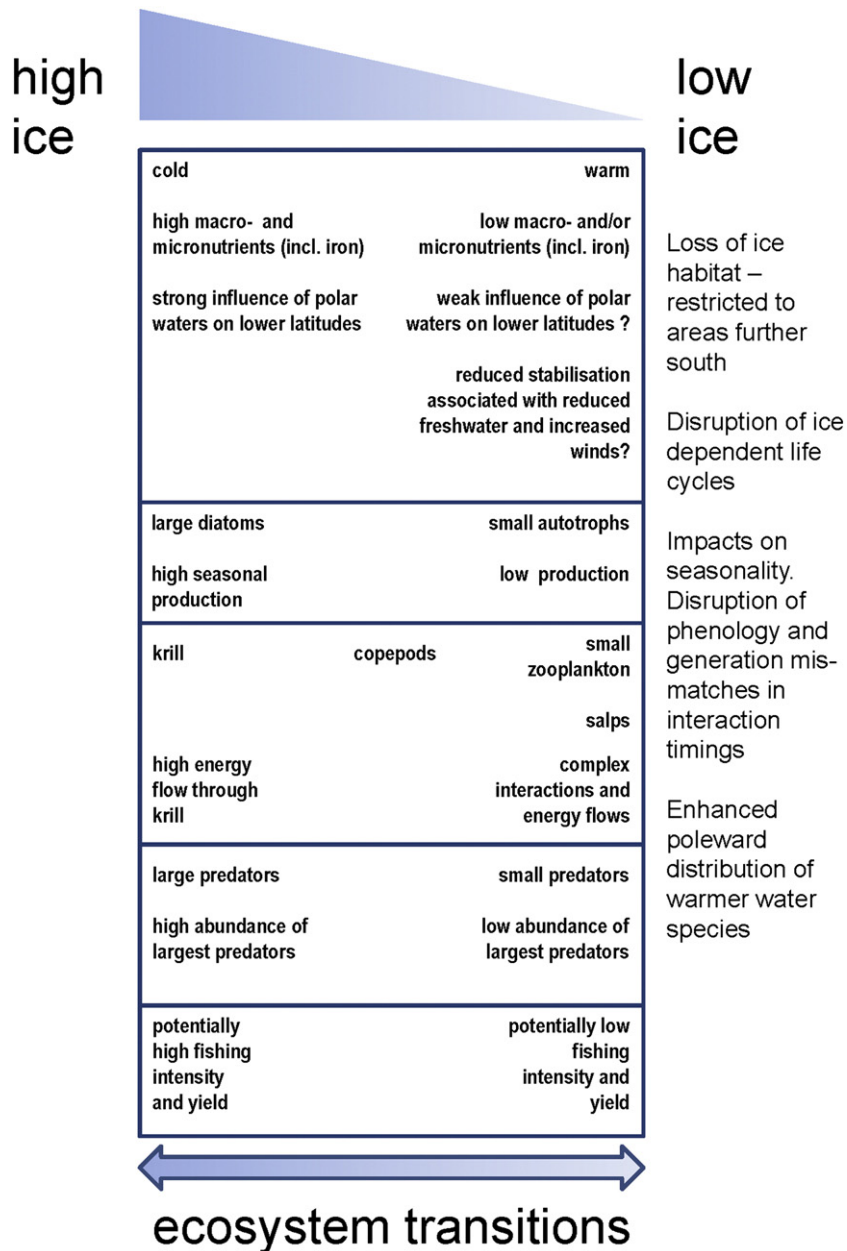


Fig. 8. Schematic summary of the known major differences in characteristics of ecosystems in ice and open water areas of the Southern Ocean. The potential ecological impacts of a transition from high ice to low ice ecosystems are indicated. Some of the ecosystem characteristics vary independently, so interactive effects involving factors other than ice, such as changing iron concentration and ocean circulation, also affect the ecosystem structure.

intense oceanic–shelf interactions, which enhance the surface and neritic influence of deeper waters, are crucial for determining Southern Ocean ecosystem structure. The biogeochemical conditions are critical, and particularly the iron inputs into the upper waters by upwelling, vertical mixing/exchange, sediment interactions and melt water, which provides the basis for large blooms under appropriate conditions, which in turn drive the production and population dynamics of large macro zooplankton (krill), which are then consumed by the large bodied air-breathing predators. This classical Southern Ocean food chain is just one of the pathways that exist within much more complex and variable food webs.

The WAP and South Georgia systems are similar in structure and function but are also distinct. The two systems are part of a continuum from the more intensely seasonal ice covered areas farther south to the more open water regions in the north. The connectivity that underpins this continuum is maintained by both the advective flows and biological

transfers and flows of material and movements of organisms. The similarity and connectivity of the two ecosystems allows development of a generic approach to modelling these ecosystems, which combines life history constraints with overall food web structure at a range of scales. Such a model provides a valuable basis for further comparative analyses of Southern Ocean ecosystems, for generating models for projections of the future state of these ecosystems under different scenarios of change, and for comparisons with other marine ecosystems. Accounting for variability and uncertainty in developing analyses of ecosystem structure and function will be critical in developing useful analyses and models.

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