

Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web

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The Scotia Sea ecosystem is a major component of the circumpolar Southern Ocean system, where productivity and predator demand for prey are high. The eastward-flowing Antarctic Circumpolar Current (ACC) and waters from the Weddell–Scotia Confluence dominate the physics of the Scotia Sea, leading to a strong advective flow, intense eddy activity and mixing. There is also strong seasonality, manifest by the changing irradiance and sea ice cover, which leads to shorter summers in the south. Summer phytoplankton blooms, which at times can cover an area of more than 0.5 million km², probably result from the mixing of micronutrients into surface waters through the flow of the ACC over the Scotia Arc. This production is consumed by a range of species including Antarctic krill, which are the major prey item of large seabird and marine mammal populations. The flow of the ACC is steered north by the Scotia Arc, pushing polar water to lower latitudes, carrying with it krill during spring and summer, which subsidize food webs around South Georgia and the northern Scotia Arc. There is also marked interannual variability in winter sea ice distribution and sea surface temperatures that is linked to southern hemisphere-scale climate processes such as the El Niño–Southern Oscillation. This variation affects regional primary and secondary production and influences biogeochemical cycles. It also affects krill population dynamics and dispersal, which in turn impacts higher trophic level predator foraging, breeding performance and population dynamics. The ecosystem has also been highly perturbed as a result of harvesting over the last two centuries and significant ecological changes have also occurred in response to rapid regional warming during the second half of the twentieth century. This combination of historical perturbation and rapid regional change highlights that the Scotia Sea ecosystem is likely to show significant change over the next two to three decades, which may result in major ecological shifts.

Keywords: Scotia Sea; ecosystem; advection; Antarctic krill; heterogeneity; interannual variability

1. INTRODUCTION

Analysis of the operation of ocean ecosystems requires an understanding of how the structure of the ecosystem is determined by interactions between physical, chemical and biological processes. Such analysis needs to consider the interactions across a wide range of spatial (approx. 10 m–10 000 km) and temporal (minutes to centuries) scales, and across all trophic levels (primary producers to top predators; [Murphy *et al.* 1988](#); [Angel 1994](#); [Werner *et al.* 2004](#)). There are, however, few areas of the global ocean where there is sufficient knowledge to achieve such an integrated analysis ([deYoung *et al.* 2004](#)). Circulation patterns of the major ocean gyres, such as the North Atlantic and

Pacific Oceans, involve movement of water masses through very different climatic regimes which favour distinctly different groups of organisms ([Longhurst 1998](#)). Generating comprehensive views of the operation of oceanic ecosystems is complicated as a result of such heterogeneity in species distribution and ecosystem structure ([Murphy *et al.* 1988](#); [Levin 1990](#); [Longhurst 1998](#)).

In contrast to other areas of the global ocean, the Southern Ocean has two major characteristics that make the development of large-scale integrated analyses a realistic possibility. The first is a circumpolar current with relatively constant environmental conditions along the streamlines, and the second is a simple food-web structure ([Everson 1977](#); [Hempel 1985a](#)). A circumpolar eastward circulation that occurs within a restricted latitudinal belt dominates the flow (between approx. 50° and 65° S; [Orsi *et al.* 1995](#)). This current system, the Antarctic Circumpolar Current

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(ACC), transports around 130–140 Sv (million $\text{m}^3 \text{s}^{-1}$) eastward at Drake Passage (Cunningham *et al.* 2003), but shows significant atmospherically forced variability on time-scales from days to years (Hughes *et al.* 2003; Meredith *et al.* 2004b). This flow around the continent results in relatively consistent surface summer temperatures south of the Polar Front (PF) of approximately 4–5°C in the north and 0 to –1°C in areas just south of the Southern Boundary (SB) of the ACC (Sievers & Nowlin 1984; Whitworth & Nowlin 1987; Moore *et al.* 1997, 1999; Brandon *et al.* 2004).

Across the circumpolar current, there are therefore relatively consistent environmental conditions within which the ecosystem operates. Within this flow regime, the other major factor that determines the structure of the ecosystem is the marked seasonality of polar environments (Clarke 1988). Changes in solar irradiance and associated fluctuations in sea ice cover result in strong seasonal variation in upper ocean temperature and light levels (Okada & Yamanouchi 2002). This seasonal variation dominates the operation of Southern Ocean ecosystems in a number of ways. Temperature changes in surface waters as a result of fluctuations in irradiance have direct impacts on the physiological processes of many marine species, and temperature tolerances are a major determinant of the geographical boundaries of species distributions (Mackintosh 1936, 1960; Hempel 1985b; Longhurst 1998; Peck *et al.* 2004; Peck 2005). However, for most species, it is marked seasonal fluctuations in the availability of food that drives key biological processes (Laws 1983; Clarke 1985a; Peck *et al.* 2005). During summer, there is a short period of only two to three months (or less in the highest latitudes) when conditions are favourable for primary production. The resulting phytoplankton blooms are often dominated by species of large diatoms (Laws 1983; Clarke 1985a; Hempel 1985a,b; Clarke & Leakey 1996; Smetacek *et al.* 2004). As with the rest of the world ocean, microbial systems are a key feature of Southern Ocean ecosystems and can dominate the processes of production in many regions and through the winter months (Smetacek *et al.* 2004). The seasonality propagates through the food web, so consumers must be able to make full use of the short summer periods to breed and survive during the low production periods of winter (Laws 1983; Clarke 1985a). Such physical and biological conditions favour the two extremes of smaller species that can develop quickly in response to favourable conditions and large-bodied predators that are often highly mobile. The smaller microbial and meso-planktonic species opportunistically use available resources and have strategies in place to survive periods of low production. The large, mid- and higher trophic level species, such as penguins and seals, have relatively long lifespans (often greater than 10 years) and are highly mobile (foraging over hundreds to thousands of kilometres), and many move away from the area during the periods of low production (Clarke 1985b; Croxall 1992). The extreme seasonality in production also means that there is little capacity to build-up long food chains involving many steps to the highest trophic levels (Everson 1977; Clarke 1985b). Southern Ocean ecosystems therefore have an apparently simple

structure, dominated by short food chains that also make them tractable for analysing large-scale system operation (Everson 1977; Laws 1983; Hempel 1985a; Clarke 1985b). The dominant food-web pathway from diatoms–zooplankton–predators also provides an important focus for studying end-to-end ecosystem processes linking primary production and highest trophic level predators.

Although there is a consistency in the structure and composition of the Southern Ocean ecosystem, it is not operationally homogeneous (Hempel 1985a). South of the ACC exist large subpolar gyres in the Ross and Weddell Seas, and there are often complex current systems at the shelf break and on the shelf of Antarctica, such as the Antarctic coastal current (Hempel 1985a; Orsi *et al.* 1995). The flow of the ACC is strongly topographically constrained in many places around its circulation, with the greatest restriction occurring at Drake Passage. Here, the ACC flows through a ‘choke point’ between South America and the Antarctic Peninsula and emerges into the Scotia Sea. The Drake Passage and Scotia Sea region is therefore an important area in the connection of the global ocean (Cunningham *et al.* 2003). To the east of Drake Passage, the ACC encounters one of the biggest topographic barriers in the Southern Ocean, the Scotia Arc, which forms the northern, southern and eastern boundaries of the Scotia Sea (figure 1). The southern section of the Scotia Sea also receives input of waters from the shelf of the Antarctic Peninsula and the Weddell Sea (Whitworth *et al.* 1994).

The combination of strong flow and mixing in an area of rugged bathymetry makes the Scotia Sea one of the most physically energetic regions of the Southern Ocean. As a result, the Scotia Sea ecosystem has different operational characteristics to those in other regions of the ACC. Over much of the oceanic Southern Ocean, the concentration of chlorophyll is low even though macronutrient concentrations are high (termed high-nutrient, low-chlorophyll or HNLC regions). In contrast, extensive blooms of large diatoms occur across the Scotia Sea during spring. The result is a high-nutrient, high-chlorophyll region, although at times nutrient concentrations can become sufficiently depleted to become locally limiting (Holm-Hansen *et al.* 2004b; Korb *et al.* 2005). The enhanced production supports some of the largest and most diverse concentrations of seabirds and marine mammals anywhere on Earth (Everson 1977, 1984). Antarctic krill (*Euphausia superba* Dana; hereafter krill) are the major link between primary production and vertebrate predators in the Southern Ocean food webs. This is particularly marked in the Scotia Sea, where about half of the overall krill population occurs (Atkinson *et al.* 2004). Historically, the Scotia Sea is also where the majority of harvesting of seals, whales and fishes in the Southern Ocean occurred (Everson 1977, 2001; Laws 1984). Although the krill fishery has declined during the last decade, a significant fishery still exists, operating almost exclusively in the Scotia Sea and the Antarctic Peninsula regions (Everson 1977, 2001; Everson *et al.* 2000a).

The Scotia Sea ecosystem is therefore a key part of the Southern Ocean ecosystem and understanding its operation has become more urgent as evidence has

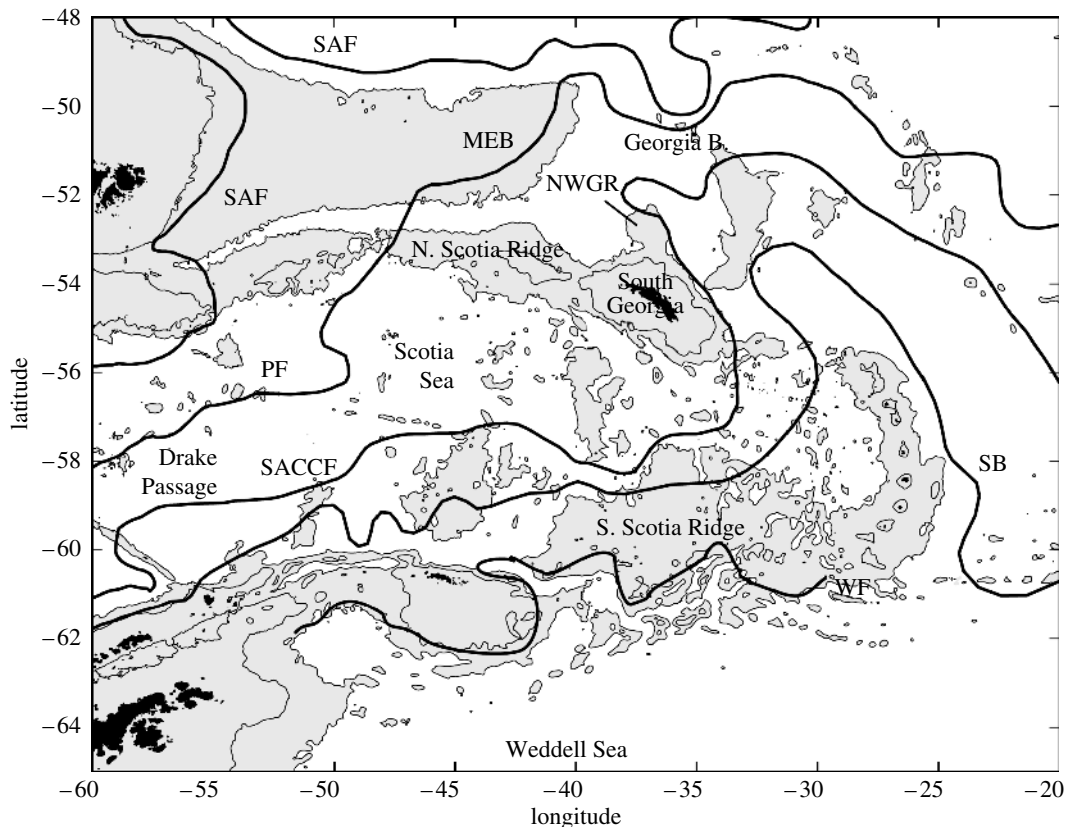


Figure 1. The Scotia Sea and surrounding areas showing the general position of the major frontal systems in relation to bottom topography. SAF, sub-Antarctic Front; PF, Polar Front; SACCF, Southern Antarctic Circumpolar Front; SB, Southern ACC Boundary; WF, Weddell Front; MEB, Maurice Ewing Bank; NWGR, North West Georgia Rise (see text for references; depth contours shown for 1000 and 2000 m).

emerged that rapid environmental change is occurring in the western Scotia Sea and west Antarctic Peninsula (WAP) region (Vaughan *et al.* 2003; Meredith & King 2005). Recent analyses have also suggested that krill abundance has reduced by over 50% in the Scotia Sea during the last 30 years and there are indications that some of the krill-dependent predator populations are in decline (Reid & Croxall 2001; Atkinson *et al.* 2004). Suggestions that these ecological changes are linked to the climate-related variations have been provided support by evidence that changes in the Scotia Sea ecosystem are linked to Southern Ocean and southern hemisphere scale variations (Forcada *et al.* 2005; Murphy *et al.* submitted; Trathan *et al.* in press).

Predicting how the Scotia Sea ecosystem will respond to the climate-related changes presents a major challenge. Traditional views of food webs have tended to consider the network of biological interactions in isolation from the environment. Such an approach is not realistic because it does not take account of process interactions of different organisms at different scales, or the ontogenetic and seasonal changes in trophic interactions. Including all such complexity is impossible, so a pragmatic scale-based approach that focuses on key species within the system is more realistic (Murphy *et al.* 1988; deYoung *et al.* 2004). Such an approach is tractable for the Scotia Sea ecosystem owing to the importance of krill. To analyse the operation of the Scotia Sea ecosystem, therefore, requires detailed analyses of the krill population dynamics as well as knowledge of the trophic

interactions (figure 2). An analysis of the Scotia Sea ecosystem also requires consideration of the wider links to surrounding regions owing to the open nature of the ecosystem. Here, we concentrate on the Southern Ocean region of the Scotia Sea south of the PF, but consider the wider links of the ecosystem to surrounding areas of the Antarctic Peninsula, the northern Weddell Sea and the regions east and north of the Scotia Arc. Earlier Southern Ocean whole system reviews were produced by Everson (1977) and Miller & Hampton (1989). Priddle *et al.* (1998a) also considered carbon flows through the food web to highest trophic levels. Lower trophic level dynamics in Southern Ocean ecosystems have been reviewed recently by Smetacek *et al.* (2004) and Smith & Lancelot (2004). Specific reviews of aspects of the dynamics of krill populations have been discussed by Siegel (2005), of predators by Ainley *et al.* (2005) and Trathan *et al.* in press and the response of the wider ecosystem to change by Smetacek & Nicol (2005). In this paper, we review the operation of the ecosystem in the Scotia Sea and surrounding areas, focusing on the dominant krill centred food web (figure 2 illustrates the structure of this paper in relation to the food web).

2. OCEANOGRAPHY AND SEA ICE

Flow through Drake Passage commenced when an initial shallow gateway opened around 50 Myr ago, but deep throughflow started only around 34–30 Myr ago, immediately after the onset of spreading of the west Scotia Ridge (Livermore *et al.* in press). The western

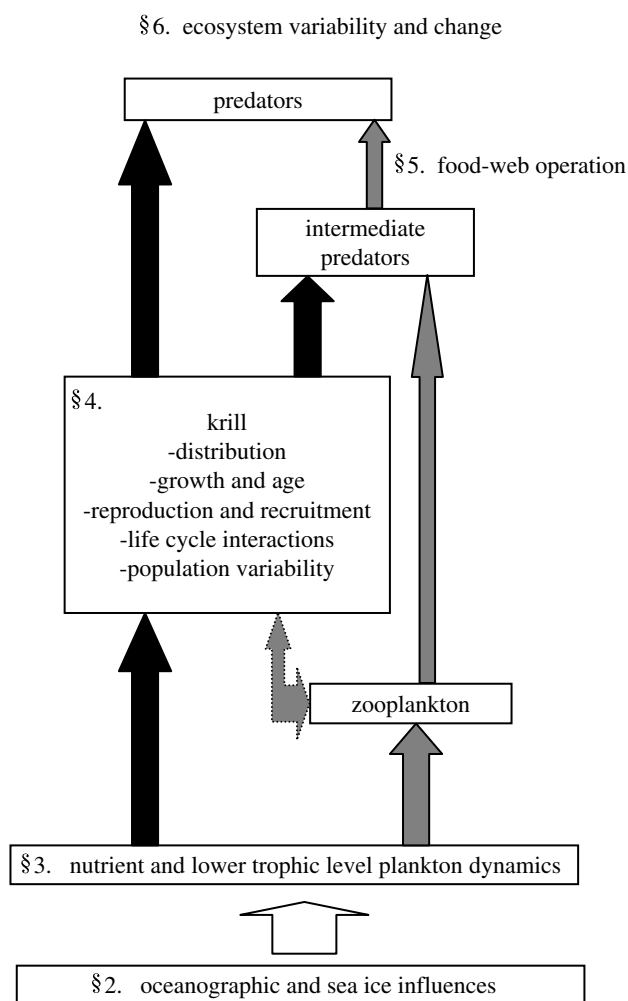


Figure 2. Schematic of the Scotia Sea food web as considered in this review. Developing the approach of *deYoung et al.* (2004), the major focus is on krill, their life history and interactions, with reduced detail on other groups and trophic levels. Numbered headings refer to the major sections and organization of this paper.

side of the Scotia Sea is bounded by Drake Passage, while the other sides are formed by the Scotia Arc (figure 1). It extends over approximately 750 km north–south and approximately 2000 km to the east from Drake Passage, encompassing an area of approximately 1.5×10^6 km². The waters of the ACC enter the Scotia Sea through Drake Passage, deflect northwards and then cross the Scotia Arc that rises from depths of around 3000–5000 m as a chain of islands from the Antarctic Peninsula to the tip of South America. Along this arc are a series of island groups and seamounts. Much of the central abyssal plain of the Scotia Sea is 3000–4000 m deep with a gradual shallowing from west to east. Across the region, there are submarine structures and seamounts such as the Shackleton Fracture Zone, the Pirie, Bruce, Discovery and Herdman Banks and the North West Georgia Rise (NWGR) to the north of South Georgia.

(a) *Upper-ocean circulation and characteristics in the Scotia Sea*

The ACC is split into several fronts, which are at their narrowest meridional constriction within Drake Passage and which then diverge as the ACC spreads

into the Scotia Sea (*Orsi et al.* 1995; *Brandon et al.* 2004). Following *Orsi et al.* (1995), the fronts are termed (from north to south) the sub-Antarctic Front (SAF), the PF, the Southern ACC Front (SACCF) and the SB (figure 1). The SAF and PF veer northward upon entering the Scotia Sea and cross the complex bathymetry of the North Scotia Ridge (*Zenk* 1981). North of the North Scotia Ridge, the PF separates into two branches over the Falkland Plateau, with one branch topographically tied to the southern flank of the Maurice Ewing Bank and the other branch continuing northward over the plateau. The transport is approximately equally split between these branches, with the classical signature of the PF being found in the former (*Trathan et al.* 1997, 2000; *Arhan et al.* 2002; *Naveira Garabato et al.* 2002). The SACCF has a more eastward course, but loops around South Georgia anticyclonically from the south before retroflecting eastward (*Thorpe et al.* 2002; *Meredith et al.* 2003c). The SB also maintains a mostly eastward course through the Scotia Sea, but has a northward topographically induced loop in the vicinity of the South Sandwich Island arc (figure 1).

South of the ACC in the Scotia Sea lies the waters of the Weddell–Scotia Confluence (WSC), formed from waters spilling off the shelf at the tip of the Antarctic Peninsula that are injected into oceanic waters flowing eastward (*Whitworth et al.* 1994). It should be noted that the flux of shelf waters into the WSC is not the only route for such waters to enter the deep ocean from close to the tip of the Peninsula: *Meredith et al.* (2003a) showed that downslope convection occurs to the north of Elephant Island, with waters dense enough to contribute to the deep waters of the Scotia Sea, including Antarctic Bottom Water.

This downslope convection is strongly seasonal and concentrated in the austral winter. It is speculated that the flux of shelf waters into the WSC will be similarly time dependent. The WSC is bounded to the north by the SB and to the south by the Weddell Front (WF) (figure 1). It has been suggested recently that the WF originates from a branching of the Antarctic Slope Front close to the northwestern limit of the Weddell Sea (*Heywood et al.* 2004). Historical observations have often depicted the WSC to be characterized by abundant eddies and meanders, but it is now thought that at least some of this complexity is caused by the fronts being strongly steered by the convoluted bathymetry of the South Scotia Ridge.

Close to South Georgia, the flow regime is dominated by the SACCF. The extent of the SACCF retroflexion has been revised since *Orsi et al.* (1995) first represented it schematically reaching to 43° W; *Thorpe et al.* (2002) compiled historical hydrographic measurements and found that the retroflexion only extended as far as 36° W. Subsequently, *Meredith et al.* (2003c) showed that the SACCF is steered away from the shelf of South Georgia by the NWGR, which rises 2000 m above the seabed. It has also been shown that the course of the SACCF in this region is traceable using sea surface temperature (SST) imagery from satellite-borne radiometers (*Meredith et al.* 2003c). Such imagery revealed a complex eddy field north of South Georgia, and this probably accounts for the

debate on the westward extent of the SACCF retroflexion. Waters on the shelf of South Georgia can differ in potential temperature and salinity characteristics from those off-shelf, due to retention processes coupled with freshwater inputs from land and warming through insolation (Brandon *et al.* 1999, 2000; Meredith *et al.* 2005). The transition between the shelf and off-shelf waters can be abrupt or gradual, with implications for baroclinic advection around the shelf break (Brandon *et al.* 1999, 2000; Meredith *et al.* 2005).

Although the circulation in the Scotia Sea broadly follows the pathways of the ACC fronts, it is important to recognize the role of bathymetry. Not only does this steer the ACC fronts themselves, but it also controls the circulation in the zones between the fronts. For example, Meredith *et al.* (2003a) presented trajectories of passive drogued drifters in the Georgia Basin and demonstrated a general anticyclonic circulation around the island shelf from the south. However, some of the drifters did not move to the east in the vicinity of the SACCF retroflexion, but continued to circulate anticyclonically around the periphery of the Georgia Basin before joining the PF to the west and north of the basin. Clearly, the advective pathways can be more strongly influenced by direct topographic steering than by the ACC frontal pathways in such circumstances. Also of note is the presence of a variable, but often intense, warm-core anticyclonic circulation above the NWGR, with velocities as large as 50 cm s^{-1} . Meredith *et al.* (2003a) presented dimensional analysis which showed that the features of this circulation were consistent with those of a stratified Taylor column and demonstrated the strong impact that it can have on primary production and biogeochemistry.

(b) Sea ice dynamics

During winter in the Scotia Sea, sea ice extends out over the southern areas of the ACC (figures 1 and 3). The ice is generated mainly in the Weddell Sea, drifting northwards driven by ocean currents and surface winds (Murphy *et al.* 1995; Harms *et al.* 2001; Parkinson 2002, 2004). The minimum ice extent in summer occurs across the Weddell Sea between February and March, with sea ice advancing across the southern Scotia Arc around May (figure 3). Although the maximum northward extent of sea ice across the Scotia Sea during winter usually occurs during September or October, it can occur anytime between July and November. The timing of both advance and retreat shows significant inter-annual variation (figure 3) and is related to changes in air temperatures and wind speed and direction reflecting regional atmospheric dynamics (Allison 1997). The mean position of the maximum winter sea ice extent generally occurs in the area of the mean summer position of the SB of the ACC (figures 1 and 3). However, in extreme years, it can occur much further north in the region of the SACCF or indeed much further south around the position of the WF. It should be noted however that there is little information on the positions of the fronts when sea ice covers the region. The average concentration of sea ice across the area during winter is between 50 and 15%, and at this time it will be approximately 0.3–0.5 m thick (Allison 1997) and drifts north and eastward at speeds ranging from 1

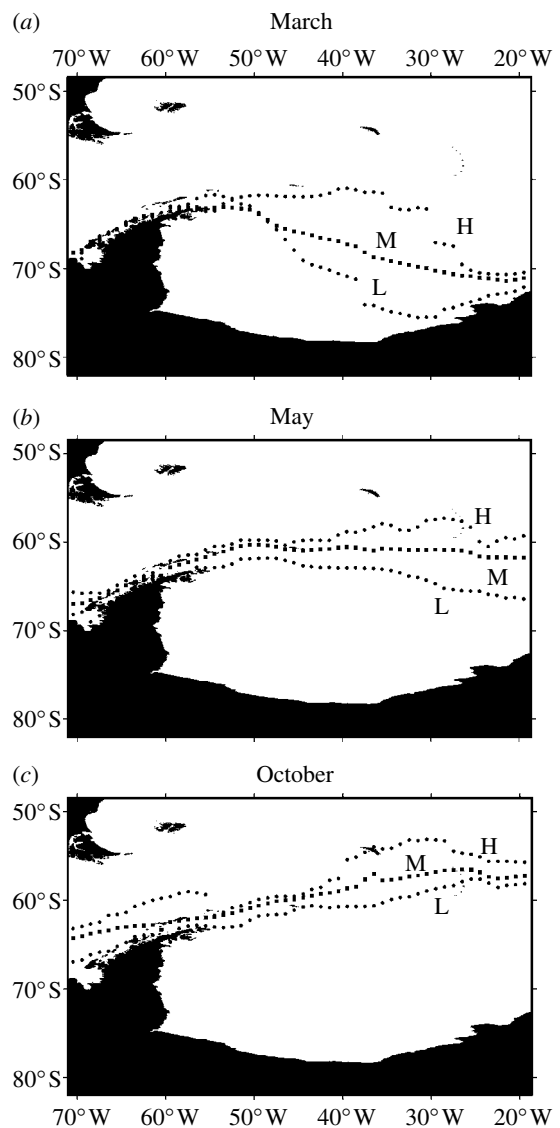


Figure 3. Seasonal and interannual changes in extent of sea ice across the Scotia Sea and Weddell Sea. Mean positions of the 15% ice edge are shown for three months in the year along with the position of the ice edge in a year of extreme north and south extent. (a) Mean sea ice extent in March (M) and extent in March 1986 (L) and 2004 (H). (b) Mean sea ice extent in October (M) and extent in 1989 (L) and 1987 (H). (c) Mean sea ice extent in May (M) and extent in May 1999 (L) and 1992 (H). Sea ice data from 1979 to 2005 from DMSP–SSM/I passive microwave data produced by NOAA/NCEP.

to 15 cm s^{-1} . These characteristics result in an eastward drifting marginal ice zone (MIZ) comprising variable sized ice floes separated by leads and more extensive areas of open water (Allison 1997). In spring, there is an asymmetric southward retreat of sea ice, with sea ice in the east retreating earlier than that in the west (October and November). The MIZ in the west is also more limited in north–south extent by the Antarctic Peninsula than areas in the eastern Scotia Sea. Some areas in the western Scotia Sea remain ice covered until late in the spring (November and December). In areas where the sea ice retreats slowly, the upper water column can be stabilized by melt water input, generating shallow surface mixed layers (10–30 m; Bianchi *et al.* 1992; Lancelot *et al.* 1993; Figueiras *et al.* 1994; Parkinson 1994; Park *et al.* 1999). However, the retreat of sea ice

across the Scotia Sea during spring is often rapid and probably mainly wind driven (Sullivan *et al.* 1988; Comiso *et al.* 1993; Parkinson 1994).

(c) *Physical variability and long-term change*

With the development of satellite-derived data series of over 25 years duration, we can now consider variability and change across the Scotia Sea system. On inter-annual time-scales, connections between remotely sensed SST close to South Georgia and the El Niño–Southern Oscillation (ENSO) have been demonstrated (Trathan & Murphy 2002). These studies show a 2–3 year lag between ENSO variability in the equatorial Pacific and response around South Georgia, implying a significant component of oceanic advection in the signal propagation (Trathan & Murphy 2002; Murphy *et al.* submitted). More recently, Meredith *et al.* (2005) examined 5 years of hydrographic data from close to South Georgia and noted particularly cold waters in early 1998. These were shown to be linked directly to the very strong 1997/1998 El Niño event (Meredith *et al.* 2005). Murphy *et al.* (submitted) have further shown that the propagating oceanic signal dominates the interannual variation from the Central and west Pacific sector through to the Scotia Sea, but further support the view that short-term (less than six months) direct impacts from atmospheric effects did occur during the major El Niño event. In contrast, variation in the WAP region appears to be dominated by the direct ENSO-related atmospheric effects rather than the signal that is propagated in the ACC (Fraser & Hofmann 2003; Quetin & Ross 2003; Meredith *et al.* 2004a).

The interannual changes in SST associated with these large-scale processes are also closely correlated with sea ice variation across the region (Fedulov *et al.* 1996). Warm periods coincide with winters of reduced ice extent and duration, while in the coldest years the ice extends further north generating longer winters in the southern Scotia Sea (Trathan *et al.* 2006; Murphy *et al.* submitted). These changes are linked with the passage of warm and cold anomalies in ocean SST through the region from the South Pacific sector of the Southern Ocean (White & Peterson 1996; Murphy *et al.* submitted). Further work is needed to fully determine the climatic forcings of interannual and longer period variability in the Scotia Sea.

There is also marked decadal and longer term change occurring in physical environments around the Scotia Sea. There is clear evidence that the region around the Antarctic Peninsula is one of the most rapidly warming on the planet, with increases in air and SSTs, and decreases in winter sea ice cover (Smith & Stammerjohn 2001; Stammerjohn *et al.* 2003; Vaughan *et al.* 2003; Meredith & King 2005). The longest record of sea ice dynamics for anywhere in the Southern Ocean also comes from the southern Scotia Sea (Murphy *et al.* 1995). Records of the duration of fast ice in the South Orkney Islands have shown a significant decline in the mean duration of fast ice between the first and the second half of the twentieth century (Murphy *et al.* 1995; de la Mare 1997). There are also some indications that upper water column temperatures around South Georgia increased between the first and the second half of the century and that this

was related to changes in sea ice extent (Whitehouse *et al.* 1996a). This warming was followed by a period of glacier retreat at South Georgia (Gordon & Timmis 1992). Taken together there is evidence that there was an abrupt and rapid change in the physical environment of the Scotia Sea in the middle of the last century. There are also clear indications that further changes have been occurring over the last three decades. Meredith & King (2005) recently showed a warming of the upper ocean on the west of the Peninsula over the second half of the last century. There has also been a reduction in the mean duration of winter sea ice around the WAP and across the Scotia Sea during the last 25 years (Parkinson 2002). It is likely that this more recent regional change reflects a downstream influence of the regional warming that is occurring around the Antarctic Peninsula in areas where sea ice formation occurs.

3. NUTRIENT AND PLANKTON DYNAMICS

In contrast to much of the Southern Ocean, which is characterized by HNLC conditions, the Scotia Sea is an area of both high nutrient concentration and high productivity (Holm-Hansen *et al.* 2004a,b). However, the production regimes are highly variable and reflect the large-scale variation in physical and chemical conditions across the region. Pre-bloom surface macro-nutrient concentrations (nitrate, silicate and phosphate) are generally high (surface values of nitrate (NO_3) > 30 mol m⁻³; silicic acid ($\text{Si}(\text{OH})_4$) > 60 mmol m⁻³; phosphate (PO_4) > 2 mmol m⁻³; Whitehouse *et al.* 1996a, 2000; Atkinson *et al.* 2001), with a gradient from south to north of reducing nutrient concentration. Across the central Scotia Sea, summer surface chlorophyll *a* concentrations are moderate, between 0.4 and 1.0 mg m⁻³, with some areas of higher concentration (> 1.0 mg m⁻³; figure 4; Holm-Hansen *et al.* 2004a,b; Korb *et al.* 2005). Most areas of enhanced mean surface chlorophyll *a* concentrations (> 1.0 mg m⁻³) occur around and downstream of islands, across shelf areas, within frontal jets and in areas recently covered by sea ice (figures 3 and 4; Mitchell *et al.* 1991; Bianchi *et al.* 1992; Treguer & Jacques 1992; Comiso *et al.* 1993; Perez *et al.* 1994; de Baar *et al.* 1995; Clarke & Leakey 1996; Korb & Whitehouse 2004; Korb *et al.* 2004, 2005; Holm-Hansen *et al.* 2004a,b). Productivity is also variable and Korb *et al.* (2005) estimated primary production rates of approximately 0.31 g C m⁻² d⁻¹ in central oceanic regions compared to rates between 0.72 and 2.04 g C m⁻² d⁻¹ across the shelf areas, around the Scotia Arc and in the region of the retreating ice edge in the southern Scotia Sea. These rates are similar to the empirically derived estimates of Holm-Hansen *et al.* (2004b) of between 0.60 and 0.99 g C m⁻² d⁻¹ for the entire Scotia Sea during January and February. In the northern areas of enhanced production, where the summer season can extend over about five months, annual productivity may be very high and has been estimated to be approximately 30–40 g C m⁻² around South Georgia (Whitehouse *et al.* 1996a). Further west, near to Drake Passage, where waters of the ACC have recently emerged from the South Pacific sector, concentrations

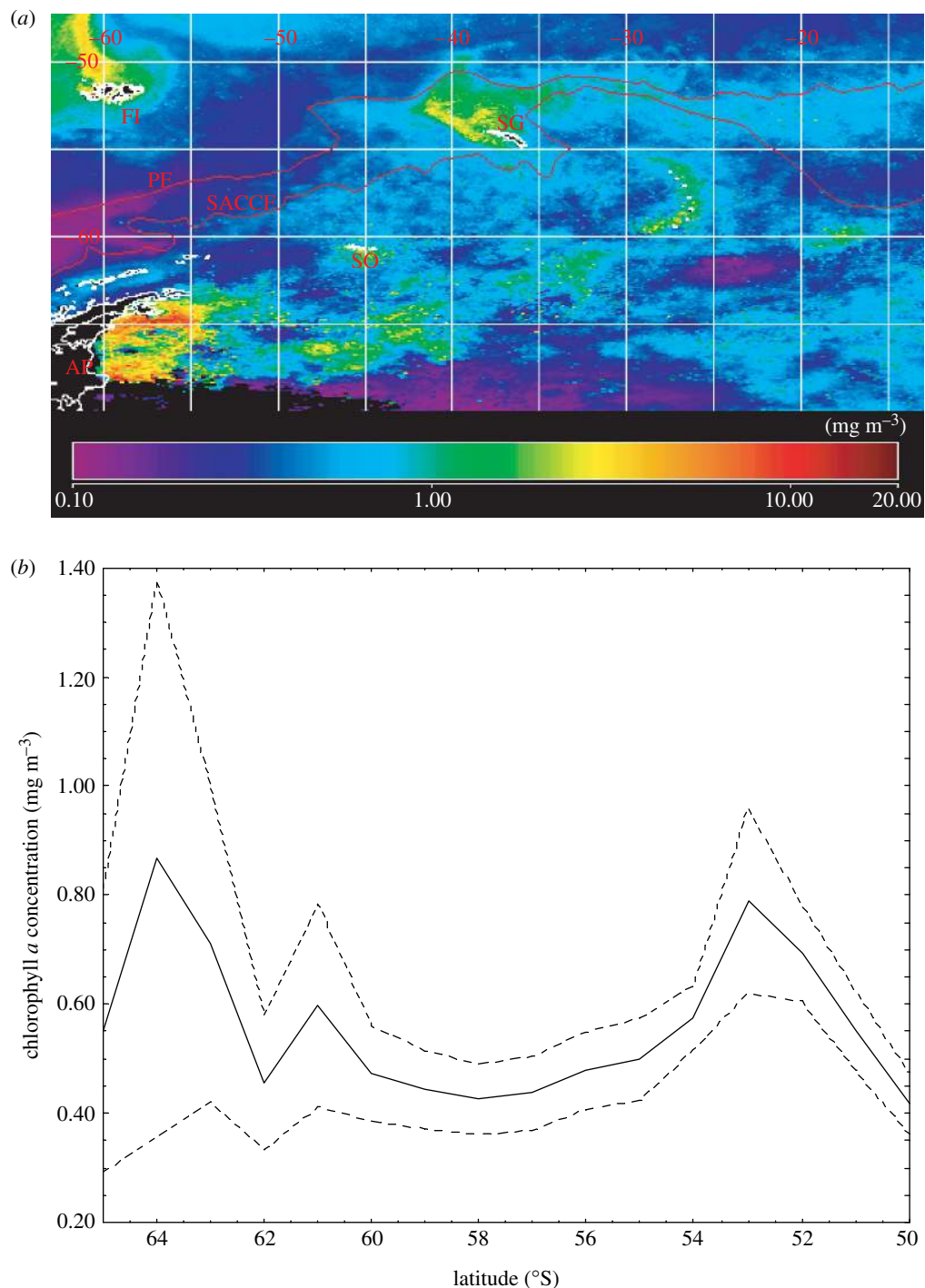


Figure 4. (a) Mean concentration of chlorophyll *a* (mg m⁻³) derived from the summer (December–February) SeaWiFS data for the period from 1998 to 2005. The position of the PF and SACCF are also shown. (b) Mean and 95% confidence intervals of the December–February concentration of chlorophyll *a* (mg m⁻³) calculated in 1° latitude bands across the Scotia Sea from 55 to 30° W. Data are from the SeaWiFS Project and the NASA Giovanni Ocean Color Project.

of chlorophyll *a* are much lower (approx. 0.1 mg m⁻³; figure 4; Holm-Hansen *et al.* 2004a). These waters are similar to much of the Pacific and Indian Ocean sectors of the Southern Ocean with high concentrations of nutrients (silicate, phosphate and nitrate, i.e. HNLC; Korb *et al.* 2005).

The development of blooms in the southern Scotia Sea is affected by the timing and pattern of sea ice retreat during spring (Sullivan *et al.* 1988; Comiso *et al.* 1993; Korb *et al.* 2004, 2005). In the areas of the northern Scotia Arc, blooms are more regular and predictable. Over much of the summer, blooms

develop in the shelf areas around South Georgia (figure 4; Atkinson *et al.* 2001; Korb & Whitehouse 2004; Korb *et al.* 2004, 2005). These blooms extend to the north in the retroflective area of the SACCF. A large spatially extended bloom is often established downstream of the island (Korb & Whitehouse 2004). This bloom can extend downstream from the island more than 2750 km to the east and at times enhanced chlorophyll *a* concentrations are observed beyond the prime meridian (Korb *et al.* 2004). These megablocks, which can occur over an area of between approximately 0.07 and 0.5 × 10⁶ km² and can last for over five

months, are potentially globally important in export of carbon from the surface to the seabed (Schlitzer 2002). In areas where intense phytoplankton blooms form, such as north of South Georgia, macronutrients can be reduced to or near to limiting concentrations (approx. $10 \text{ mmol m}^{-3} \text{ NO}_3$, approx. $1 \text{ mmol m}^{-3} \text{ Si(OH)}_4$ and approx. $0.3 \text{ mmol m}^{-3} \text{ PO}_4$; Whitehouse *et al.* 1996a,b; Korb & Whitehouse 2004; Korb *et al.* 2005).

These views of large-scale chlorophyll *a* distribution across the Scotia Sea are based on satellite data (Comiso *et al.* 1993; Korb *et al.* 2004; Holm-Hansen *et al.* 2004a,b), which are known to underestimate high chlorophyll *a* concentrations in large blooms ($>5 \text{ mg m}^{-3}$; Korb *et al.* 2004). A further problem is that satellites cannot detect sub-surface chlorophyll maxima which are known to occur in the Scotia Sea (Korb *et al.* 2004; Holm-Hansen *et al.* 2005; Whitehouse *et al.* submitted). Such sub-surface production is likely to be regionally and temporally important, but presently remains an uncertain aspect of the operation of the food web.

It is likely that the waters of the Scotia Sea are naturally iron enriched and this promotes high productivity of large diatoms throughout the region. There is now good evidence, from artificial iron enrichment experiments, that a lack of iron in surface waters is a major factor limiting phytoplankton growth (de Baar *et al.* 1995; Boyd 2002c). The natural iron enrichment in the Scotia Sea is likely to come from a range of sources, including shelf water inputs from the Antarctic Peninsula region associated with the WSC, upwelling and interaction of the ACC with the shelf sediments of the Scotia Arc introducing dissolved iron into surface waters (de Baar *et al.* 1995; Korb *et al.* 2004, 2005; Holm-Hansen *et al.* 2004b). This enhanced concentration of iron, which is a crucial micronutrient in the growth process of large diatoms, is considered to be the major factor that allows phytoplankton to bloom across the Scotia Sea (Hart 1942; Korb & Whitehouse 2004; Korb *et al.* 2004, 2005; Holm-Hansen *et al.* 2004a). A recent study of phytoplankton growth across the northern Scotia Arc region gave further support to this view. Holeton *et al.* (2005) obtained direct iron measurements which showed enhanced iron concentrations around South Georgia that arose from a benthic source. A range of indirect evidence gives further support for the view that iron concentrations are high and a major factor generating the large phytoplankton blooms across the Scotia Sea; these include the dominance of large diatoms, large depletions of NO_3 concentration, observed nutrient deficit ratios and high photosynthetic efficiency (Korb & Whitehouse 2004; Korb *et al.* 2004, 2005; Holm-Hansen *et al.* 2004a; Holeton *et al.* 2005; BAS 2006, unpublished data).

In the Scotia Sea, we therefore see a region of transition with waters of low iron concentration in the west that emerge from Drake Passage (Korb *et al.* 2004; Holm-Hansen *et al.* 2004a) and then mix with waters of high iron concentration that have recently flowed around and across the Antarctic Peninsula shelf and southern Scotia Arc. The iron levels of these waters are likely to be further enhanced as the currents flow over the northern Scotia Arc, allowing blooms to develop

around the shelf areas. Over time, these blooms develop downstream away from the shelf areas; therefore, they are a function of both the flow and the iron enhancement (Korb *et al.* 2005). The strong gradient north-south in irradiance and ice cover and duration will affect the timing and development of the planktonic system.

Although iron is important in phytoplankton growth, a range of studies have shown that realized population growth rates are the result of multiple controls (Lancelot *et al.* 2000; Holm-Hansen *et al.* 2004b; Korb *et al.* 2005). The interactive effects of light, nutrients (micro and macro), temperature and grazing will all be important in determining the concentrations of phytoplankton (Smith & Lancelot 2004; Holm-Hansen *et al.* 2004b). Silicic acid levels decrease further north across the Scotia Sea and, as previously noted, are more likely to become limiting late in the season in northern areas where summer lasts longer. The long-lasting blooms observed in these areas are also therefore likely to show shifts in species composition from diatoms to non-siliceous species. It is also likely that the dynamics and fate of iron from the Scotia Sea will also be important in determining the food-web structure downstream. Indeed, studies of the food-web operation along the region north of the Scotia Arc may reveal the time-scales for iron recycling and its fate in the food web (Smetacek *et al.* 2004). Of the grazing controls on production, the impacts of meso- and macro-zooplankton on phytoplankton production can often be low, particularly during summer when blooms have already developed (Atkinson *et al.* 2001). However, krill and copepods also exploit microbial and heterotrophic production, so grazing impacts on new production will be determined by food-web structure and interactions (Atkinson *et al.* 1996; Atkinson & Snyder 1997; Pakhomov *et al.* 1997a,b; Giesenhagen *et al.* 1999; Lancelot *et al.* 2000).

Like much of the global ocean, microbial populations are undoubtedly an important component of Scotia Sea nutrient and production systems, but relatively little is known about connections between the microbial components and higher trophic levels and much of the relevant work comes from adjacent areas of the Weddell Sea and Antarctic Peninsula and elsewhere in the Southern Ocean (Lancelot *et al.* 1991; Mordy *et al.* 1995; Wright & van den Enden 2000; Walsh *et al.* 2001). During summer, the dominant pathway for energy flow in the Scotia Sea will be through new production by the larger diatoms, but ammonium is likely to be an important nitrogen source over the Scotia Sea (Priddle *et al.* 2003). Outside of the summer period, the recycling pathways are much more important. The seasonal changes in relative importance of new versus recycled production however is unknown (Cota *et al.* 1992; Mordy *et al.* 1995). In winter, the microbial communities associated with the sea ice are important in the food web (Becquevort *et al.* 1992; Garrison & Close 1993; Mordy *et al.* 1995). Bacteria have an important role in transferring energy through the consumption of dissolved organic matter and are in turn consumed by protozoa which are fed upon by smaller zooplankton (Bak *et al.* 1992; Kuparinen & Bjornsen 1992; Grossmann 1994; Tupas *et al.* 1994;

Mordy *et al.* 1995; Moran *et al.* 2001). These microbial systems introduce important temporal delays into the food web, making key compounds, organic substrates and energy available at times during the season when little new production is available. This will be particularly important in maintaining energy flows in the food web during autumn and winter in the Scotia Sea, where extensive meso- and macro-zooplankton populations require food (Walsh *et al.* 2001; Smith & Lancelot 2004). The recycling pathways are likely to be the major components of coastal food webs around the Scotia Sea. In more pelagic waters during winter, there will be significant sea ice-associated microbial production in the drifting ice habitat of the MIZ of the southern Scotia Sea that will maintain higher trophic level production (Garrison & Close 1993; Ackley & Sullivan 1994; Murphy *et al.* 1998a). Temporal delays in the food web introduced by recycling will also result in a spatial disconnect between regions of production and consumption as the material is advected in the ocean (Garrison & Buck 1991; Becquevort *et al.* 1992; Garrison & Close 1993; Grossmann 1994; Grossmann & Dieckmann 1994).

The high productivity of the Scotia Sea ecosystem makes it an important region for examining the effects of natural iron fertilization on the development of planktonic systems. The impacts on the wider operation and structure of the ecosystem provide a valuable natural contrast with much of the rest of the oceanic Southern Ocean.

4. KRILL IN THE SCOTIA SEA FOOD WEB

(a) *Krill distribution in the Scotia Sea*

The physical environment sets the context within which any species must operate. For Antarctic krill, the biggest influence may have been the opening of Drake Passage and the development of the ACC to generate the relatively isolated circumpolar Southern Ocean (Patarnello *et al.* 1996; Jarman *et al.* 2000; Zane & Patarnello 2000; Livermore *et al.* 2005, *in press*). This has generated an oceanic environment in the Scotia Sea which is the most advective in the world (Cunningham *et al.* 2003). The life cycle of Antarctic krill, which appears to have originated at about the time the ACC became established (Patarnello *et al.* 1996; Jarman *et al.* 2000), will have developed in this dispersive system, which had characteristics similar to the general pattern of oceanic circulation and seasonality that is observed today (Spiridonov 1996).

Understanding the factors controlling the large-scale distribution of krill has become a major focus of research during the last 5–10 years. These studies have been advanced by the development of complementary large-scale modelling, field studies and data syntheses (Murphy *et al.* 1998b; Murphy & Reid 2001; Atkinson *et al.* 2004; Hofmann & Murphy 2004; Murphy *et al.* 2004a,b; Siegel 2005; Fach & Klinck 2006; Fach *et al.* 2006; Nicol *et al.* 2000; Nicol 2006). The large-scale distribution of krill is a function of production (recruitment and growth), mortality, retention and dispersal. The resultant circumpolar distribution is highly asymmetric (Marr 1962; Mackintosh 1973), with at least half of the entire krill population occurring

in the southwest Atlantic sector of the Southern Ocean (Atkinson *et al.* 2004). The distribution of krill in the Scotia Sea also extends further north than in any other region of the Southern Ocean, with high densities occurring north of 53° S (figure 5a). Elsewhere in the Southern Ocean, krill tend to occur mainly near the continent (between approx. 75 and 65° S). Marr (1962) suggested that the large-scale distribution was dominated by the surface currents generally, and that the ACC, WSC and outflows from the Weddell Sea were the major determinants of the horizontal distribution in the Scotia Sea. A recent modelling study has further indicated that the mixing of surface waters in the Scotia Sea is a key determinant of the large-scale distribution of krill and brings together plankton from around the Southern Ocean (Thorpe *et al.* submitted).

Within the Scotia Sea, high and relatively predictable concentrations of krill occur in waters less than 1000 m deep (Miller & Hampton 1989; Murphy *et al.* 1997). Detailed analyses of fishery and acoustic survey data from around South Georgia in the northern Scotia Sea have shown that maximal values occur in the shelf-break region (Murphy *et al.* 1997; Trathan *et al.* 1998a; Trathan *et al.* 2003). However, significant amounts of krill also occur in oceanic waters across the Scotia Sea (Siegel 2005). The *Discovery Investigations* (1925–1951) found large concentrations of krill in off-shelf regions (Marr 1962). The most recent comprehensive acoustic survey to date also showed a large biomass of krill in the central southern Scotia Sea during summer 2000 (figure 5a; Hewitt *et al.* 2004). Further support to this view is given in an analysis of historical net data, which shows large amounts of krill in off-shelf areas during summer (Atkinson *et al.* 2004). These central Scotia Sea regions were also areas of commercial whaling and are strongly influenced by oceanic frontal systems (Hofmann *et al.* 1998; Tynan 1998; Hofmann & Murphy 2004; Murphy *et al.* 2004a,b). During autumn and winter, a combination of dispersal and mortality leads to a decline in the abundance of krill across northern oceanic regions. Higher abundances are maintained across shelf and off-shelf areas further south through retention, recruitment and seasonal dispersal (see discussions in Marr 1962).

(b) *Krill growth and age in the Scotia Sea*

Growth of krill is highly variable, and a function of animal size and maturity, food availability and temperature (Ross *et al.* 2000; Fach *et al.* 2002; Reid *et al.* 2002; Daly 2004; Atkinson *et al.* 2006; Candy & Kawaguchi 2006; Kawaguchi *et al.* 2006). The Scotia Sea during summer appears to be a generally favourable habitat for krill growth and development. Atkinson *et al.* (2006) and Tarling *et al.* (2006) recently measured post-larval growth rates based on samples from across the entire Scotia Sea in mid-summer. They derived empirical relationships between krill growth rates, size and development state with local temperature and chlorophyll *a* concentration. Here, we use these relationships to estimate growth rates across the whole Scotia Sea during summer (figure 5b). Highest growth rates, predicted for the 2000 season, are across the southeast Scotia Arc, down to the eastern Weddell Sea, across the southern Scotia Sea and in the east

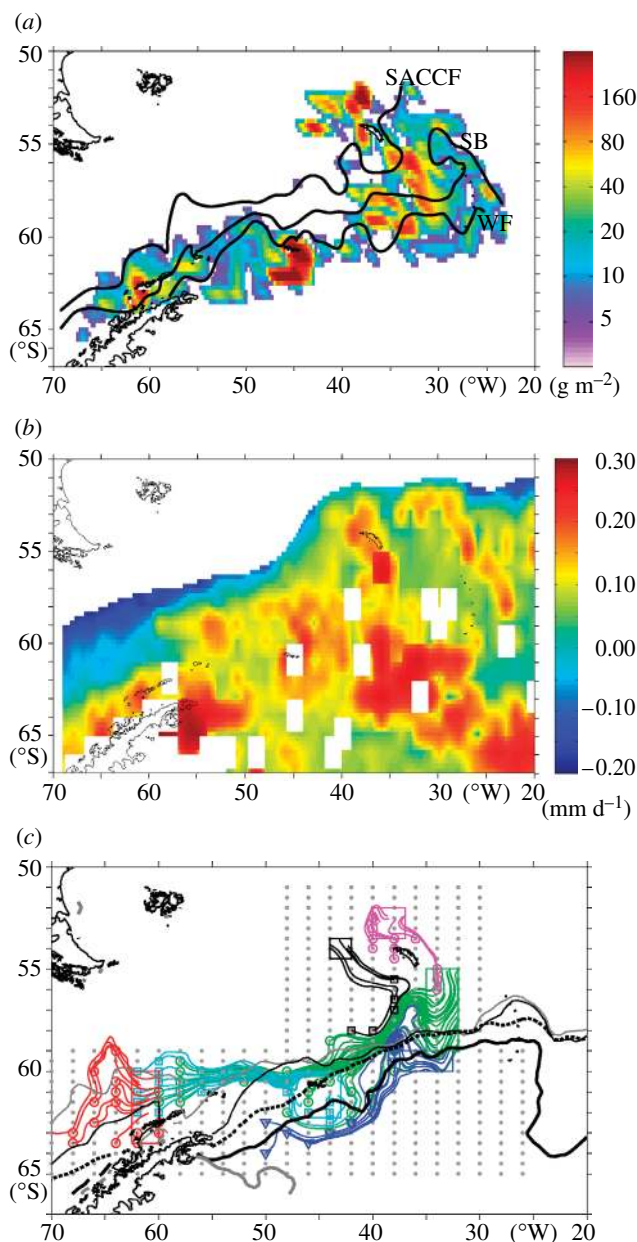


Figure 5. (a) Krill biomass across the Scotia Sea based on CCAMLR Synoptic Survey during January and February 2000. The positions of the major fronts as determined during the survey are also shown (Murphy *et al.* 2004a). (b) Estimated growth rates (mm d^{-1}) of krill across the Scotia Sea during January and February 2000. Values based on empirical relationships derived by Atkinson *et al.* (2006; Calculations use Model 3, Table 5, for all krill sampled) and Tarling *et al.* (2006) using satellite-derived mean SST field and chlorophyll *a* (SeaWiFS) concentrations for January and February and assuming a mean length of 40 mm. Blank cells are where no data were available or where the SST was less than -1 or greater than 5°C . (c) Lagrangian particle tracks passing through major biomass regions (a) based on tracks from previous three months using output from the OCCAM circulation model (Murphy *et al.* 2004a). (a,c) Reproduced from Murphy *et al.* 2004a with permission from Elsevier.

Antarctic Peninsula region. Predicted growth rates are consistently above zero over most of the area, except in the more northern and warmer regions nearer the PF. Calculations of carbon flux indicate that rates of growth of krill of approximately 3–6% of animal body mass per day would have occurred in the high growth regions

where the animals were 20–30 mm long. This was mainly in the central and the eastern Scotia Sea. Further west and north 40–60 mm animals would have shown lower rates of 0.5 to 2%. The relationships indicate that higher temperature regions, to the north of the Scotia Sea, are poor areas for krill growth and especially for larger animals. However, it should be noted that significant growth rates can be maintained by larger animals in relatively warmer more northern regions if the chlorophyll *a* concentrations are sufficiently high. Areas to the north and northeast of South Georgia show consistent blooms during summer in areas where temperatures can be more than 3°C , and these could be areas where positive growth rates could be maintained.

As there are currently no reliable methods to age individual krill, the variability in growth rate makes it difficult to examine the development of individual year classes (Miller & Hampton 1989). There is a fragmented picture of year class development at South Georgia compared to that from the WAP. Analyses of predator diet data have suggested that growth rates across the Scotia Sea over extended summer periods are sufficient for animals to reach a size of between 35 and 40 mm in 1 year having overwintered only once (1+ age class; Reid *et al.* 2002). This view of rapid growth in the north compared to southern regions of the Scotia Sea is also supported by analyses of year class fluctuation across the Scotia Sea (Brierley *et al.* 1999; Reid 2002; Reid *et al.* 2002). However, analyses of length frequency distributions from net samples have suggested that the same year classes dominate around South Georgia and the Elephant Island and WAP regions (Quetin & Ross 2003; Siegel *et al.* 2003). In this interpretation, which is based on a view that the size of age classes is the same across the Scotia Sea, the animals would have overwintered twice (2+ age class) before they appear in the population at South Georgia (Siegel 2005).

This lack of agreement arises from the absence of a definitive ageing method, the capacity of krill to shrink in conditions of low food availability, and the short duration of the available time-series of recruitment strength data in which the mean size of cohorts are highly variable and consecutive year classes tend to occur together. Uncertainty in identifying exactly which year the animals were spawned affects our ability to interpret interannual changes in abundance. The predator and net series also relate to different parts of the krill population (Reid *et al.* 1996b; Murphy *et al.* 1998b; Watkins *et al.* 1999; Murphy & Reid 2001). The net sampling has occurred around the whole island on and off the shelf, which combined with the small mesh size of the nets can sample size groups in the year before they dominate the predator diet (Watkins *et al.* 1999). Most of the sampling of the length frequency of krill in the diet of predators is based on animals that forage in the west of the region, often mainly over the shelf (Reid *et al.* 1996b). Comparison of net and predator data has shown that the sampling needs to be local and contemporaneous to be comparable (Reid *et al.* 1996b). Thus, discrepancies can arise through mismatches in the scale of sampling, thereby generating

difficulties in interpretation of population processes across the region.

(c) *Krill reproduction and recruitment in the Scotia Sea*

Spawning followed by successful recruitment probably occurs to some extent right across the southern Scotia Arc and the Scotia Sea between about November and February (Marr 1962; Hofmann & Husrevoglu 2003; Tarling *et al.* in press). Depending on food availability, krill can probably spawn several times in a year (Ross & Quetin 1986; Siegel 2005). Mature krill have been found throughout the Scotia Sea in both on- and off-shelf areas, and a recent study off South Georgia has shown that krill complete spawning and produce viable eggs in the region (Tarling *et al.* 2006b). Around the Antarctic Peninsula region mature krill appear to migrate to the shelf-break regions to spawn (Siegel 2005). Eggs sink rapidly to depths of greater than 500 m, so spawning in shallow shelf areas is unlikely to be viable as it would result in physical damage when the eggs come into contact with the substrate and predation from the benthos (Marr 1962; Miller & Hampton 1989; Hofmann & Husrevoglu 2003). Larvae develop as they return to the surface where they begin to feed, in a process that takes about two to three weeks to complete. Model simulations of egg development and larval hatching have shown that there are restricted regions of the shelf-slope, where the sinking eggs come into contact with upwelling, relatively warm Upper Circumpolar Deep Water, where egg development and larval hatching and ascent can be successfully completed (Hofmann & Husrevoglu 2003). In the Scotia Sea sector, these areas are restricted to the WAP and a few places around the east Antarctic Peninsula. Although shelf-slope regions around the Scotia Arc do not favour egg development and larval retention, the model simulations indicate that oceanic waters right across the Scotia Sea are suitable for spawning and larval development (Hofmann & Husrevoglu 2003; Tarling *et al.* 2006b). This suggestion is supported by large-scale surveys of larval distribution that have shown that the Scotia Sea is an area where high densities of larval krill occur during the summer months (Marr 1962; Brinton 1985; Ward *et al.* 2004). These larvae are generally considered to have come mainly from the major spawning regions further south along the southern Scotia Arc and around the Antarctic Peninsula (Marr 1962; Fach *et al.* 2006). Through a combination of further spawning and drift, the distribution of larvae then develops across the southern regions of the Scotia Sea and north towards South Georgia in the east. However, recent findings have focused on the fate of larvae spawned and released over oceanic waters across the Scotia Sea (Murphy *et al.* 2004a; Tarling *et al.* 2006). Analyses of spawning status have shown that krill at South Georgia probably complete their maturation process and spawn over slope and off-shelf areas, where eggs and larvae will be rapidly transported away from the island (Murphy *et al.* 2004a; Tarling *et al.* 2006b).

Winter survival and growth of the larval krill produced during summer require access to alternative food sources. Sea ice is considered to be a key overwintering habitat for krill generally (Quetin &

Ross 1991; Spiridonov 1995). Ice algae, which develop on the undersurface and within sea ice, are an important source of energy that help sustain krill during the periods of low water column productivity (Daly & Macaulay 1991; Quetin & Ross 1991, 2001; Melnikov & Spiridonov 1996; Quetin *et al.* 1996; Ross & Quetin 1999; Fraser & Hofmann 2003; Meyer *et al.* 2002; Pakhomov *et al.* 2004). The sea ice also acts as a potential refuge from predators, reducing mortality rates (Daly & Macaulay 1991). A relationship has been found between sea ice conditions during winter and krill recruitment around the Antarctic Peninsula (Siegel & Loeb 1995; Loeb *et al.* 1997; Quetin & Ross 2003; Siegel *et al.* 2003; Siegel 2005). It also appears that consecutive years of extensive sea ice are required to generate large year classes around the WAP (Loeb *et al.* 1997; Fraser & Hofmann 2003; Quetin & Ross 2003). However, the extension of this concept that greater winter sea ice extents lead to better food and refuge conditions as a linear function in every region is likely to be too simplistic to explain changes across the whole region. Sea ice conditions vary across the region, with an area in the west around the Peninsula where the MIZ is small compared to areas further east, where low-concentration sea ice cover can extend over much of the Scotia Sea. Sea ice conditions around the WAP are dependent on factors to the west, with much of the ice brought into the region on ocean currents and driven by wind. Areas around the tip of the Antarctic Peninsula into the Scotia Sea will be affected by conditions in the Weddell Sea as well as further west. It is therefore surprising that a simple relationship of krill recruitment with ice extent appears to dominate, given the complexity of the processes generating the distribution of sea ice. Recent studies have suggested that the relationships between krill recruitment and sea ice are more complex. In the Palmer and Marguerite Bay region, years of enhanced recruitment were found to be associated with winters of average ice conditions (Quetin & Ross 2001, 2003). Algal concentration and abundance in sea ice will not depend on sea ice extent, but will be a function of the degree of open water, the floe size and thickness, and may also be dependent on when the ice formed and under what conditions. The complexity of the habitat for krill has been highlighted by Daly (2004), who showed that larval grazing on sea ice algae in southern areas of the WAP is low in winter, but becomes more important in spring as the ice melts and the light levels increase. The successful survival of krill through various critical stages of the life cycle will therefore be a complex function of interaction between sea ice habitats in winter and open ocean regions in summer (Quetin & Ross 2001, 2003; Siegel 2005). Final recruitment success, when animals are at least 1 year old, will reflect conditions over at least the previous 2 years, which would have affected maturation and spawning of mature animals and larval survival in summer and winter.

An apparent consistency of year class recruitment at the Antarctic Peninsula and across the Scotia Sea has been noted and a number of explanations have been proposed (Priddle *et al.* 1988; Murphy *et al.* 1998b; Brierley *et al.* 1999; Quetin & Ross 2001, 2003; Siegel

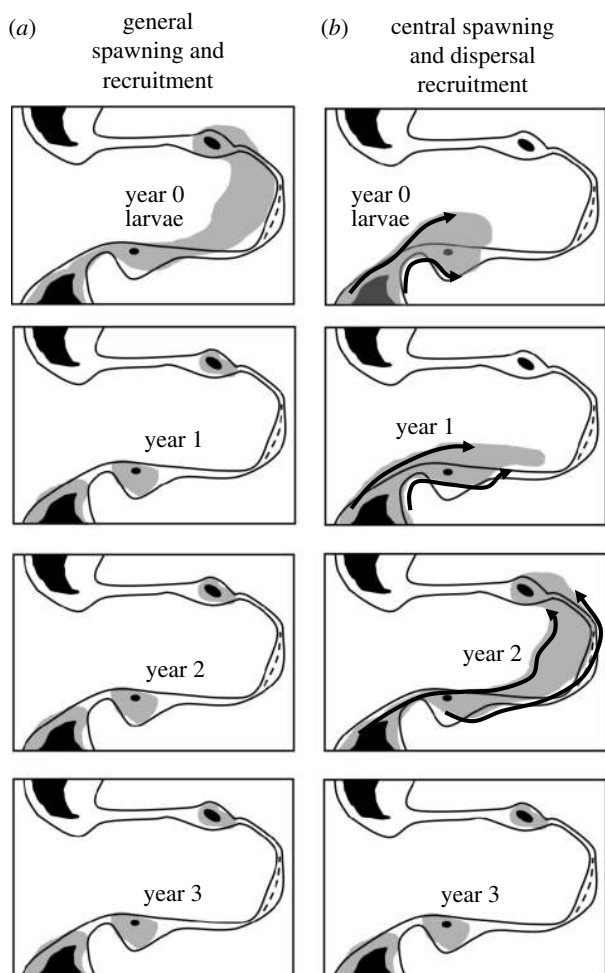


Figure 6. Schematic of two alternative spawning and recruitment scenarios that can both generate concordance in recruitment across the region. (a) Spawning occurs generally across the region and then recruitment is maintained in all shelf regions. (b) Spawning and successful survival during the first year occur mainly in central and southern areas of the Scotia Sea, and the year class is dispersed through interactions with the ocean and sea ice over the next 1–2 years. Intermediate scenarios between these extremes can also be envisaged.

et al. 2003; Atkinson *et al.* 2004). Spawning may be occurring right across the region, under similar large-scale physical and growth conditions, generating successful regional recruitment (figure 6). Alternatively, spawning and larval survival may be occurring mainly in a central area in the south with drift taking the older individuals into a larger habitat over the next 1–2 years (figures 5c and 6; Priddle *et al.* 1988; Hofmann *et al.* 1998; Murphy *et al.* 1998b; Quetin & Ross 2003; Hofmann & Murphy 2004; Fach *et al.* 2006). Analyses of sea ice data indicate that conditions show marked variation across the region, suggesting that recruitment success will also vary. We also know that large animals occur in off-shelf areas in regions of rapid current flow, indicating that there is significant transport of both larvae and adult krill, and a general oceanic mixing of year classes across the region (Hofmann & Murphy 2004; Murphy *et al.* 2004a,b). These observations tend to support the view of a central spawning region with dispersal into the larger habitat (figure 6), but this is based on limited information. At local scales, around

islands, how the krill get onto the shelf from off-shelf areas is unknown, although vertical migration strategies may be important in areas where exchanges of water occur at depth (Murphy *et al.* 2004a). In some areas close to the Scotia Arc, larvae may be entrained back onto the shelf by cross-shelf transfers of water associated with upwelling or surface water mass exchange (Dinniman & Klinck 2004; Klinck *et al.* 2004). These exchange mechanisms are likely to be important in larval retention along the Antarctic Peninsula and around the South Orkneys. However, there is no evidence that there is a significant larval recruitment onto the shelf in more northern regions such as South Georgia (Ward *et al.* 1990; Watkins *et al.* 1999; Atkinson *et al.* 2001).

The implication of this view of krill dynamics is that a large proportion of the young produced will be immediately lost from the regional system (Murphy *et al.* 2004a,b). This can be a viable strategy for a species as long as some animals are retained in the major spawning zones or there is some reverse mixing against the flow towards the south and west. However, this view of a broadcast spawner, in which the majority of the larvae drift away from a central favoured habitat and are lost from the population, may not be appropriate for this species. The chances of successful development of larvae in the pelagic areas of the Scotia Sea will depend on food availability (Meyer *et al.* 2002, 2003; Ross *et al.* 2000; Meyer & Oertl 2005). As previously mentioned, the southern Scotia Sea and Arc show variable but moderate chlorophyll *a* concentrations that are likely to be adequate for krill growth (Atkinson *et al.* 2004).

(d) *Krill–habitat interactions in the Scotia Sea*

This large-scale view of krill dynamics indicates that the more northerly regions of the Scotia Arc will be unfavourable areas for krill with an apparent lack of larval recruitment and low growth rates as a result of high temperatures (Atkinson *et al.* 2006). A longer growing season at low latitudes may offset this situation, but it raises the question of whether these northern areas are part of a linked system where animals are returned south to the major spawning areas or whether they are effectively a dead end, where krill are consumed, starve or are transported out of the system. A direct active migration (Siegel 1988; Nicol 2006), towards favoured spawning areas in the south, would be successful even in the rapid flow of the ACC with a sustained swimming speed of 15 cm s^{-1} . Such a sustained swimming speed may be possible for krill (Marr 1962; Kils 1982; Miller & Hampton 1989), although there is no evidence of a large-scale migratory strategy (Marr 1962). The proposed evidence of active directed horizontal migration of krill over extended distances could also be largely explained by small-scale interaction effects and interactions with larger scale environmental structure. One such small-scale strategy would be a vertical migration to exploit changes in flow speed and direction with depth (Hardy 1967). Simulation studies have shown that diurnal vertical migration in surface waters (less than 200 m) can modify the direction that krill are transported within the main current flow (Murphy *et al.* 2004a). Krill do

not however appear to undertake a deep (greater than 300 m) migration during winter, although there are suggestions that vertical migration during winter in shelf and slope regions may be more important than first recognized (Siegel 2005; Taki *et al.* 2005). Even if such a seasonal vertical migration does occur, there is little southward flow at any depth in the Scotia Sea sector as intermediate water masses enter through Drake Passage and not from the Atlantic Sector, so a deep winter migration will not move krill south in the Scotia Sea.

A change in vertical distribution in the water column through the year does however occur owing to the winter association with the sea ice, which is a crucial part of the life history. The association with the sea ice has so far been assumed to be a strategy for accessing alternative sources of food and for the avoidance of predators (Loeb *et al.* 1997). However, the association may also be a strategy for retention and life cycle closure. The direction of the drift of ice is different from the underlying ocean circulation because the motion of ice is mainly wind driven (Thorndike & Colony 1982; Steele *et al.* 1997). A recent modelling study (Thorpe *et al.* submitted) has suggested that drifting with the sea ice over winter can generate retention of krill in southern regions where conditions for larval growth over the whole year are most favourable. A strong physical association of the krill with the sea ice could lead to a rapid southward redistribution as the retreat of sea ice in spring is often wind driven. This process may be particularly important in the Antarctic Peninsula region where the sea ice tends to move towards the continent from the Bellingshausen Sea region rather than offshore and northwards (Stammerjohn *et al.* 2003).

The link with the sea ice will also be important in generating the large-scale distribution of krill. Simulations of the growth and development of larval krill (Fach *et al.* 2002) showed that krill drifting east from the Antarctic Peninsula region would encounter sea ice advancing north across the region (Murphy *et al.* 1998b). Thus, larvae would be entrained in the west and central Scotia Sea during autumn. Modelling studies (Thorpe *et al.* submitted) indicate that krill entrained with the sea ice in the southern Scotia Sea in autumn would drift east and north with it during winter. During the spring ice retreat, the krill would either be entrained into the water column in the eastern or southern Scotia Sea or remain with the ice as it retreats and become entrained in the eastern Weddell. Further drift and entrainment in sea ice in the following season may release the krill into the favourable growth conditions of the Scotia Sea or in the Antarctic Coastal Current in the following year (figure 5c). The sea ice interaction is therefore potentially important in generating the distribution of krill in the Scotia Sea (figure 5; Murphy *et al.* 2004a).

During winter, the sea ice zone across the Scotia Sea system will also provide a very different habitat to that of the WAP region and probably favours ice algae growth even during mid-winter (Garrison & Close 1993). Day length in mid-winter across the southern Scotia Sea is more than 5 h, whereas there is no daylight in areas further south in the Weddell Sea and along the WAP. The sea ice zone will be an area of ice divergence where

leads and floes are consistently changing, generating a MIZ system right across the southern Scotia Sea. During winter, the mean concentration of sea ice is approximately 42%. Even for the peak months of July, August and September, the concentration averages below 50%. An area of approximately 0.5×10^6 km² is covered by sea ice at this time and over 0.17×10^6 km² will be covered by sea ice less than 30% in concentration. These characteristics of low-concentration sea ice and relatively high irradiance are likely to favour the growth of sea ice algae and other components of the microbial community across the southern Scotia Sea during winter (Garrison & Close 1993). These are areas where krill are known to occur during spring and are likely to be an important habitat for krill and the whole food web during winter (Marr 1962; Hopkins *et al.* 1993b; Brierley *et al.* 2002a).

Although the South Georgia population depends on inputs from areas further south, there does appear to be some local retention of krill over a number of years (Reid *et al.* 1999b; Murphy & Reid 2001). There are consistent changes over weeks to months and between summer and winter and also between years in krill length in the diet of Antarctic fur seals (Reid *et al.* 1999a). This raises key questions about how krill overwinter in these more northern regions. At South Georgia, krill overwinter on shelf where they are the target of a fishery that operates over a series of banks off the north coast (Murphy *et al.* 1997). However, we do not know what these krill feed on during winter, nor do we have much information on the winter dynamics of local plankton populations. We do know from studies around the Antarctic Peninsula that krill can feed on benthic material, so a benthic food source may be available (Ligowski 2000; Daly 2004). We also know that krill occur near the sea bed in other regions. Activity recorder studies on penguins foraging from Signy Island have shown that at times they are feeding close to the bottom around 200 m and consuming krill (Takahashi *et al.* 2003). Krill can also feed on a range of planktonic species and groups other than large diatoms, including microbial species and meso-zooplankton (Marr 1962; Quetin & Ross 1991; Hopkins *et al.* 1993b; Huntley *et al.* 1994; Pakhomov *et al.* 1997a, 2004; Atkinson *et al.* 2002; Meyer *et al.* 2002, 2003; Daly 2004). These alternative food sources will be important in allowing the krill to survive in winter away from the sea ice, and further information on krill diet in winter in areas outside the sea ice is required.

There have also been suggestions that the Scotia Sea krill stock is maintained by two separate inputs of krill from populations in the Weddell Sea and the WAP regions (Siegel 2005). There are some indications of an east–west split in krill dynamics with different-sized krill dominating in the east or west in some years. However, there is no physical or planktonic community distinction between these areas, indicating that there is no simple ecological distinction (Marin 1987; Ward *et al.* 2004, 2006). It is also likely that krill are produced right across the region in areas of the WAP, the southern Scotia Arc, Weddell Sea and possibly right across the Scotia Sea (Hofmann & Husrevoglu 2003; Tarling *et al.* in press). However, we do not observe

large numbers of larval krill regularly around South Georgia, and those that are present do not appear to recruit successfully to the local population (Ward *et al.* 1990). It is possible that larval development may be constrained by high temperatures in these more northerly regions. The view of a mixed Scotia Sea population is also supported by the observed consistency of recruitment success across the region and indicates that a discrete two-source view is inappropriate (Fach *et al.* 2006). Modelling studies have also suggested that krill will recruit into the Scotia Sea from right across the southern region (around the Antarctic Peninsula and northern Weddell Sea) and that successful recruitment will be a complex function of krill life cycle and feeding interactions (Fach *et al.* 2006). The apparent east–west split might therefore be the result of a combination of oceanic and sea ice interactions (Siegel *et al.* 2004; Siegel 2005). Krill larvae generated around the Antarctic Peninsula (east or west) will be moved eastwards over winter and will emerge in areas in the eastern Scotia Sea in spring (Fach *et al.* 2002, 2006; figure 5c). This could result in a separation in the distribution of different year classes, with annual waves of recruitment moving east, associated with local year class retention in shelf areas (figures 5c and 6).

Larger scale closure of the life cycle of krill from eggs to mature adult and spawning may involve connections between krill in areas that occur outside the Scotia Sea. Simulation studies indicate that after the ice retreats, a lot of the krill in the Scotia Sea would be transported out of the region to the east around the South Sandwich Islands (Murphy *et al.* 2004a). Such eastward movement may facilitate transport to areas further south in the eastern Weddell Gyre and Lazarev Sea (Thorpe *et al.* submitted). The link with sea ice areas in the southern Scotia Sea requires more specific study, focusing on larvae in ice edge regions encompassing both oceanic and neritic waters particularly during spring and autumn. Understanding the links and potential sources in this highly distributed system requires large-scale coupled simulations of the life cycle in association with oceanic and sea ice dynamics.

These analyses of population dynamics indicate that the central southern Scotia Sea and Arc may be a much more important habitat for maintenance of the krill population across the whole area than previously considered. The habitat of the central southern Scotia Sea appears particularly crucial in both winter and summer and will be a valuable focus for studies to determine larger scale controls on the distribution of krill.

(e) *Krill population variability and change in the Scotia Sea*

A number of studies have developed integrated analyses of krill population dynamics across the Scotia Sea. These built on earlier studies of variability of the ecosystem such as those of Maslennikov & Solyankin (1988) and Priddle *et al.* (1988). Together these have shown that fluctuations in the numbers of larval krill produced and their subsequent survival is the major driver of variation in the abundance of krill across the Scotia Sea (Murphy *et al.* 1998b; Murphy & Reid 2001;

Reid *et al.* 2002). The importance of year class strength in driving changes in abundance in krill populations in the WAP and Elephant Island regions has been known for some time (Quetin & Ross 1991, 2003; Siegel & Loeb 1995; Ross & Quetin 1999; Quetin & Ross 2001). However, despite the evidence of a large-scale relationship between krill density and sea ice extent (Atkinson *et al.* 2004), the situation at South Georgia and across the northern Scotia Sea is more complicated. Smaller size/age (less than 30 mm and 1-year-old) classes of krill are generally not observed at South Georgia (Watkins *et al.* 1999). Size classes of older age groups merge together as the animals increase in size owing to the asymptotic nature of krill growth (Priddle *et al.* 1988). As noted earlier, this has made it difficult to determine whether abundance changes are driven by individual year class variations or bulk changes across all year classes. Initial studies suggested that bulk shifts in distribution of all age groups, linked to large-scale atmospherically driven changes in ocean currents, were generating the observed variation (Priddle *et al.* 1988). Subsequently, Murphy *et al.* (1995) and Fedulov *et al.* (1996) showed that these changes were also linked to sea ice changes further south and that they affected the availability of krill to the fishery. Model studies showed how the observed rapid reductions and recoveries in abundance could be the result of year class fluctuations in a system where older age groups dominated (Murphy *et al.* 1998b). Further analyses of krill size in the diet of Antarctic fur seals at South Georgia showed consistent changes in length frequency between years (Reid *et al.* 1999a), indicating that year class fluctuations were generating the observed abundance and biomass changes at South Georgia (Murphy & Reid 2001; Reid *et al.* 2002). The abundance changes are therefore driven by the influx of a large cohort of young krill which dominate the population and maintain regional biomass for 1–2 years. The biomass then declines until the next influx event. For the northern Scotia Sea, there is therefore a second-stage distributional effect on top of the original recruitment variation occurring elsewhere (Murphy *et al.* 1998b). The two effects are however linked, i.e. cold periods favour recruitment success and disperse krill further north, so it is unlikely to be possible to simply separate physical and biological effects.

These events of influx of young krill into the northern Scotia Sea are strongly related to the physical conditions across the Scotia Sea. At South Georgia, it is krill that have overwintered at least once under the ice that are transported to the island during the early summer (Murphy *et al.* 1998b). The further north the sea ice extends across the region, the colder the conditions in the north (Fedulov *et al.* 1996; Whitehouse *et al.* 1996a). Analyses of recruitment of krill into the population at South Georgia (Murphy *et al.* submitted) and particle-tracking studies, including interactions with sea ice (Thorpe *et al.* submitted), indicate that more extensive winter sea ice leads to enhanced dispersal and transport of young krill into northern regions. The effect is that during cold periods, influx recruitment is enhanced, while there is little or no influx during warm periods. In years of little or no flux, mortality rates will also increase as the predators attempt to maintain food supply,

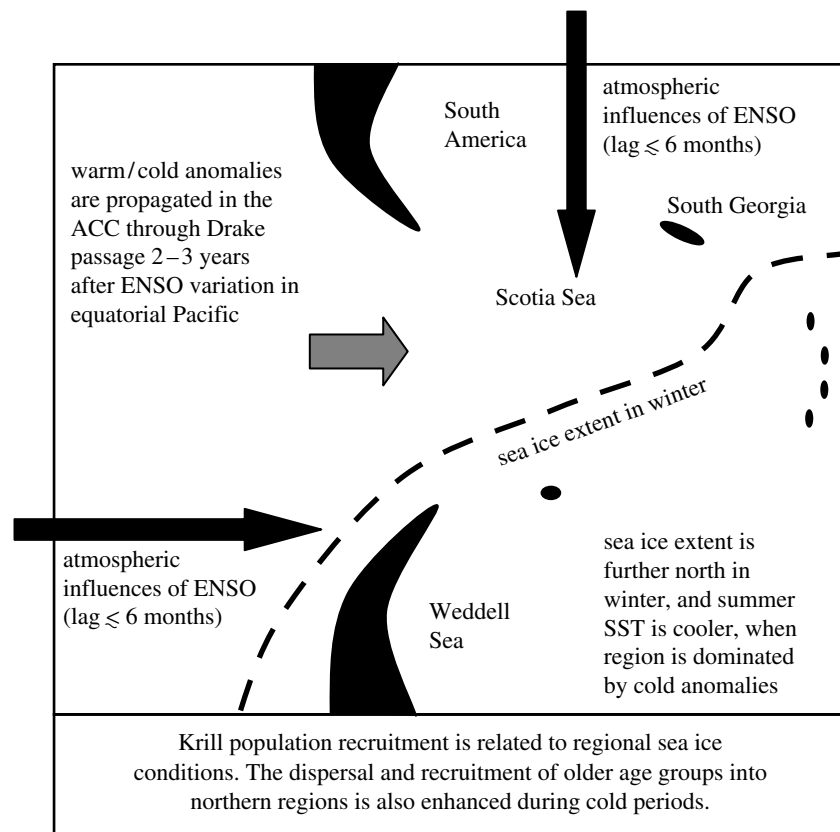


Figure 7. Schematic of the main physical processes generating variation in the Scotia Sea ecosystem. These factors also affect krill recruitment and dispersal across the region, generating observed correlations of changes in krill density and biomass and higher trophic level predator foraging and breeding performance with sea ice and larger scale indices of oceanic and climatic variation.

reducing abundance more quickly (Murphy & Reid 2001; Constable *et al.* 2003). These interactive effects of varying krill abundance and predator demand mean that mortality will be a key process in determining the interannual variability and may enhance the amplitude of the observed variation. However, although we can estimate the mortality rates of older krill, rates for larval and juvenile krill are unknown (Murphy & Reid 2001; Siegel 2005). Higher temperatures are likely to exacerbate the decline in krill biomass through reduced rates of growth (Atkinson *et al.* 2006), and may also affect survival. As the duration of the warm period extends over 2–3 years, biomass declines further so that the lowest biomasses occur at the end of the warm period (Reid *et al.* 1999a; Murphy & Reid 2001). A recent study of population changes at South Georgia (Murphy *et al.* submitted) indicates that influx events are most clearly detected after the warmest, lowest biomass years. During the colder periods, influx events are less obvious as the biomass is generally higher due to consecutive years of reasonable or high recruitment.

The influx of krill to the South Georgia area depends on transport from the southern Scotia Sea in spring (Murphy *et al.* 2004a,b). Some of the transport is associated with the SACCF which has been shown to be important in advecting krill (Hofmann *et al.* 1998; Fach *et al.* 2002, 2006; Murphy *et al.* 2004b). Further analyses of fluctuations in the position of the SACCF have also indicated that this may affect the large-scale transport of krill across the Scotia Sea (Thorpe *et al.* 2002; Trathan *et al.* 2003; see also Priddle *et al.* 1988).

The sea ice and SST variation in the Scotia Sea is related to larger scale atmospherically driven changes (Murphy *et al.* 1995; Turner 2004; Murphy *et al.* submitted). ENSO variation influences the region oceanically through a signal that propagates across the southern Pacific sector and through Drake Passage into the South Atlantic region, 2–3 years after the variation in the ENSO region (figure 7; Murphy *et al.* 1995; Trathan & Murphy 2002; Murphy *et al.* submitted). During the most intense ENSO periods, the signal can be modified by direct, short-term, atmospherically driven changes (Meredith *et al.* 2005; Murphy *et al.* submitted). Low SST in the South Atlantic is also associated with greater sea ice in winter (Trathan *et al.* 2006; Murphy *et al.* submitted). As previously noted, these changes in sea and SST affect the recruitment in southern ice-covered regions and dispersal of older age groups to the north. This will introduce biological lags that affect the northern Scotia Sea through dispersal of krill 2–3 years after the recruitment in the south. The coherent nature of the physical variability provides the potential for prediction of physical and biological changes in the Scotia Sea.

A lack of information on seasonal changes in krill abundance limits our understanding of these interannual fluctuations. Seasonal variation in krill abundance has been recorded in the Antarctic Peninsula region and may be a key aspect of the interannual fluctuations (Siegel 2005). Data from krill predators at South Georgia also indicate that there are marked seasonal changes in krill population structure in

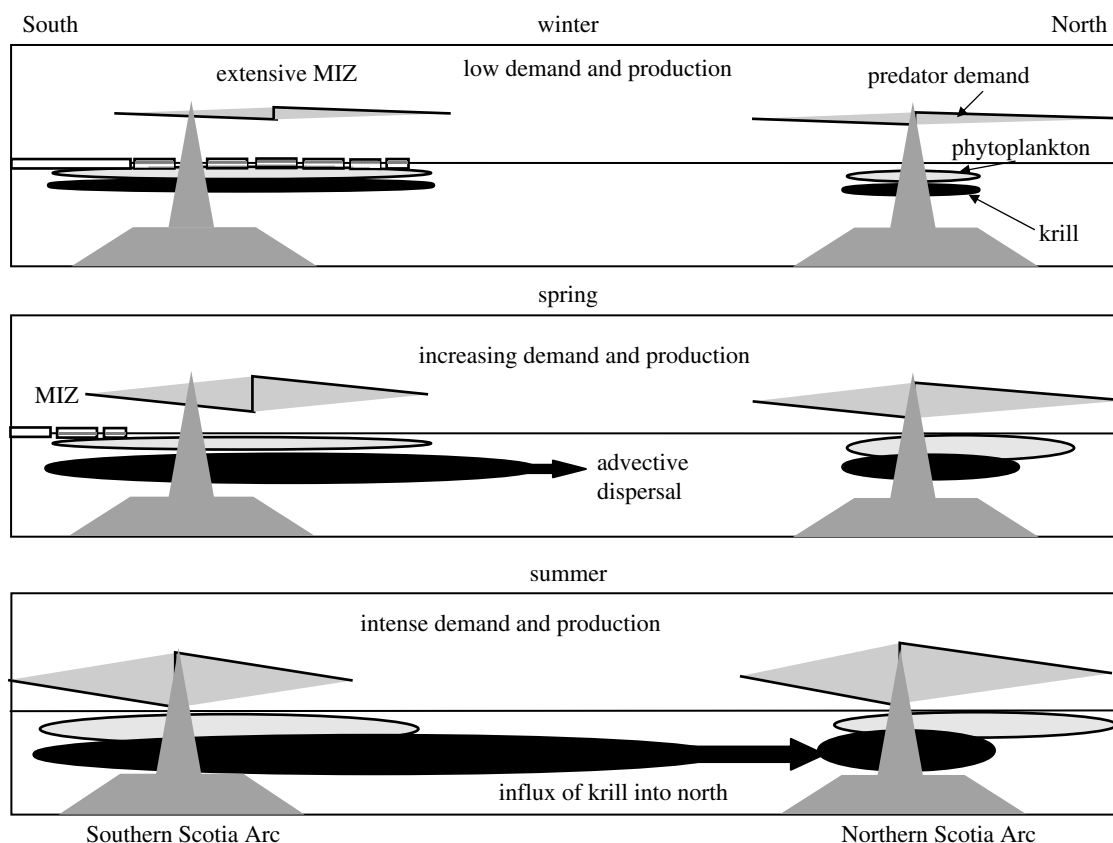


Figure 8. Schematic of seasonal development (winter, spring and summer) of the Scotia Sea ecosystem, highlighting major spatial connections and the development of the spatial distribution of krill.

northern regions (Reid *et al.* 1999b) and biomass peaks during the summer (Brierley *et al.* 2002b; BAS unpublished data). In the northern regions, changes in timing of influx, growth and mortality during the season will all affect local krill abundance and hence their availability to predators. There is little knowledge of these processes and it is important that further information on seasonal changes in krill abundance across the Scotia Sea is obtained.

On longer time-scales, analyses of historical net data have shown a decline (50–80%) in the abundance of krill across the Scotia Sea over the last 30 years (Atkinson *et al.* 2004). Across the region, annual krill density is related positively to the previous winter sea ice cover in the Scotia Sea (Atkinson *et al.* 2004). Although it is tempting to infer a causal relationship from these observations, sea ice changes over the last three decades have been complex and show marked interannual, sub-decadal and decadal changes (Murphy *et al.* 1995; Murphy *et al.* submitted). The long-term decline in overall abundance could be interpreted as a stock that has become more dependent on fewer years of successful recruitment and which are consequently subject to high mortality rates (Murphy *et al.* 1998b; Reid *et al.* 1999b; Murphy *et al.* submitted). The effect on population dynamics will therefore be expressed more clearly than in higher biomass periods that dominated two to three decades ago. When the population size was larger, single year class fluctuations would have had less effect on biomass (Murphy *et al.* 1998b). With this view, we would expect that across the Scotia Sea, correlations between

environmental variation and krill abundance fluctuations will be stronger now than in previous periods when biomass was higher. However, as both recruitment and dispersal of krill are related to sea ice, it is difficult to determine whether the changes in density in the Scotia Sea are due to reductions in overall abundance or changes in distribution (Murphy *et al.* 1998b; Constable *et al.* 2003).

(f) *Krill in the Scotia Sea food web*

The analysis of the life cycle of krill highlights the spatial operation of the krill population in the Scotia Sea. Krill are therefore a variable and dynamic component of the food web across the Scotia Sea (figure 8). As we have noted, krill are omnivorous and consume other zooplankton or microbial groups. In sea ice-covered regions, they can consume sea ice algae and, in shelf areas, have been found to be feeding on benthic algae (Ligowski 2000). However, a major source of energy for krill during spring and summer is diatoms (Cadee *et al.* 1992; Pond *et al.* 2005). Each year, as the ice retreats, large blooms of diatoms occur across the Scotia Sea, particularly in the regions of the Scotia Arc and downstream (Holm-Hansen *et al.* 2004b), and these are exploited by krill (figure 8). Later in the spring, as the ice retreats southward, large blooms of diatoms in southern regions will fuel the growth of post-larval krill in areas where they are retained over the shelf or as they drift north across the Scotia Sea (figure 8). In the more northern regions, krill will benefit from the occurrence of large blooms associated with the Scotia Arc that are maintained for

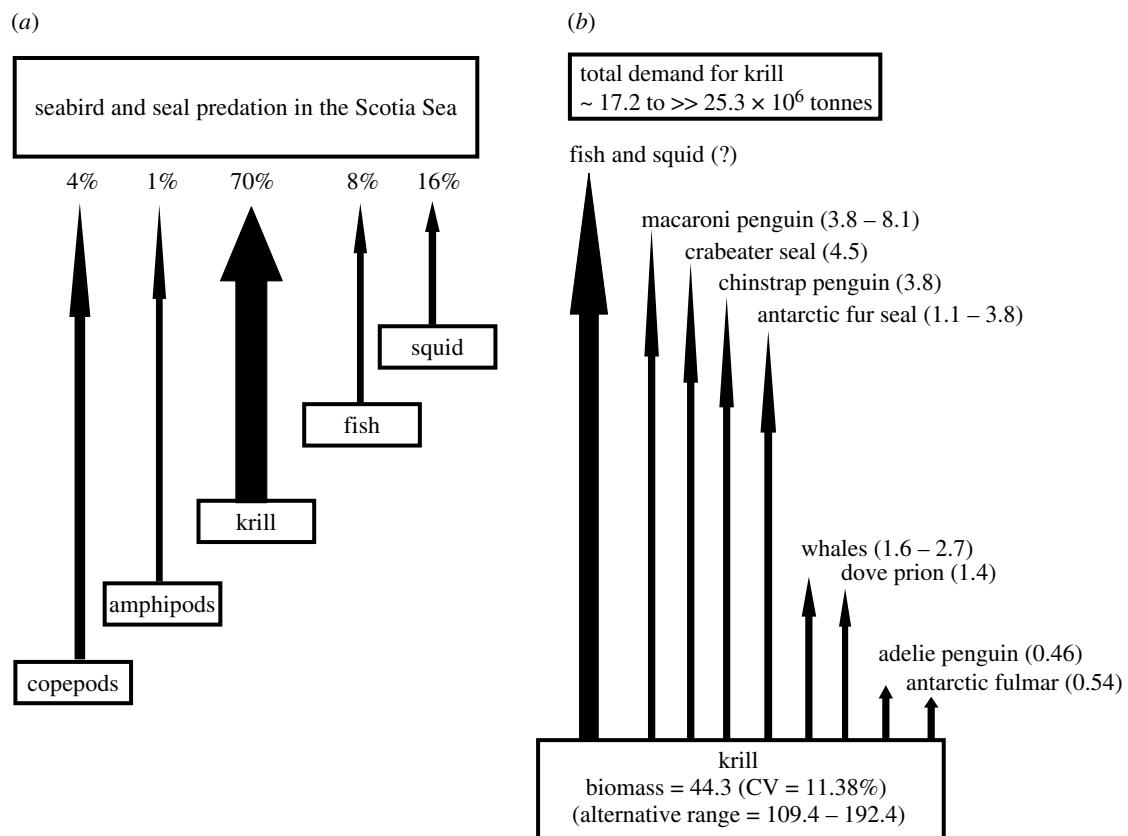


Figure 9. Predator links in the Scotia Sea food web. (a) Proportional consumption of different groups of prey by the major predators. (b) Estimates of annual consumption of krill (10^6 tonnes yr^{-1}) by the main krill predators. Where available a range of estimates are given to illustrate the uncertainty. Information on predator diet and consumption is from Croxall *et al.* (1984, 1985), Boyd (2002a) and Reilly *et al.* (2004). Estimates of krill standing stock are from Hewitt *et al.* (2004) and values in parentheses are from Demer & Conti (2005). Estimates are based mainly on summer studies and are likely to overestimate the importance of krill in the diet (Croxall *et al.* 1985). Values for fish and squid consumption have not been included, but may be very large (Kock 1985; Pusch *et al.* 2004).

extended periods during summer (Atkinson *et al.* 2001; Korb *et al.* 2005).

The resultant krill distribution is highly heterogeneous with the highest densities occurring in areas of shelf around the Scotia Arc, but with a significant biomass in areas off-shelf, particularly at the ice edge during spring (Marr 1962; Atkinson *et al.* 2004; Hewitt *et al.* 2004; Siegel 2005). Large numbers of predators require land-based breeding sites during summer, from where they operate over a restricted local area as centrally placed foragers (Croxall *et al.* 1988). These areas occur on islands around the Scotia Arc where enhanced concentrations of krill are found on the shelf. These are also the regions where most of the commercial fishing for krill occurs (Murphy *et al.* 1997). There is therefore a spatially heterogeneous demand for krill, with intense hotspots, where krill concentrations are high and predator demand is greatest (figure 8; Murphy & Reid 2001). In areas of low production or retention of recruits, the demand for prey is maintained by the advective influx of krill. Rates of mortality of krill across the Scotia Sea will therefore be highly heterogeneous (Murphy & Reid 2001).

Within these regions of high concentration, krill show further spatial structure associated with meso-scale (tens to hundreds of kilometres) physical features, such as frontal regions, plumes and the edges of submarine canyons (Brinton 1985; Watkins *et al.*

1986; Murphy *et al.* 1988; Witek *et al.* 1988; Miller & Hampton 1989; Watkins & Murray 1998). Biological and physical process interactions within these aggregations generate swarms in response to predatory and feeding stimuli (Murphy *et al.* 1988). This patchiness across a range of scales allows a variety of predator species with very different foraging strategies to exploit krill (Murphy *et al.* 1988). The longevity of krill is also an important factor in their role in the food web. The long lifespan of krill (5–7 years) means that at a population level, they are able to cope with the strong seasonal and interannual variability (Murphy *et al.* 1998b; Fraser & Hofmann 2003). By exploiting a wide range of food sources, they can survive periods of starvation. Long lifespan allows for the potential of spawning several times during their life and means they can cope with unfavourable years (Fraser & Hofmann 2003). This combination of high abundance, longevity, dispersal and heterogeneity is why krill have such a central role in the food web of the Scotia Sea (figure 9).

5. FOOD-WEB OPERATION

The Scotia Sea ecosystem encompasses high production regions around areas of shelf and sea ice retreat during spring, and low production regions in the west near Drake Passage. The advective nature of the system also makes a narrow geographical view inappropriate. Some locally detailed studies, mainly based on summer

data, have been undertaken on various aspects of the ecosystem (Croxall *et al.* 1985; Gowing & Garrison 1992; Hopkins *et al.* 1993a,b; Bathmann *et al.* 2000; Atkinson *et al.* 2001), but there have been few attempts at a broader synthesis (Everson 1977; Hempel 1985a,b). The focus for carbon flow analyses has been on primary production and lower trophic level interactions where the flows are greatest (Bathmann *et al.* 2000). In contrast, analyses of variability have focused mainly on higher predator interactions with their prey, which has generated datasets extending back almost 30 years (Croxall *et al.* 1988; Reid & Croxall 2001). Here, we highlight some of the key features of the food web, considering trophic and spatial links.

(a) Trophic links

Within the lower trophic levels, a particular focus has been on the role of copepods and their interactions with krill. Copepods in the northern Scotia Sea, around South Georgia, can at times be the dominant grazers (Ward *et al.* 1995; Atkinson & Snyder 1997; Pakhomov *et al.* 1997b; Atkinson *et al.* 1996, 1999). Shreeve *et al.* (2005) found that daily gross krill production was $0.022 \text{ g C m}^{-2} \text{ d}^{-1}$ compared with $0.026 \text{ g C m}^{-2} \text{ d}^{-1}$ of the older stages (CIV and CV) of the copepod *Calanoides acutus* (which represented approx. 25% of the total copepod biomass at South Georgia). These analyses give a valuable view of the summer situation and indicate that copepods may be the dominant zooplankton secondary producers across the Southern Ocean (Shreeve *et al.* 2005). Developing more detailed analyses of the relative impact of krill and copepods on production requires a seasonal view. These are highly dynamic systems where the timing of interactions will generate multiple and varying controls that are not easily resolved by short-term sampling programmes. The situation is complicated by associated spatial changes in the operation of the food web. Krill biomass around South Georgia is greatest on the shelf where local temperatures and chlorophyll *a* concentrations are generally low. In contrast, copepods tend to dominate in warmer waters, off-shelf to the west, where chlorophyll *a* concentrations are higher. Both competitive interactions and 'bottom-up' processes (physical and chemical) in the food web have been invoked to explain these relationships between copepods and krill (Atkinson & Snyder 1997; Priddle *et al.* 1997, 2003; Atkinson *et al.* 1999; Shreeve *et al.* 2005; Ward *et al.* 2005).

The extended lifespan of the larger zooplankton species may be an adaptation to survive in highly seasonal and variable systems. However, they may also be an important factor in determining the influence of zooplankton on lower trophic levels (Priddle *et al.* 2003; Shreeve *et al.* 2005). Overwintering zooplankton will affect the development of phytoplankton populations during spring. Large numbers of zooplankton rising from depth in spring (copepods; Atkinson *et al.* 1997; Ward *et al.* 1997; Tarling *et al.* 2004), or already present in surface waters (krill), will have an instantaneously high grazing impact, affecting the net growth rates of phytoplankton (Lancelot *et al.* 1991, 1993). Krill grazing impacts may therefore affect bloom development even though their impact on overall productivity during the summer is low. This may be

particularly important in the Scotia Sea where copepods and krill are a dominant part of the food web.

The relative importance of grazing through copepods and krill will impact the fate of carbon (Cadee *et al.* 1992; Gonzalez 1992; Ross *et al.* 1998; Schnack-Schiel & Isla 2005). Krill generate large faecal pellets that sink quickly (rapidly removing carbon to depth), whereas copepod waste material is smaller and likely to sink less rapidly. However, copepods spend a large part of the year in diapause at depths of greater than 1000 m where they may die, generating a direct carbon flux at depth, whereas krill remain in surface waters. The complexities of such vertical interaction effects in the food web, including links to microbial systems, are largely unknown but are likely to be important in determining vertical fluxes of carbon (Tarling & Johnson 2006). These life cycle and behavioural effects demonstrate that analyses of carbon fluxes in the Scotia Sea, and indeed biogeochemical cycles generally, will require detailed knowledge of the life cycles of key planktonic species, particularly krill and copepods (Giesenhausen *et al.* 1999).

Of the other zooplankton groups, two in particular deserve further study in the Scotia Sea. Firstly, salps are distributed across the Scotia Sea and have an important role in regional biogeochemical cycles and food webs (Foxton 1966; Fortier *et al.* 1994; Pakhomov *et al.* 2002). However, it is unclear whether they are as important as in other regions around the Southern Ocean, particularly in the WAP region and in warmer areas to the north (Marchant & Murphy 1994; Loeb *et al.* 1997; Atkinson *et al.* 2004; Kawaguchi *et al.* 2004; Smetacek *et al.* 2004). This may be the result of high concentrations of diatoms that adversely affect salp feeding, or the result of competitive or predatory interactions with other species (Smetacek *et al.* 2004). Recent suggestions that their abundance is increasing in high-latitude Southern Ocean ecosystems (Pakhomov *et al.* 2002; Atkinson *et al.* 2004) make the need to improve understanding more urgent.

The second group for which information is very limited are the predatory amphipods, particularly *Themisto gaudichaudi* (Pakhomov & Perissinotto 1996). These amphipods can become a major component (more than 50%) in the diet of mackerel icefish around South Georgia in years of low krill abundance and are also consumed by a range of other pelagic and seabird predators (Rodhouse *et al.* 1992; Kock *et al.* 1994; Pakhomov & Perissinotto 1996; Reid *et al.* 1997b; Bocher *et al.* 2001). It is likely that they are a significant predator on a wide range of species, including krill and copepods (Pakhomov & Perissinotto 1996) and may exert predatory control on the dynamics and interactions of lower level species (Bocher *et al.* 2001).

Top-down controls are important in Scotia Sea planktonic ecosystems (Atkinson & Snyder 1997; Priddle *et al.* 2003; Shreeve *et al.* 2005), but much more specific studies of plankton interaction effects are required to elucidate mechanisms and generate dynamic models. Feedbacks within the food web will also affect the dynamics of phytoplankton productivity (Priddle *et al.* 2003; Shreeve *et al.* 2005). For example, large aggregations of krill grazing on

phytoplankton can generate locally high concentrations of ammonium through excretion (Priddle *et al.* 1997, 2003; Atkinson & Whitehouse 2000). As ammonium is a preferred nitrogen source for many phytoplankton species, this will lead to enhanced phytoplankton growth rates (Priddle *et al.* 1998b). Ammonium levels can also be enhanced around local predator colonies, again increasing potential growth rates of phytoplankton (Whitehouse *et al.* 1999). Such interaction and feedback effects are likely to be particularly significant in the Scotia Sea, which has such high concentrations of copepods, krill and higher predators.

Across the Scotia Sea, there is no simple relationship between the structure of plankton communities and any major physical features, such as frontal boundaries between water masses. In recent analyses of zooplankton community structure, Ward *et al.* (2004, 2006) found that the major Scotia Sea frontal systems did not act as significant boundaries for species or between communities. Instead, the variation of community structure in spring was dominated by north–south differences in the state of development of the different zooplankton species. Species in communities further north were generally in a more advanced state of development than areas to the south during mid-summer. This development-related variation has been generally linked to timing changes in water temperature and sea ice cover related to latitude and seasonal variation in production and planktonic system development (Hempel 1985a; Marin 1987; Atkinson & Sinclair 2000; Ward *et al.* 2004, 2006). This difference was further shown in analysis and modelling of the development status of key copepod species (Tarling *et al.* 2004). Overwintering stages reach the surface waters earlier in the season in the more northern regions (Voronina 1970). The short and later season also impacts the overall life cycle, with animals in the north completing their life cycle in a single year, whereas further south, more of the population take 2 years (Tarling *et al.* 2004). These variations in timing, growth and development will affect interactions with krill and modify the dynamics of the food web and will be a valuable focus for the next generation of model studies.

Even though krill dominate the energy flows to higher trophic levels (figure 9), the pathways of energy transfer through the food web are complex (Croxall *et al.* 1984, 1985; Hopkins *et al.* 1993a,b). Most of the studies of krill consumption are from analyses of the diet of land-based predators (figure 9). However, krill are also consumed by a wide range of pelagic species, especially squid and fish, although consumption estimates are extremely uncertain (Kock 1985; Rodhouse & Nigmatullin 1996; Pakhomov *et al.* 1996; Pusch *et al.* 2004). The importance of copepods as prey items in the food web is even less well quantified than for krill. Shreeve *et al.* (2005) recently discussed the potential importance of the copepods in the food web and noted that *C. acutus* is an important part of the diet of the mesopelagic fish, *Electrona antarctica*. Another copepod species, *Drepanopus forcipatus*, is consumed by the larvae of the commercially exploited icefish (*Champsocephalus gunnari*). Copepods are also important to the flying seabirds such as Antarctic prions (*Pachyptila desolata*) and diving petrels (*Pelecanoides* sp.; Reid *et al.* 1997a,b).

Groups and species other than copepods and krill can also be locally or seasonally important in the diet of a range of pelagic and land-based predators. For example, the diet of icefish varies markedly around South Georgia; euphausiids other than krill (e.g. *Thysanoessa* spp.), the amphipod *T. gaudichaudi* or mysids (Siegel & Muhlenhardtsiegel 1988) are a significant component of the diet in different areas. These groups and species are also an important, but variable, component of the diet of other fish, seabird and squid predators (Kock *et al.* 1994; Croxall *et al.* 1999; Everson *et al.* 1999; Bocher *et al.* 2001; Dickson *et al.* 2004). Variations in trophic links as zooplankton and fish species grow and develop are largely unknown. The impact of chaetognaths, jellyfish and other pelagic species on young stages of fish and krill is also unknown, but may be an important component of variability of recruitment of fish and krill.

Around South Georgia and across the Scotia Arc, demersal and pelagic predators such as fish and squid provide alternatives to krill as prey for higher predators during the summer (figure 9). For example, the mackerel icefish, *C. gunnari*, which is semi-demersal on the shelf, is an important prey item for Antarctic fur seals at South Georgia (Reid & Arnould 1996; Everson *et al.* 1999). Equally, squid are an important prey for several groups of higher predators including seabirds, seals and toothed whales (Rodhouse *et al.* 2001; Collins & Rodhouse 2006). Mesopelagic species of myctophid fish are also important in the diet of various predators, including Antarctic fur seals (Reid & Arnould 1996), squid (Rodhouse *et al.* 1992) and king penguins (Olsson & North 1997). A number of these predator species forage in the vicinity of the PF and Rodhouse *et al.* (1992, 1994) considered explicitly some of the trophic links in this region. Further south in winter in MIZs, *E. antarctica* can be a more important prey item in the diet of flying seabirds (Ainley *et al.* 1991; Hopkins *et al.* 1993b). Salps and jellyfish also appear to be a potentially significant dietary component in a range of pelagic and land-based predators but their importance is unknown (Cтры *et al.* 2004). As well as being key components of the diet of many of the predators, squid and myctophid fish species will also be important in links between pelagic and mesopelagic communities (Collins & Rodhouse 2006). There will also be important pelagic–benthic links, and a number of species develop in shallow waters and migrate deeper to shelf–slope regions as they grow. For example, in coastal ecosystems along the northern Scotia Arc, the commercially exploited Patagonian toothfish (*Dissostichus eleginoides*) will be a significant predator with dynamic trophic interactions that vary between pelagic and benthic systems as it grows. Short-term variations in trophic interactions involving diurnal and seasonal changes in depth are also known to be important. However, although descriptive analyses are available, quantitative studies of abundance and fluxes associated with most of these interactions are not available.

These less well-known alternative pathways to the traditionally studied krill links will be important in maintaining the ecosystem structure and determining the dynamics of individual species. These alternative

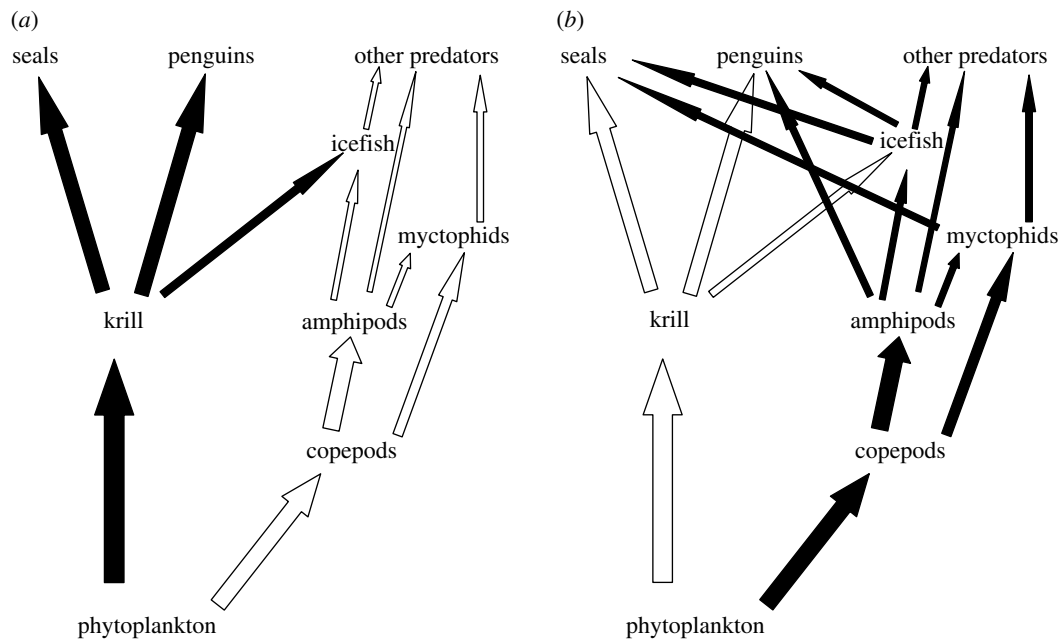


Figure 10. Schematic illustration of alternative pathways in part of the Scotia Sea food web, showing shifts between (a) years when krill are abundant across the Scotia Sea and (b) years when krill are scarce. Major pathways shown as black arrows.

pathways cannot however support the same level of predator demand as the krill–predator pathway, because more complex pathways involve more trophic transfers and associated energy losses at each step (figures 10 and 11).

The upper trophic level structure of the food web is dominated by different predator species across the Scotia Sea. In the north, there are extensive land areas that are not covered by snow during the summer which allow access to suitable breeding sites for macaroni penguins and Antarctic fur seals, which are the major krill predators (Croxdall *et al.* 1984, 1985; Boyd 2002a). Further south, in regions covered by sea ice for much of the year, it is chinstrap or adelic penguins and Weddell or crabeater seals that are the major krill consumers (Croxdall *et al.* 1985; Trathan *et al.* 1996; Priddle *et al.* 1998a; Boyd 2002b; Takahashi *et al.* 2003; Lynnes *et al.* 2004). The dietary differences and specific habitat requirements that generate niche separation of the many predator species across the Scotia Sea have been described in detail. Krill predators often dominate local Scotia Sea food webs, but large numbers of other seabird species, such as petrels and albatrosses, are dependent on groups other than krill, particularly copepods, amphipods, fishes and squid (Croxdall *et al.* 1984, 1985; Reid *et al.* 1996a; Lynnes & Rodhouse 2002; Xavier *et al.* 2003a,b, 2004). We have some knowledge of the diet and foraging of many of these species, particularly in one or two localities such as South Georgia, Signy Island and around the Antarctic Peninsula, but little information for much of the area (Croxdall *et al.* 1985; Reid *et al.* 1996a, 2004).

There is also very little data on the overall abundance and distribution of most of these predator species across the Scotia Sea. Much more detailed information is required on trophic links at local and regional scales combined with data on geographical distribution and abundance. There are major gaps in our knowledge about the operation of the mesopelagic

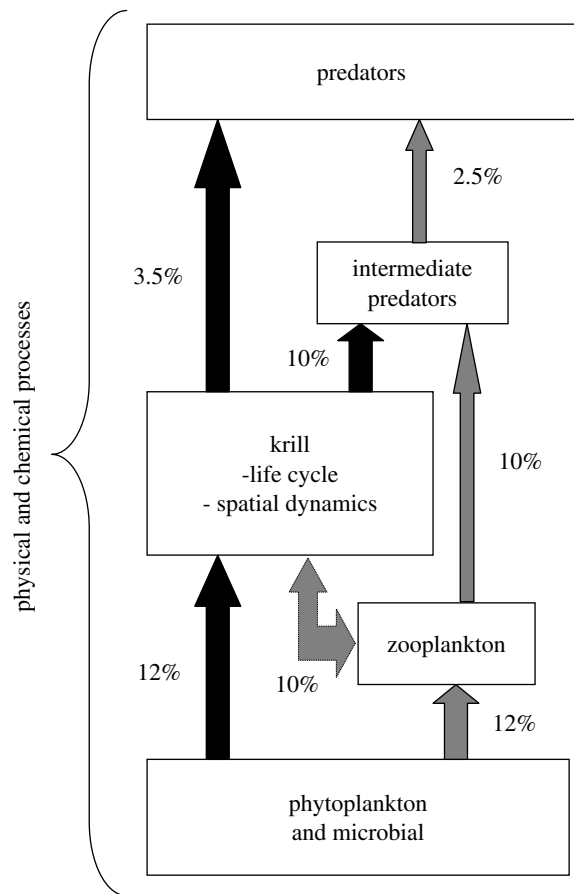


Figure 11. Estimated transfer efficiencies in the Scotia Sea krill-based food web with transfer efficiencies for alternative routes through other zooplankton species and intermediate predators. Based on Priddle *et al.* (1998a).

systems across the Scotia Sea and the links between pelagic and benthic systems. These systems will be crucial, both in terms of the fate of upper ocean production (and hence carbon) and in terms of the effects on the long-term dynamics of pelagic food webs.

It is not possible to examine all pathways in the food web, so we need to focus effort. Specific studies of the role of key predator groups for which we have very little information, such as the whales and crabeater seals, will be important. With a changing climate, copepod and mesopelagic fish interactions, that are crucial in more sub-Antarctic ecosystems, are likely to become more important across the northern Scotia Sea. Focusing effort on these pathways as alternatives to energy flow through krill will be a valuable basis for future research on trophic links.

(b) Spatial operation of the food web

In a highly advective physical environment, the food-web structure can only be maintained by a combination of local and externally generated production. That both local (see also Atkinson *et al.* 2001; Gilpin *et al.* 2002) and external production are important in krill population processes and in maintaining food webs was recognized as far back as the *Discovery Investigations* (Marr 1962; Hardy 1967; Mackintosh 1972, 1973). This view has been supported by field analyses that have shown that large amounts of krill do occur in high-flow areas off South Georgia (Ward *et al.* 2003; Murphy *et al.* 2004b). These flows will be important in taking krill around the island and onto the shelf, although the exact pathways and connections will be complex and variable (Thorpe *et al.* 2002; Meredith *et al.* 2003b,c). Field measurements have shown that the flows will be variable, but at times their influence will dominate the local food-web structure (Murphy *et al.* 2004a).

Even conservative estimates suggest that local krill production around islands such as South Georgia is rapidly consumed through predation. Calculations of predator demand are however complex, and it is especially difficult to account for all the potential demand (Boyd 2002a; Murphy *et al.* 2004b; Shreeve *et al.* 2005). The relatively low growth rate of krill in warm regions of high predator demand around South Georgia during summer further indicates that production will not supply local demand in key regions of the Scotia Sea (Atkinson *et al.* 2006). Such a large impact should generate rapid changes in numbers that would need to be replenished to maintain local krill populations (Murphy *et al.* 1998b). The lack of very young krill on the shelf at South Georgia, combined with the strong flow of the ACC past the island, further indicates that the population in the northern regions is maintained by recruitment from further south (Ward *et al.* 1990; Thorpe *et al.* 2002; Meredith *et al.* 2003c; Murphy *et al.* 2004b). Variations in these inputs will have profound effects on the krill population dynamics and the local system operation. Input of krill into more northern regions probably peaks during spring and early summer following the retreat of the sea ice in the southern Scotia Sea, and is likely to be lowest in winter (Murphy & Reid 2001; Murphy *et al.* 2004a,b). On top of these input effects, further variation will be introduced through fluctuations in rates of growth and mortality. Growth rates may be highest in early spring and summer, while mortality rates are likely to peak in mid to late summer. Together these factors will generate the apparent mid-season peak in the biomass of krill, the timing of which is likely to vary.

Although it is difficult to estimate the total predator demand for krill, it is clear that top-down control on plankton communities will be important in areas around the major predator colonies in the Scotia Sea (Reid *et al.* 2004; Murphy *et al.* 2004b). At South Georgia, in areas of shelf to the east of Cumberland Bay, the concentration of krill is variable, but usually exceeds that observed in areas further west around Bird Island, where the variation is lower (Brierley *et al.* 1997). The majority of seabird and seal demand for krill around South Georgia is concentrated in the west around Bird Island (Croxdall *et al.* 1985; Trathan *et al.* 1996). Long-term data on predator breeding performance has demonstrated that there are periods where krill availability in the western regions has been sufficiently low that they result in catastrophic mortalities of predator offspring (Croxdall *et al.* 1988; Reid & Croxdall 2001; Reid *et al.* 2005; Trathan *et al.* 2006). During these periods of reduced krill biomass, foraging trips become extended as the predators forage further offshore in the search for prey (Boyd & Murray 2001). These factors indicate that predator demand is at times sufficient to deplete local krill biomass. This top-down influence will in turn modify the dynamics of the planktonic communities on the shelf, although the actual effects are unknown. The processes of replenishment of plankton on the shelf through cross-shelf exchange are unknown as we have little real understanding of the detailed circulation on the shelf (Brandon *et al.* 1999; Meredith *et al.* 2003b; Meredith *et al.* 2005). This is also true in terms of understanding the links along the shelf around South Georgia between areas that are fished in winter, which are mainly in the east, and areas further west where the predators forage during spring and summer (Murphy *et al.* 1997). Development of high-resolution models of on-shelf circulation will be an important component in generating the required understanding.

The role of fronts in transferring material across the Scotia Sea is likely to be important, as these are areas of high flow rate (Hofmann *et al.* 1998; Nicol 2006; Murphy *et al.* 2004b). However, analyses of the large-scale distribution of krill during summer indicate that a simple view of a 'conveyor belt' of krill across the Scotia Sea connecting the Antarctic Peninsula region to South Georgia is not appropriate (Hewitt *et al.* 2004; Murphy *et al.* 2004a). The distribution of krill and other plankton in spring will be a function of the timing and pattern of sea ice retreat, affecting local production, krill emergence from the MIZ and copepod migration from depth. Thus, the summer distribution of plankton across the Scotia Sea will be strongly dependent on the system development during spring (Murphy *et al.* 2004a). The importance of advective transfers and dispersal of species other than krill, many of which are more planktonic, such as copepods, has not been the focus of as much study, but is likely to be important. The importance of advection in generating the observed distribution of phytoplankton was demonstrated in a detailed analysis of the planktonic system on the northern side of South Georgia (Ward *et al.* 2002). The analysis showed that the planktonic system around the island was strongly influenced by inflows associated with the SACCF. Enhanced

the grey-headed albatross and king penguins, which consume more squid and fish, operate more widely across the Scotia Sea or in areas further north around the PF (Collins & Rodhouse 2006).

The predators in the South Georgia ecosystem, and at other islands across the Scotia Sea, are therefore not only dependent on local production, but also forage out across the Scotia Sea and surrounding areas, bringing energy back to feed their young in the large and spatially restricted colonies (Croxall *et al.* 1984, 1985). This concept was developed in predator–prey modelling by Murphy (1995) and it generates a distance–demand relationship away from the centre of foraging. The result is intense heterogeneity in the demand for prey, which is centred around the islands with most of the demand within approximately 200–250 km of the islands. This concept has been further developed by Trathan *et al.* (1998b) and Reid *et al.* (2004), who used data from large-scale at-sea observations to derive more specific species-based relationships of foraging in relation to distance from land in the Scotia Sea. Such analyses provide the basis for generating spatially distributed demand maps, and hence prey mortality distributions, across the Scotia Sea.

Food webs in the Scotia Sea also show marked seasonal changes with major shifts in structure between summer and winter. Thus, for example, around South Georgia the diet of fur seals changes during late summer and autumn, from being dominated by krill to one where myctophid and other fish species are proportionately more important (Reid & Arnould 1996). Many of the higher trophic level species also show shifts in foraging areas or disperse across the region during winter (Boyd *et al.* 1998). This includes many of the krill-eating species of penguins, such as the adelic and chinstrap penguins in the southern regions, which disperse as the sea ice advances north from about May. In the north, fur seals disperse south towards the advancing sea ice, but also north across the PF to areas of the Patagonian Shelf (Boyd *et al.* 1998, 2002). However, a significant number of animals remain in areas around the islands such as South Georgia during winter (Boyd *et al.* 1998, 2002). Macaroni penguins also disperse away from South Georgia during the winter months, but there is little available information on winter distribution. Many of the seabirds also leave the region, as illustrated by the wandering albatross which forages right around the Southern Ocean. Other species and groups leave the Southern Ocean completely and move north across the southern hemisphere. This large-scale dispersal is most well known for the whales, which migrate north along the east coast of South America and the west coast of Africa. There is therefore a movement out of the region of a potentially significant, but unknown, proportion of the upper trophic level predators. This dispersal across the Scotia Sea, the Southern Ocean and southern hemisphere is crucial in understanding the operation of the food web. The effect is to reduce the upper trophic level demand for energy during the low production winter season, so that a significant proportion of the potential demand leaves the ecosystem during the winter (figure 8). More broadly, it also means that these

predators connect the dynamic operation of the Scotia Sea ecosystem with ocean ecosystems across the South Atlantic.

Improving our understanding of the spatial and temporal operation of Scotia Sea food webs requires a multi-scale approach. In particular, we need to understand how localized food webs, such as around the island areas of the Scotia Arc, interact as part of the larger scale Scotia Sea and Southern Ocean ecosystems. Understanding how physical and biological processes and interactions operating over different scales impact the regional food web will be crucial in analyses of the long-term dynamics of the ecosystem (figure 12).

6. ECOSYSTEM VARIABILITY AND LONG-TERM CHANGE

As we have noted, the major focus of studies aimed at understanding the factors generating interannual variability in Scotia Sea ecosystems has been on changes in the distribution and population dynamics of krill. However, the development of that focus has been generated in part through studies of the impact of variability on other trophic levels in the food web (Croxall *et al.* 1988; Priddle *et al.* 1988; Constable *et al.* 2003). Unique long-term monitoring datasets of the breeding biology and population size of upper trophic level predators across the Scotia Sea highlighted that there were years in which availability of krill was very low and predator breeding performance was significantly reduced (Boyd & Murray 2001; Fraser & Hofmann 2003). These impacts have been shown across a range of predators for which krill are a significant component of their diet, including the land-based breeding predators, such as macaroni penguins, gentoo penguins, Antarctic fur seals, black-browed and grey-headed albatrosses and Antarctic prions at South Georgia, and chinstrap and adelic penguins at Signy Island and on the Antarctic Peninsula (Priddle *et al.* 1988; Boyd & Murray 2001; Reid *et al.* 1997a, 2005). Pelagic predators are also affected as shown in the earliest observations of interannual variability, which were revealed by changes in the distribution and feeding of fin and blue whale species between years (Priddle *et al.* 1988 and references therein). Growth and condition indices of the mackerel icefish also show marked interannual changes (Everson *et al.* 1997, 2000b; Everson & Kock 2001). These changes have shown that predator performance can be used to monitor changes in krill availability (Boyd & Murray 2001; Reid & Croxall 2001). However, although indices of predator performance do identify periods of low krill abundance, they cannot resolve changes in abundance above approximately $25\text{--}30\text{ g m}^{-2}$ (Boyd & Murray 2001). Above this level, increases in density do not generate improved performance of predators (Reid *et al.* 2005). It is likely that above this concentration foraging constraints, competitive effects and other density-dependent factors dominate the dynamics. More recently, relationships have been revealed between the variation in predator performance and local and large-scale indices of physical variation (Forcada *et al.* 2006;

Trathan *et al.* 2006; Trathan *et al.* in press). At South Georgia, warm conditions in the previous season precede low reproductive success in penguins and seals (Forcada *et al.* 2006; Trathan *et al.* 2006; Trathan *et al.* in press). Detailed studies of krill population dynamics have shown that these relationships reflect changes in krill availability which are linked to changes in the ocean and sea ice regimes (Murphy *et al.* 1998b; Murphy & Reid 2001; Constable *et al.* 2003; Murphy *et al.* submitted).

The variability reveals shifts in food-web structure between years of high and low krill availability (figure 10). At South Georgia, when krill are scarce, the diet of the large numbers of seals, penguins and fish shifts. Fur seals consume mackerel icefish and myctophids, penguins consume fishes and amphipods, and icefish consume more amphipods (Croxall *et al.* 1999). Energy flows through these alternative pathways are insufficient to support the demand required to generate a large number of offspring, so we see failures in reproductive performance (figure 11; Croxall *et al.* 1988). However, the switching does allow the survival of adults and hence maintains the populations during years of low krill abundance. The switching therefore reveals a property of the food web that buffers the system response to variability. These weak pathways can appear unimportant in terms of energy flow compared to the main krill-related flows, but they are crucial in maintaining the system in the longer term. These alternative, weaker interaction pathways linking production to highest trophic level predators are likely to be crucial in determining the dynamics of the food web and its stability properties (Rooney *et al.* 2006).

There are also direct physical effects that modify the food-web operation when the region is dominated by warm or cold conditions. During colder, longer duration winters, the sea ice extends further north and more ice obligate species will occur across the Scotia Sea. Leopard seals (*Hydrurga leptonyx*) usually occur in ice-associated environments, but they are present around South Georgia in winter although their abundance varies between years. Jessopp *et al.* (2004) analysed a time-series of leopard seal occurrence from South Georgia. They found that in winters which are cooler and of longer duration, when winter sea ice extends further north, leopard seals occur in greater numbers at South Georgia, arriving earlier and leaving later. It is also likely that at these times, the general influence of ice-associated species will extend further north across the region. Of the predator species, the role of crabeater seals is likely to be particularly significant across the region at these times.

The physical and biological process interactions underpinning the structure of the food web make it sensitive to regional and hemisphere scale changes in climate (Trathan & Murphy 2002; Murphy *et al.* submitted). As we have noted, changes in this region not only reflect local processes, but are also linked to global scale processes. This has given us a short-term predictive capacity that will be tested over the coming years.

The rapid regional reductions in sea ice concentration and SST associated with increases in air temperature are generating major changes in the Scotia

Sea ecosystem (Murphy *et al.* 1995; Vaughan *et al.* 2003; Meredith & King 2005). Along the Antarctic Peninsula, shifts in the breeding distributions of penguins have been related to reduced ice extents (Fraser *et al.* 1992; Smith *et al.* 1999). Across the Scotia Sea, the abundance of krill has declined by between 50 and 80% over the last 30 years (Atkinson *et al.* 2004). These declines have been linked to changes in sea ice distribution and, as we have discussed, probably reflect regional variations in recruitment and dispersal (Murphy *et al.* 1998b). At South Georgia, there have also been significant changes in penguin and albatross populations (Reid & Croxall 2001; Barlow *et al.* 2002). However, although the changes have been linked to a general reduction in krill abundance over the last 20 years (Reid & Croxall 2001), other effects are also likely to be important. Although there have been clear regional changes in sea ice and ocean temperatures, the effects on the ecological system are complicated by the long-term dynamics of the food web (May 1979; May *et al.* 1979). The regional food web has been strongly perturbed over the last two centuries, as a result of harvesting of seals, whales, fishes and krill (Everson 1977; Murphy 1995). It has been suggested that the reductions in whales and seals may have generated a 'krill surplus' and that this will have been used by other groups of predators (Laws 1985). Although the extent to which this occurred has been debated, the exploitation will have had long-term consequences (Everson 1977; Croxall 1992; Murphy 1995). Populations of many of the exploited whale species have not recovered to pre-exploitation levels. In contrast, Antarctic fur seal populations have recovered rapidly from very low numbers (less than hundreds) in the first half of the twentieth century to around 2–3 million just around South Georgia, while their range has expanded across the Scotia Sea. These large-scale and rapid ecological changes are likely to be generating intense competition for krill (Barlow *et al.* 2002) and be a major factor influencing the dynamics of the food web. It is also worth noting that two species whose populations are expanding in the northern Scotia Sea, the Antarctic fur seal and king penguin, both exploit the myctophid *P. choriodon* as part of their diet. This myctophid is the major component of the diet of both predators in sub-Antarctic areas, outside the main krill zones. The success of these predator species may reflect a shifting competitive balance favouring species that can exploit prey other than krill.

Over the last 30 years, the Scotia Sea and surrounding regions have also been the major area of exploitation of living resources in the Southern Ocean (Everson 2001). It is currently the main area where krill are harvested and is the focus for the development of ecosystem-based approaches to the management of exploited fish and krill stocks (Constable *et al.* 2000). The long-term effects of the disturbance are unclear as we have little knowledge of the population size of the major predator species across the Scotia Sea (Everson 1977; Everson 1984). If we are to predict the long-term dynamics of key species in the ecosystem, we need much better information on the size of populations, their distribution and their dynamics across the Scotia Sea. We also need to consider the larger scale physical

processes affecting the region (such as ACC, ENSO and Southern Annular Mode variability), as well as the biological processes (such as krill transport processes and predator migration) and their interactions (figure 12; Murphy *et al.* 1988, 1998*b*, submitted; Constable *et al.* 2003; Fraser & Hofmann 2003; Ainley *et al.* 2005; see also Clarke *et al.* 2007*a,b*). This will be crucial in developing models of the response of the system to change and in developing long-term sustainable approaches to management of exploitation. This is a key region in global fisheries and an area where the potential for expansion of the demand of fisheries in the coming years is generating real concern, particularly among scientists involved in developing management procedures within the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). It is urgent that a comprehensive understanding of the operation of this regional ecosystem is developed. The Scotia Sea system is changing so quickly that in a short time regions in the north may not be influenced by polar waters and could undergo rapid changes in ecosystem structure.

7. CONCLUDING COMMENTS

The food web of the Scotia Sea is highly heterogeneous, widely distributed but dynamically connected. The fundamental determinant of the operation of the Scotia Sea ecosystem is the ocean circulation and its interaction with the Scotia Arc. The interaction of the flow with the regional topography generates a highly energetic environment of intense vertical and horizontal mixing. The ecosystem is therefore dominated by the flows of the major current systems (the ACC and the WSC), but it is also strongly influenced by the seasonality manifest most clearly by the advance of sea ice across the region during winter. This combination of mixing and seasonality generates a unique environment in the ACC which is high in both nutrients and chlorophyll *a*. The generation of megablooms of large diatoms is the result of the flow of the ACC across the Scotia Arc, affecting macro- and micro-nutrient concentrations. These blooms are a particularly consistent feature across the northern Scotia Sea towards the PF. This production fuels the food web, and krill are particularly reliant on the development of these large diatom blooms during spring. Krill are the major link between lower trophic level production and consumption by higher trophic level predators across the Scotia Sea. The regional food web, which has developed in this dispersive and seasonal context, is therefore highly distributed with production at higher trophic levels maintained by advective flows. The advective regime that disperses krill is therefore a fundamental factor in determining the structure of the whole ecosystem. Energy is generated in restricted regions in spring, particularly in areas of the retreating ice edge in the south. This energy is dispersed across the region and over the summer to be used in more northern regions in areas where large numbers of predators are concentrated during breeding.

The role of krill in the ecosystem is crucial, not only owing to their high abundance, but also because of a number of biological characteristics that make them a

major prey item for many of the predators. Krill are heterogeneously distributed over a wide range of scales from tens of metres to hundreds of kilometres. This makes them available as prey over very different scales, so that predators of very different size and foraging strategies can all exploit krill as food. This heterogeneity generates a highly spatially structured and variable ecosystem in which food-web connections involve complex spatial as well as temporal and trophic interactions. Relative to other species of zooplankton, krill attain a large maximum size (approx. 60 mm) and are long lived (5–7 years). This makes them available to large-bodied predators over extended periods, especially during periods of reduced primary production. This longevity is therefore important in allowing them to be dispersed across the Scotia Sea, surviving through winter and across low production regions, connecting regions of production with remote areas of consumption. Krill production and development are not limited to the shelf areas of the Scotia Sea and the central Scotia Sea area is a key region for overwintering of post-larval and larval krill. The interaction with the sea ice during winter and spring will be crucial in determining survival and dispersal during summer. The retreating ice edge across the Scotia Sea generates high productivity which drives the regional production of krill. The MIZ across the southern Scotia Sea in winter and spring is therefore a key habitat for krill, where production of both sea ice algae and phytoplankton will occur during winter and spring. The sea ice is therefore a link between the southern and northern Scotia Sea and between winter and summer.

The importance of krill to the higher trophic level predators means that any examination of Scotia Sea food webs requires not only descriptions of distribution, abundance and production, but also detailed knowledge of the life cycles of key species. The debate about whether advection is important in transporting krill has developed to focus on quantifying the relative roles of these different processes and the factors controlling their operation. This requires a specific focus on key stages of the life history of krill, particularly the larval and juvenile phases in oceanic waters during spring. Developing the models of krill requires detailed analyses of the operation of the life cycle. This will require coupled physical–biological models that involve not only the oceanic system but also the sea ice. Taking account of the interactions of krill at different scales will be important and will require a multi-scale modelling strategy that links behavioural and population processes with physical models which can resolve appropriate physical processes. In particular, this will require high-resolution shelf models embedded in lower resolution oceanic models.

To develop a wider understanding of the dynamics of the food web, the detailed life cycle operation of krill and other key species will need to be analysed in the context of the regional food-web interactions. Improving knowledge of winter processes across the Scotia Sea is crucial, as it is gaining more information on poorly studied species or groups such as the fishes (especially mesopelagics), squid, crabeater seals and whales. Developing studies of the importance of alternative

pathways involving groups such as copepods and myctophid fish will also be valuable. The importance of large-scale physical and biological interactions in determining the dynamics of the Scotia Sea ecosystem has also highlighted that any analyses and modelling must take account of the wider circumpolar and southern hemisphere atmospheric, oceanic and biospheric connections (figure 12). The Scotia Sea ecosystem is highly spatially and temporally variable, so future research effort aimed at understanding the effects of a changing environment must be focused on aspects of the food web that determine long-term behaviour of the system. To deal with the complexity, we need to focus effort on analyses of food-web structure that centre on the dominant energy flow pathway (through krill) and some of the alternative weaker pathways to higher predators. These links will be crucial in determining the operation of the food web and its long-term dynamics (Rooney *et al.* 2006).

In analysing the Scotia Sea ecosystem, the biggest challenge we face is to determine what has happened in the last two centuries of major ecological change. This requires detailed analyses of long-term datasets and the development of models that account for the spatial and temporal complexity of the ecosystem operation. This will allow the development of models to predict the responses of Southern Ocean ecosystems to change and procedures for the sustainable exploitation of resources. Developing such models is an urgent requirement because we know that there is rapid regional change occurring in the ocean and sea ice. There is clear evidence that there was a stepwise change in the physical regime of the Scotia Sea during the last century. This change has occurred simultaneously with the ecological changes driven by harvesting. Ecological systems are dynamic and particular states represent dynamic equilibria or transient effects, so they are always varying and changing. However, the rapid changes over the last 20–30 years on top of the changes that have occurred in the last two centuries may already be driving the Scotia Sea ecosystem into a very different operational state. It is likely that we will see major changes over the next 50 years, with the potential for extremely rapid and locally catastrophic changes in species distribution and abundance across the northern Scotia Sea.

8. SUMMARY

- (i) The ecosystem of the Scotia Sea and the Antarctic Peninsula region is undergoing some of the most rapid regional environmental and ecological change in any area of the ocean.
- (ii) Advection and the interaction of the circulation with the regional bathymetry generate intense mixing and are major factors determining the structure of the Scotia Sea ecosystem.
- (iii) Interactions of the circulation with the regional topography probably generate elevated concentrations of iron in regions of high macronutrients. This fuels regular blooms of extended duration (more than one month) across areas around the northern Scotia Sea. In the south, blooms are more irregular and associated with areas of melt water stabilization, following the spring retreat of the sea ice, or with shallow areas of the Scotia Arc. The variability of the sea ice system and its spring retreat results in highly variable productivity.
- (iv) Krill are a long-lived and key species in the food web, maintaining the majority of higher trophic level production. The dynamics of their population operates across the Scotia Sea and is linked to adjacent regions of the Weddell Sea and Antarctic Peninsula. Analyses of the operation of the Scotia Sea food web require a detailed understanding of the spatial and temporal dynamics of krill populations.
- (v) Krill occur in predictable densities across the Scotia Arc. High concentrations of krill also occur across the central oceanic regions of the Scotia Sea in areas seasonally covered by sea ice. The drifting MIZ of the central Scotia Sea is likely to favour ice-associated production, and its relatively low latitude for a polar region means that the light cycle will fuel production even during winter. These central sea ice-covered regions will be a key overwintering and spring habitat for krill, connecting areas further south with regions to the north.
- (vi) There is marked variability in the spatial structure of the food web across the Scotia Sea. There is also marked temporal variation in the connections within the food web. During winter many of the higher predators disperse or leave the region, reducing the energetic requirements at higher trophic levels.
- (vii) The food-web structure is maintained by horizontal advection of energy, for which krill are the key vector. Biological dispersals and active movements further maintain the regional food-web structure.
- (viii) There is clear evidence of top-down control effects of grazers on the primary production systems. Grazing and predatory impacts on the plankton affect the dynamics of the plankton community, and shifts between krill and copepods affect the regional production and phytoplankton community development.
- (ix) There is also evidence that top-down control is exerted by higher predators on macro-plankton in shelf regions. High local demand for krill reduces density and variance in the distribution of krill, which in turn affects plankton dynamics.
- (x) There is marked interannual variability in the operation of the Scotia Sea ecosystem that is driven by changes in regional sea ice and SST conditions that are linked to hemispheric-scale variations (linked to ENSO).
- (xi) These variations affect the population dynamics and dispersal of krill across the Scotia Sea during spring and summer. This generates a reduction in the recruitment of krill into northern regions during warm periods.
- (xii) The removal of the large seal and whale predators over the past two centuries has undoubtedly generated long-term top-down cascade effects and modified the local plankton

populations. These effects are probably continuing today and will affect the interpretation of the ecosystem responses to change.

- (xiii) There has been marked regional climate and oceanic change over the last 20 years. A rapid change occurred in the duration of winter sea ice across the Scotia Sea between the first and the second half of the last century.
- (xiv) A decline in krill abundance has been linked to changes in sea ice, but these changes are confounded by ecological shifts in the predators.
- (xv) The Scotia Sea ecosystem has many key features that make it ideal for examining the effects of harvesting and climate change on processes in large-scale oceanic ecosystems, from primary production through to the highest level predators.

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