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Advection, krill, and Antarctic marine ecosystems

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Abstract: Advective processes are recognized as being important in structuring and maintaining marine ecosystems. In the Southern Ocean advective effects are perhaps most clearly observed because the Antarctic Circumpolar Current (ACC) provides a connection between most parts of the system, including open ocean and continental shelf regions. The ACC also provides a mechanism for large-scale transport of plankton, such as Antarctic krill (*Euphausia superba* Dana), which is an important component of the Southern Ocean food web. This overview provides a summary of recent observational and modelling results that consider the importance of advection to the Southern Ocean ecosystem and, in particular, the role of advection in structuring the large-scale distribution of Antarctic krill. The results of these studies show that advection is a dominant process controlling Antarctic krill distribution and by inference an important process affecting overall structure and production of the Southern Ocean food web. The overview shows that quantifying the roles of advective and retentive physical processes, and population dynamic and behavioural biological processes in determining the regional and local distribution of krill and abundance will be an important research focus. Strategies for future Antarctic multidisciplinary research programmes that are focused on understanding advective processes at a circumpolar scale are suggested.

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Key words: Antarctic krill, advection, ecosystem, Southern Ocean, transport

Introduction

Processes of ocean circulation control the distribution and transport of heat, salt, and nutrients in the oceans, and the advective component of this flow has been identified as a major process controlling the distribution of biological material in marine systems (e.g. Margalef 1978, Mann & Lazier 1991). Advection has been explicitly identified in many modelling studies of primary production processes as a major factor structuring ocean ecosystems (e.g. Walsh 1975, Smith *et al*. 1983, Klein & Steele 1985, McGillilcuddy *et al*. 1998, Friedrichs & Hofmann 2001). Observational and modelling studies show that advection disperses phytoplankton and zooplankton away from their main centres of production, thereby extending the regions of enhanced concentrations and distributing these populations over wider geographical ranges. Thus, oceanic biological distributions may be viewed as a balance between processes of production, dispersal, and loss.

Advection is known to be important in the maintenance of zooplankton populations through movement of larvae to distant locations where they then recruit to remote populations (e.g. Werner *et al*. 1993, 1996, Heath *et al*. 1998*)*, as well as in dispersal of adult phases (e.g. Wroblewski 1982). Such dispersal generates a space and time separation for biological processes by moving zooplankton from centres of production to areas where they die or are consumed but do not necessarily reproduce. In recent years extensive studies have focused on *Calanus finmarchicus* (Gunnerus), which is a key zooplankton species of the North Atlantic Ocean. Studies of the distribution of this species have shown that ocean currents are important in maintaining individual populations (Backhaus *et al.* 1994, Bryant *et al.* 1998, Miller *et al*. 1998, Durbin *et al.* 2000, 2003, Gaard 2000, Gaard & Hansen 2000, Harms *et al.* 2000, Pedersen *et al.* 2000, Lewis *et al.* 2001, Edvardsen *et al.* 2003) and in maintaining connections between populations (Gislason *et al.* 2000, Heath *et al.* 2000a, 2000b, Durbin *et al.* 2003). Moreover, advective processes are considered to be important in linking sub-decadal variation in North Atlantic atmospheric processes reflected in the North Atlantic Oscillation (NAO) with changes in *C. finmarchicus* abundance in continental shelf areas in the Northwest Atlantic (Greene & Pershing 2000, Greene *et al.* 2003). An implication is that changes in *C. finmarchicus* populations at trans-Atlantic scales and long time scales are likely to be driven primarily by changes in advective processes (Greene *et al.* 2003). Advective processes have also been identified as important in generating observed distributions of other calanoid copepod species, such as *C. agulhensis* DeDecker populations on the Agulhas Bank (Huggett & Richardson 2000) and *C. australis* Brodsky populations in Patagonian and New Zealand continental shelf waters (Sabatini *et al.* 2000).

Zooplankton population distribution studies frequently consider advection as an important process in the dispersal of individuals. However, although advection is often mentioned as an important process affecting plankton distributions most studies that encompass a range of trophic levels tend to assume homogeneous conditions. Such an assumption does not include potential effects of advective processes, which have major implications for the dynamics of marine systems and are crucial in determining space and time variability in food web structure (Murphy 1995).

The Southern Ocean provides an environment where the effects of advective controls can be considered at a circumpolar scale because the Antarctic Circumpolar Current (ACC) provides a connection for most of the system. Unlike other large-scale ocean currents, such as the Gulf Stream, across its range the ACC encompasses marine ecosystems that have similar characteristics, although there is heterogeneity in the exact form of the ecosystem in any area. This provides an opportunity to observe the effects of advection without the compounding effect of vastly different climates and ecosystems. An assumption is that the observed heterogeneity of the circum-Antarctic ecosystem arises in part from variability generated and/or maintained by advective processes. Much of the ecosystem is centred on one species, Antarctic krill (*Euphausia superba* Dana) which occurs throughout much of the Southern Ocean. Other groups of zooplankton, such as copepods and salps, may be more important than krill in terms of abundance, production and wet weight for certain locations and times (e.g. Atkinson *et al*. 1996, Atkinson & Sinclair 2000, Pakhomov *et al*. 2002). However, understanding the influence of advective processes on the distribution and abundance of Antarctic krill will give valuable insight into the potential effects of a changing physical environment on the operation of a large-scale marine ecosystem.

The main objective of this study is to describe aspects of the role of advection in the generation of Antarctic krill distributions. We do not review all aspects of the biology of Antarctic krill but rather highlight some of the major biological and physical processes and interactions that are important in determining the distribution of krill.

Circumpolar ecosystems: controls on krill distributions

Ecosystem characteristics

Antarctic krill is a key component of Southern Ocean food webs, being the major prey item in the diet of many of the higher trophic level predators, and supporting large populations of air-breathing vertebrate predators, such as penguins, seals, whales, and sea birds. However, the ecosystem is not homogeneous as there is marked spatial and temporal variation in its structure. So, for example, the major species of higher trophic level predators in the food web, the major consumers of krill, change with latitude. At higher latitudes ice-obligate predators, such as crabeater seals and Adélie penguins (Laws 1984, 1985), dominate, while at lower latitudes Antarctic fur seals (Doidge *et al.* 1986) and chinstrap penguins or macaroni penguins can dominate (Laws 1985).

As well as variation in the higher trophic level food web structure, the importance and complexity of the lower trophic levels is now being increasingly recognized (e.g. Brown & Landry 2001). Microbial components have long been known to be important in Southern Ocean ecosystems, particularly in carbon and nutrient cycles (Hall & Safi 2001, Dubischar & Bathmann 2002, Hense *et al.* 2003, Froneman & Bernard 2004). In some regions zooplankton species other than Antarctic krill are the dominant grazers (Dubischar & Bathmann 2002). Salps are considered to be major grazers of primary production in the warmer waters mainly to the north of the seasonal pack-ice zone (Pakhomov *et al.* 2002). Further south, in the more permanent pack-ice zone, a different species of krill, *E. crystalorophias* Holt & Tattershall, can be the dominant euphausid (Brierley & Thomas 2002). Thus, there are spatial variations in the form of the food web that characterizes the Southern Ocean.

Even within areas where Antarctic krill are considered to be dominant, the characteristics of the food web can show marked variation (Atkinson *et al*. 2001). Krill are known to feed on a range of food types (Kawaguchi *et al*. 1986, Daly 1990, Huntley *et al*. 1994, Atkinson & Snÿder 1997, Pakhomov *et al*. 1997) and pathways that connect higher

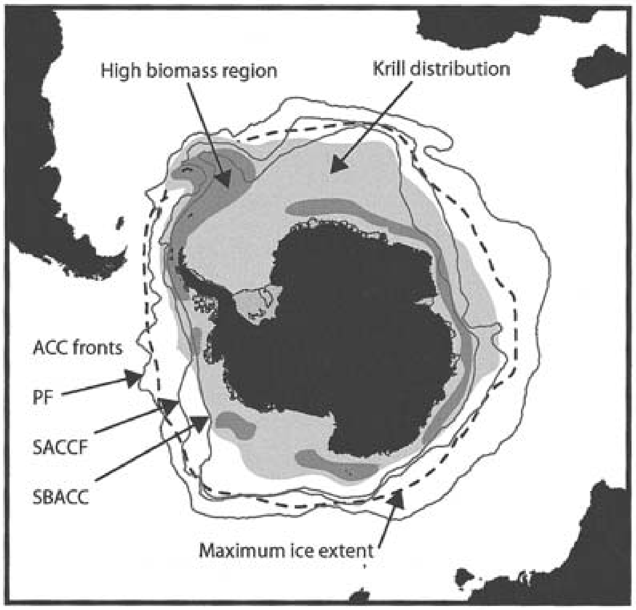

Fig. 1. Circumpolar distribution of Antarctic krill constructed from data presented in Marr (1962), Everson & Miller (1994), Nicol & Endo (1997) and Everson (2000). The climatological locations of the fronts associated with the Antarctic Circumpolar Current (ACC) determined by Orsi *et al*. (1995) are shown and are identified as: PF = Polar Front, SACCF = Southern Antarctic Circumpolar Current Front, and SBACC = Southern Boundary Antarctic Circumpolar Current.

and lower trophic levels have been identified that are important for times and locations when Antarctic krill are not dominant or present. However, while these other pathways are important, the majority of the energy flow to the higher trophic levels, over much of the Antarctic, is through Antarctic krill (Croxall *et al*. 1988, Ainley & DeMaster 1990, Atkinson *et al*. 2001). Thus, understanding the factors that affect the distribution and availability of Antarctic krill has implications for the entire Southern Ocean ecosystem.

Antarctic krill have a circumpolar distribution (Fig. 1), but one that is asymmetric in terms of areas of the highest concentration. High densities of krill occur in shelf areas, but they also occur in oceanic regions within the ACC, particularly across the Scotia Sea (Miller & Hampton 1989). The overall distribution does not show any simple relationship with the fronts that make up the ACC, with winter sea ice distribution, or with the maximum extent of winter sea ice (Fig. 1). Thus, the question arises of what is controlling the large-scale distribution of Antarctic krill?

In any one place the abundance of Antarctic krill is a function of production and survival as well as retention and export. Post-larval krill can swim, undergo diurnal vertical migrations and form swarms, all of which affect their small-scale movement. There are also indications that Antarctic krill undertake directed migrations across the continental shelf during particular times of the year (Siegel 1988). Thus, behaviour is a potentially important factor determining large-scale movement of Antarctic krill (see Murphy *et al*. (in press) for a discussion). However, there is no evidence that Antarctic krill can undertake directed migration against the open ocean currents of the ACC for extended periods. Such movement would require high energy expenditure for long periods and directed movement in relation to some other environmental cue. Movements of adults, such as vertical migrations, may affect the absolute trajectory, but they will generally be transported with the major ocean flows (Marr 1962, Mackintosh 1973, Everson & Murphy 1987, Murphy *et al*. in press). Moreover, the larvae and juvenile stages have limited swimming abilities so they will be transported as mainly passive particles. For some areas of the ACC, current speeds may be sufficiently reduced and the direction so irregular that directed swimming will be important. However, in open ocean regions away from the continental shelf, advection will be a major factor determining the distribution of krill.

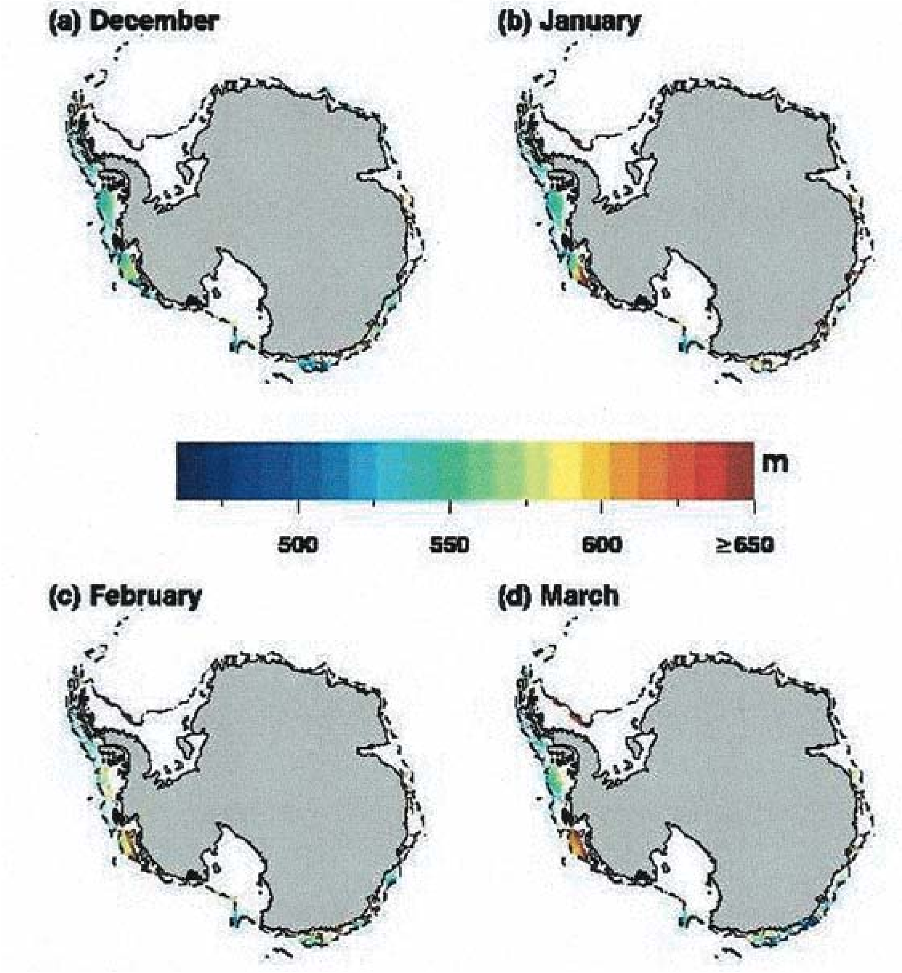

Fig. 2. Simulated circumpolar distribution of locations that allow hatching of Antarctic krill embryos above the bottom for areas inside the 1000-m isobath for: **a.** December, **b.** January, **c.** February, and **d.** March. The 1000-m isobath is indicated by the dashed line. Figure reproduced from Hofmann & Hüsrevoğlu (2003).

The processes of production depend on suitable spawning habitats, which define the centres from which the larger distribution develops. Environmental factors affecting the development and survival of individuals in particular year classes include water mass structure and sea ice variations. Factors affecting dispersal are local retention, behavioural patterns, and large-scale advective and migration effects. Aspects of these key processes and factors that determine the large-scale distribution of Antarctic krill are considered in the sections that follow.

Spawning habitat

Antarctic krill embryos sink after release in the upper water column, hatch between 500 m and 1000 m, after which the larvae return to the sea surface (Fraser 1936, Marr 1962, Hempel 1979, Hempel *et al*. 1979, Hempel & Hempel 1986). Completion of the descent-ascent cycle takes about 15 to 30 days depending on ambient water temperature. The larvae begin feeding after reaching the calyptopis stage, which occurs about 2 to 8 days post-hatch and usually prior to reaching the sea surface. Thus, the carbon reserves in the embryo are all that is available to sustain the larva through much of the upward ascent. Modelling studies (Hofmann *et al*. 1992) show that the presence of Circumpolar Deep Water (CDW), which is a warm salty water mass found below 200–400 m throughout the Southern Ocean (Sievers & Nowlin 1984, Whitworth *et al*. 1998), is important in controlling the embryo hatching depth and the larval ascent rate. When the embryo sinks into CDW its rate of development is accelerated by the warmer temperatures, resulting in hatching at shallower depths and shorter larval ascent distances. Larval ascent rates also increase in warmer water, which shortens the ascent time.

The descent portion of the Antarctic krill life cycle provides one of the first constraints in its life history because failure to complete this results in lack of recruitment of new individuals to existing populations. This in turn affects the overall population distribution. Many of the regions where Antarctic krill are known to spawn are in continental shelf areas, especially in the vicinity of the Antarctic Peninsula (Marr 1962). Water depth over much of the Antarctic continental shelf is 200–500 m which is shallower than the embryo hatching depth, especially where CDW is not present. Thus, spawning in some shelf areas around the Antarctic may not result in successful recruitment and could provide an explanation for some of the asymmetry observed in the large-scale distribution of Antarctic krill (Fig. 1).

The circumpolar success or failure of the Antarctic krill descent-ascent cycle was examined in a modelling study (Hofmann & Hüsrevoğlu 2003). The circumpolar distribution of locations where Antarctic krill embryos hatch above the bottom, for regions shallower than 1000 m (Fig. 2), shows that not all parts of the Antarctic are equally able to support completion of the descent cycle. The continental shelf regions where successful hatching does occur, such as along much of the west Antarctic Peninsula, are characterized by on-shelf movement of CDW below 200 m (e.g. Smith *et al*. 1999). In these areas a krill embryo either hatches above the bottom or spends a limited amount of time on the bottom prior to hatching (Hofmann & Hüsrevoğlu 2003). The implication of the hatching distribution is that there are a limited number of continental shelf regions that support the production of new individuals that can recruit to the Antarctic krill population. For regions deeper than 1000 m, hatching always occurs prior to the embryo reaching the bottom.

The regions where CDW moves onto the Antarctic continental shelf are characterized by phytoplankton assemblages that are dominated by diatoms, a preferred food for Antarctic krill, and by higher primary production throughout the year (Prézelin *et al*. 2000, 2004). Thus, these regions may partially explain the asymmetry that is observed in the larger scale concentrations of Antarctic krill; concentrations near spawning regions and areas of dependable food supply would be higher. However, the asymmetry in regions of spawning success alone does not fully explain the larger circum-Antarctic distribution. Antarctic krill still need to be dispersed from these regions.

Circulation characteristics

The Antarctic continental shelf regions identified as successful spawning habitats (Fig. 2) are regions where the Southern Boundary of the Antarctic Circumpolar Current Front (SBACC), which is the southernmost front associated with the ACC (Orsi *et al*. 1995), is near the shelf edge (Fig. 1) and where the Antarctic Slope Front is absent (Jacobs 1991, Whitworth *et al*. 1998). In these regions the southern portion of the ACC flows along the outer edge of the continental shelf and has a direct influence on the shelf circulation. Antarctic krill are known to migrate offshore to spawn in some areas (Siegel 1988). The reasons for this are unknown but it may be to allow embryos to be released into deeper water and into water with CDW present at depth. Interactions of the CDW with the regional bathymetry may result in retention and return of larval krill onto the shelf and into more inshore regions. Release of embryos at the outer shelf edge during a time when the SBACC is present could also result in transport of the embryo and/or larva away from the spawning region. The SBACC meanders along the outer Antarctic continental shelf (Klinck 1998) so the interaction between timing of spawning and the meander frequency of the SBACC is important in determining the percentage of the spawned embryos that are transported downstream. If Antarctic krill are picked up from the outer continental shelf by the SBACC the result would be a plume that extends downstream from the source region. The large-scale Antarctic krill distribution (Fig. 1) does suggest a plume extending downstream from the Antarctic Peninsula region, across the Scotia Sea, and towards South Georgia (Marr 1962). This area is however, also a region with complex bathymetry, the Scotia Arc, which is a key influence on regional ocean circulation and hence probably contributes to producing the observed krill distribution (Murphy *et al*. in press).

The band of higher concentration of Antarctic krill throughout the Indian Ocean is a region where the SBACC is near the continental shelf edge (Fig. 1). Simulations show several regions of successful completion of the descent-ascent cycle that form a narrow band along the 1000 m isobath throughout the Indian Ocean sector (see fig. 4 in Hofmann & Hüsrevoğlu 2003). Successful completion of the descent-ascent cycle at depths shallower than 1000 m is minimal (Fig. 2). The large-scale coherent region of high Antarctic krill concentration throughout the Indian Ocean region may result from advection produced by the presence of the SBACC interacting with regions of successful krill reproduction that occur at smaller spatial scales.

The time-scales and pathways of transport of particles from near the Antarctic Peninsula and across to South Georgia were examined with Lagrangian particle tracking models (Hofmann *et al*. 1998, Murphy *et al*. 1998). These studies showed the potential for direct pathways of flow from the Antarctic Peninsula to South Georgia and indicated that it would take 2–6 months for particles to be moved across the Scotia Sea. The ecologically important time scales for questions relating to possible population connection are those associated with the high surface current speeds in the ACC. The studies found that transport times were most rapid in areas associated with the (Southern Antarctic Circumpolar Current Front (SACCF), where the enhanced flows moved particles rapidly across the Scotia Sea to the South Georgia region (Hofmann *et al*. 1998). The SACCF retroflects around the eastern end of South Georgia (Fig. 1) and the suggestion from the Lagrangian particle trajectories in which the frontal flows were resolved was that the front was important in bringing krill into the South Georgia region (Hofmann *et al*. 1998).

Food supply and sea ice variations

Transporting Antarctic krill downstream from a source region is only a start at developing a large-scale distribution. For the distribution to persist the krill need to survive and grow, which requires food. Krill spawning occurs between December and March (Spiridonov 1995) and late spawning results in individuals that are entering the system at the start of autumn when light levels are decreasing and overall primary production is declining. Open ocean regions, such as the Scotia Sea, are characterized by low background levels of chlorophyll (Comiso *et al*. 1993). Transport across these regions during and subsequent to the spawning season would place larval and juvenile krill in a low food environment during a time when food levels are declining. Thus, while transport from the west Antarctic Peninsula to South Georgia, for example, is possible, survival and viability of the krill for the 2–6 months required for transit is not guaranteed. However, Antarctic krill are omnivores and feed on zooplankton (Kawaguchi *et al*. 1986, Huntley *et al*. 1994), sea ice algae (Marschall 1988, Daly &

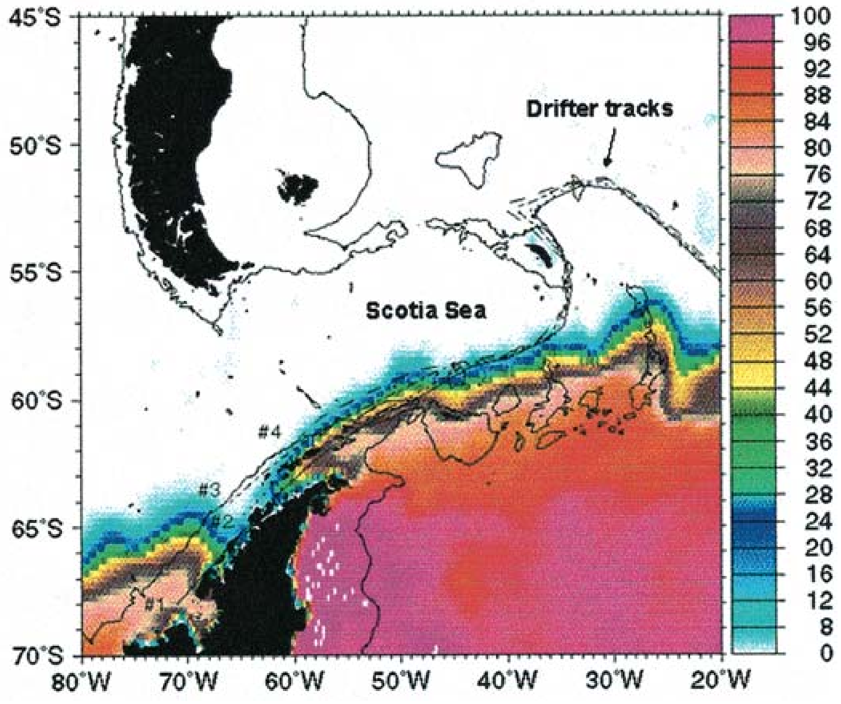

Fig. 3. Special Sensor Microwave Radiometer-derived sea ice concentration (% coverage) for the Antarctic Peninsula and Scotia Sea for July 1985. The four trajectories show the simulated path followed by particles released in a flow field constructed from historical hydrographic data from the region as described in Hofmann *et al*. (1998). Figure reproduced from Fach *et al*. (2002).

Macaulay 1991), and detrital material (Holm-Hansen & Huntley 1984, Kawaguchi *et al*. 1986, Daly 1990) in addition to pelagic phytoplankton.

The importance of alternative food supplies to Antarctic krill during transport between the Antarctic Peninsula and South Georgia was examined with Lagrangian modelling studies that included circulation, food and krill growth components (Fach *et al*. 2002, Fach 2003). These simulations showed that pelagic phytoplankton concentrations were not sufficient to support growth of Antarctic krill during transport. The inclusion of a supplemental food supply, such as sea ice algae, which is available during part of the transport time, did not significantly alter this result. The availability of mesoscale patches of high chlorophyll concentration and hetrotrophic and detrial food sources were found to be important for survival of all krill stages undergoing transport (Fach *et al*. 2002, Fach 2003).

The trajectories of krill that are transported from the Antarctic Peninsula region to South Georgia place krill under or near sea ice as it develops northward in the autumn and winter (Fig. 3). This then provides another potential scenario for transport in which Antarctic krill entering the eastward flowing waters off the Antarctic Peninsula in austral summer overwinter under sea ice in the Scotia Sea. This would allow the krill to spend the winter in a potentially better food environment in which there is access to sea ice algae and the planktonic community associated with sea ice. Transport continues during winter in association with the drifting sea ice and ocean currents. The following austral spring, as the sea ice recedes, krill are transported towards South Georgia. Simulations based on this two-stage transport scenario (Fach *et al*. 2002, Fach 2003) show that ovewintering in a sea ice environment produces krill that are 22 to 42 mm (1+ and 2+ krill) when arriving at South Georgia the next spring, which is similar to the observed dominant sizes (Murphy *et al*. 1998, Watkins *et al.* 1999). Thus, variations in winter sea ice extent can interact with krill transport pathways to potentially modify growth and survival of Antarctic krill (Murphy *et al.* 1998), which in turn can modify the large-scale distribution (Murphy *et al*. 1998).

The degree of association of Antarctic krill with the surface sea ice appears to vary. In some areas the krill are thought to be closely associated with the sea ice, while elsewhere they have been observed in the water column beneath the ice and in other regions are found close to the sea bed (Marschall 1988, Daly 1990, Gutt & Siegel 1994). The sea ice movement is driven by the surface wind field (Washington & Parkinson 1986) so that krill associated with the sea ice will be transported into different regions compared to those in the water column. This differential movement of the water column and sea ice associated with variation in the degree of association of krill with the sea ice

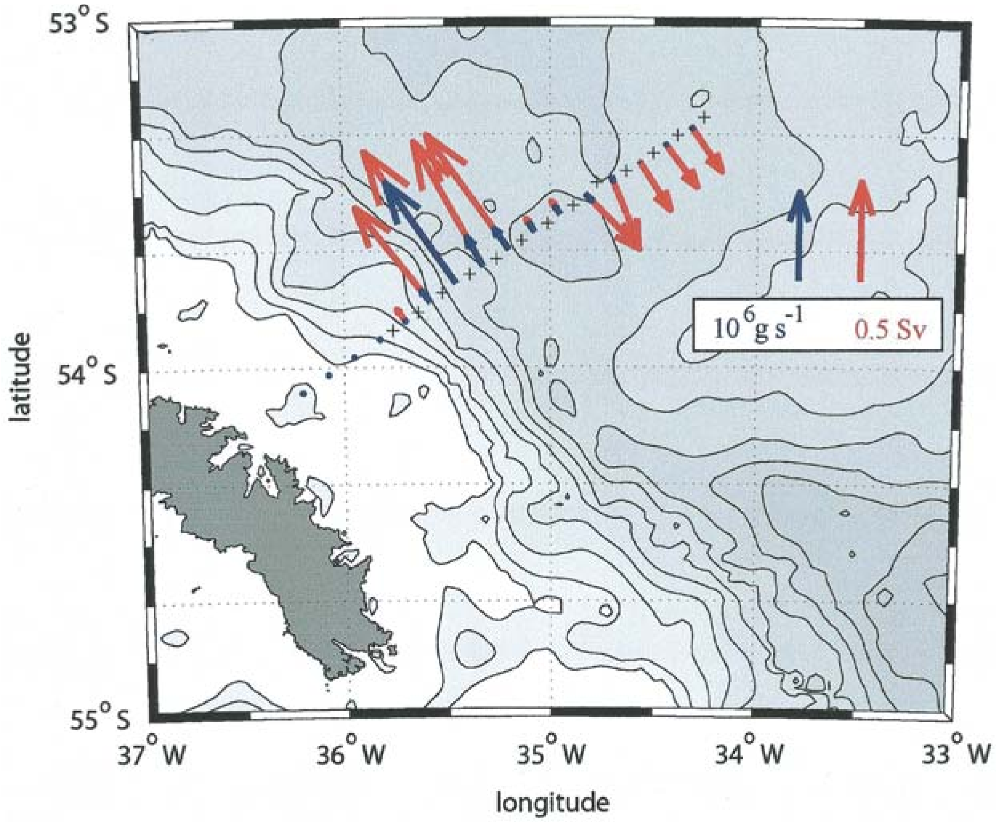

Fig. 4. Magnitude and direction of circulation and zooplankton biomass flux obtained from measurements near South Georgia. Ocean current data and acoustically-derived biomass data were combined to estimate the potential transport flux of krill orthogonal to each section of the transect in the upper 250 m. The water volume transport (Sv, 1 Sv = 10^6 m^3 s^{-1}) between each station pair is shown by the red arrows and the blue arrows show the associated krill flux (10^6 g s^{-1}). Reproduced from Murphy *et al.* (2004).

means that the resultant over-winter transport trajectories may also be highly variable.

Observations and modelling of krill transport

Field studies were recently undertaken with the objective of testing the hypothesis that the SACCF is the primary means by which Antarctic krill are brought into the South Georgia region. These studies consisted of concurrent measurements of circulation and krill biomass distribution in January 2001 for a region on the north-east side of South Georgia that includes the SACCF retroflection (Trathan *et al.* 2000). The circulation measurements (Fig. 4) revealed enhanced flow rates along the north coast of South Georgia, which are associated with the westward flow of the SACCF (Meredith *et al.* 2003). Combined analyses of water volume transports and krill biomass were used to derive estimates of krill flux through this region. The study showed that during January 2001 a large amount of zooplankton, which were mainly krill, was associated with the SACCF, which generated an estimate of the krill flux, which was large and to the west along the coast of South Georgia (Fig. 4; Murphy *et al.* 2004). A few days after the first study, a second less robust estimate was derived and indicated that the zooplankton biomass was much lower than the first estimate, showing that the flux of krill was variable.

The enhanced zooplankton biomass in the SACCF was associated with enhanced chlorophyll *a* and copepod concentrations and reduced nutrient concentrations (Ward *et al.* 2002). The copepods in the frontal region were also further advanced in their seasonal development from their over-winter state compared to those outside of the front. Analyses of the time-scales of development of the ecosystem indicated that it would have taken 3–4 months to generate the observed conditions from a winter situation. Studies based on Lagrangian particle tracking model simulations that were designed to determine the origin of the zooplankton associated with the SACCF showed that the observed community originated in the central southern Scotia Sea. Analyses of the sea ice conditions 3–4 months prior to the study also showed that sea ice covered the southern Scotia Sea (Murphy *et al*. in press). The modelling studies indicate, therefore, that the observed krill being transported around South Georgia during January 2001 were probably associated with the sea ice covered regions further south during the late winter to early spring period (Murphy *et al*. 2004). These krill were then transported north across the Scotia Sea to South Georgia arriving during the summer. These modelling studies are consistent with the modelling results presented in Fach *et al*. (2002) and Fach (2003) that indicated the importance of the association of krill during winter with the sea ice covered regions in the southern Scotia Sea.

Antarctic krill are vulnerable to predation throughout transport, but especially while near coastal and island regions such as South Georgia, where large land-based breeding predator colonies occur during the summer. Estimates of local krill growth rates indicate that it may be possible to maintain the predator demand through local production. However, it is recognized that the krill around South Georgia are part of a wider stock so at some periods through the year krill will be input into the region to maintain the stock. As noted previously, krill in the off-shore ocean currents are also likely to have been generated in more southern regions of the Scotia Sea. To be available to the predators the krill must either be brought in close onto the South Georgia shelf or the predators must forage off-shelf. Although the detailed circulation and cross-shelf exchange processes around South Georgia are not well understood, drifter analyses do show that particles tracking across the Scotia Sea can be transferred onto the shelf. Satellite tracking has also shown that the predators do forage in off-shelf regions. These studies indicate that krill being transported in off-shelf regions further east will be available to predators foraging on the north coast, potentially in on-shelf as well as off-shelf regions further west. Thus, the through-flow rates associated with the SACCF can be compared with the regional food web flows (Murphy *et al*. 2004). These calculations showed that the inflow of zooplankton associated with the SACCF was very large compared to the estimated requirements for krill by local predators. The study also showed that the through flows are an important aspect of the regional food-web, both in maintenance of the local krill stocks, but also in the overall regional abundance of krill. The study further highlighted the need for an improved understanding of the detailed circulation patterns around South Georgia. In particular, improved understanding is required of the potential mechanisms and extent of any transfer of krill from off-shelf regions further south and east into areas further west where the predator demand for prey appears to be greatest.

Predator breeding performance is enhanced during periods of high krill abundance, and these will occur when the regional inflow and flux is high. Modelling studies also indicate that there is enhanced input of krill into the South Georgia region during cold conditions. These periodic inputs then sustain the local system until the next major input, which might be two or three years after the last recruitment event (Murphy *et al.* 1998, Murphy & Reid 2001). This observed interannual variability means that the input into shelf regions and flux in the currents around South Georgia will be variable both within and between years (see also Murphy *et al*. in press).

Recently, Murphy *et al.* (in press) extended the South Georgia observations and krill transport modelling analyses to examine the within-season advection of krill in areas of high abundance observed during summer in the Scotia Sea. These analyses, which were based on Lagrangian modelling studies, highlighted that the transport trajectories that led to

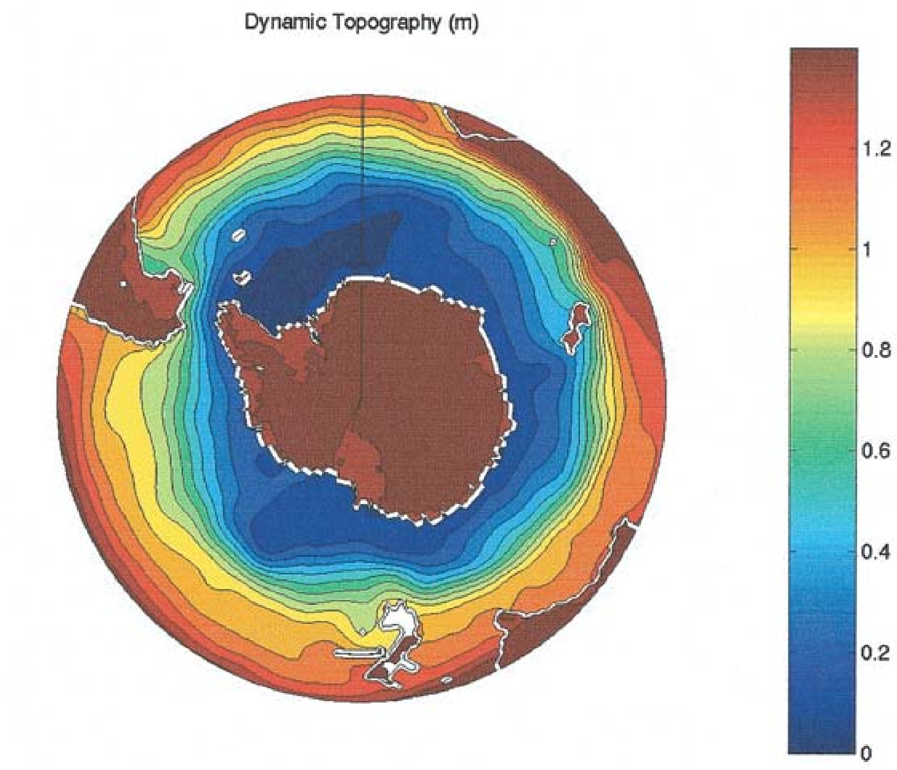

Fig. 5. Dynamic topography (0/1000 m) constructed from historical hydrographic data that are available in the World Ocean Atlas 2001 (Conkright *et al*. 2002).

the development of the observed high krill biomass regions originated in ice-covered regions in the southern Scotia Sea a few months previously. These studies utilized output from the eddy-permitting Ocean Circulation and Climate Advanced Modelling (OCCAM) Project (Webb 1996, Webb *et al*. 1998), which resolves the high surface current speeds of the ACC. Murphy *et al*. (in press) also noted that krill in these areas could have been produced across much of the southern Scotia Sea and Antarctic Peninsula region, so that the association with the sea ice complicated the determination of the point of origin. The horizontal resolution of the OCCAM simulations is 0.25° x 0.25° with 36 vertical levels ranging in thickness from 20 m at the surface to 255 m at depth. The model therefore resolves both the areas of rapid flow at the surface associated with the frontal regions of the Scotia Sea, as well as the lower velocity flows in areas away from the fronts. The model output is therefore useful not only for examining the ecological time-scales of population connection, but also for considering the broader temporal and spatial development of the distribution of krill biomass during transport across the Scotia Sea. Using time-varying output from OCCAM, Eulerian analyses of the development of the biomass distribution across the Scotia Sea were undertaken by Murphy *et al*. (in press). The Eulerian analyses indicated that, although much of the krill would be transported near to South Georgia, much of the observed biomass was not associated with the SACCF and would have been transported to the east in the Scotia Sea. These krill would probably have been under the sea ice in the south-eastern Scotia Sea, or in the northern Weddell Sea, a few months prior to the observations and would have exited the Scotia Sea mainly to the east around the South Sandwich Islands. The study highlighted the potential complexity of the pathways of flow and associations with the sea ice. The potential variability of the pathways of transport has also been highlighted recently in Lagrangian particle tracking studies where the flow field has been driven by seasonally varying wind fields. These have shown the potential for large variations in the numbers of particles being transported across the Scotia Sea and reaching South Georgia (Thorpe *et al.* 2004).

Discussion and summary

Large-scale advective effects

A comparison of the general distribution of krill (Fig. 1) with a map of the circumpolar dynamic topography (Fig. 5) highlights some associations between the two distributions. In the Antarctic Peninsula and Scotia Sea regions the distribution of krill is deflected northwards in association with the northward shift of the flow of the ACC after it flows through Drake Passage. The relatively zonal flow of the ACC is reflected in the overall krill distribution. The maximum speeds associated with the fronts of the ACC, 0.4 to 0.5 m s^{-1}, are such that krill in the ACC could, in theory, be transported around the Antarctic during their lifetime. In reality, outside of the frontal regions, where krill often occur, much of the ACC flow is too slow for individual krill to circumnavigate the Southern Ocean in a lifetime. However, the potential exists for low level continuous exchange of krill around the continent over long time scales and limited genetic studies of Antarctic krill suggest that this may happen (Fevolden & Ayala 1981, Fevolden & Schneppenheim 1988, 1989, MacDonald *et al*. 1986), although there is also the suggestion of localized populations (Zane *et al*. 1998). Studies that are focused on understanding the extent of the genetic exchange or genetic isolation of Antarctic krill populations provide one approach for further investigation of the role of advective transport in structuring the large-scale population distribution.

Around much of the Antarctic the major krill concentrations appear to be near the continental shelf regions and in areas to the south of the SBACC. In many of these regions the krill will be in the westward flowing Antarctic Coastal Current. This association, and the many localized gyres that overlie portions of the Antarctic continental shelf (e.g. Smith *et al*. 1999), imply the existence of relatively complex pathways of connection between the Antarctic krill populations of the Southern Ocean. This may generate very much more complex connections, exchange rates and time-scales for transfer between populations than would be expected by simple views of the eastward flow of the ACC (Thorpe personal communication 2003).

Interannual and sub-decadal fluctuations in krill abundance are a major feature of Southern Ocean ecosystems and may be the result of fluctuations in the dynamics of local populations. However, many regions within the krill population are dependent on immigration for maintenance so local fluctuations may be the result of variations in spawning and recruitment success upstream of the local stock or due to variations in ocean circulation affecting the krill transport (Priddle *et al*. 1988, Murphy *et al*. 1998). Interannual and sub-decadal variations in regional environments in the Southern Ocean have also been linked to circumpolar and Southern Hemisphere processes, such as the El Niño–Southern Oscillation (ENSO) and the Antarctic Circumpolar Wave (Murphy *et al*. 1995, White & Peterson 1996, Trathan & Murphy 2002). Further understanding the factors determining variation in advective processes and the effects on the distribution and abundance of Antarctic krill will be crucial in examining the impacts of climate variations in regional ecosystems.

Potential climate change effects

The current generation of climate models indicate uncertainty in what changes may occur in the Southern Ocean in response to climate variability and that there may be regional trends in cooling or warming (Anisimov *et al.* 2001). Even with this uncertainty, it is possible to provide some speculations on the potential effects of some of these anticipated changes on the large-scale Antarctic krill distribution.

Temperature changes have many obvious potential biological and environmental effects that range from changes in krill growth rate to changes in the heat capacity of the ocean. Changes in physiological processes affect survival and recruitment as can changes in environmental structure. Also, air and water temperature changes will modify sea ice extent and concentration. Sea ice is an important part of the life history of Antarctic krill. Larval Antarctic krill are dependent on sea ice (Daly 1990) and a reduction in sea ice extent removes habitat that these animals need for survival and subsequent recruitment to the population. Extensive and long duration sea ice conditions favour krill maturation and dense winter sea ice promotes early female gonadal development and spawning (Siegel & Loeb 1995). The early seasonal maturity development and spawning can result in high recruitment the following year through increased spawning success and larval survival (Siegel & Loeb 1995). The dependence of many other organisms on krill implies that changes in sea ice can potentially alter the production and structure of the Southern Ocean food web.

Changes in surface heating and atmospheric forcing could potentially affect the speed of the ACC, the location of the ACC fronts, or the distribution of CDW. The latter effect could potentially alter the distribution of viable spawning habitat for Antarctic krill. An interesting potential feedback is that reduced heat input to the continental shelf could result in more sea ice, which may mitigate changes in spawning success by providing more habitat, and a higher survivorship, for larval krill. Small changes in the location of the ACC fronts, the SACCF in particular, can alter potential source areas for Antarctic krill and affect the ability of the current system to transport krill to South Georgia (Fach 2003). Thus, climate change scenarios that produce a persistent shift in location of a few tens of kilometres in the ACC fronts could result in extinction of those local Antarctic krill populations that depend on immigration of new individuals for survival, such as those at South Georgia. This in turn would potentially result in severe reductions or local extinctions in the higher trophic level predators that depend on Antarctic krill. The potential effects of the many possible climate change scenarios on the large scale distribution of Antarctic krill are therefore varied, with the potential for both increases and decreases in local abundance. To improve our capability to predict the effects of change on the distribution of Antarctic krill, much better regional climate change scenarios are needed. The generation of such scenarios requires the development of improved coupled ocean circulation-sea ice models that are of a sufficiently high resolution to adequately represent the processes of shelf-deep ocean interaction that are crucial in the life cycle of Antarctic krill.

Future studies

Advective connections occur at circumpolar, regional and local scales in the Southern Ocean. The dependence of Antarctic krill populations at South Georgia on upstream inputs that come from the west Antarctic Peninsula and Weddell Sea regions is one example of these connections. Spatial and temporal differences in the distribution of juveniles, adults and where spawning occurs is well documented for many marine species (e.g. Cushing 1995) and advective transport is part of the processes structuring these distributions. The circum-polar nature of the Antarctic system allows advective transport to develop over large spatial scales and hence be a potentially primary control on the productivity in this system. The degree to which processes other than advective transport influence the observed Antarctic krill distribution is relatively unknown (Marr 1962, Miller & Hampton 1989, Nicol 2003, Murphy *et al*. 2004). Future studies are needed to determine how interactions at particular scales, such as vertical migrations or horizontal swimming responses to environmental cues in shear zones, shelf break frontal regions or within mesoscale eddies can affect the large-scale distribution (Murphy *et al*. 2004).

Furthering the understanding of the role of advective effects in structuring Southern Ocean ecosystems across a wide range of space and time scales will require development of new modelling approaches and extensive observational work. Models that simulate the life cycle of Antarctic krill, including ontogentic behaviour, need to be explicitly embedded in circulation models, which will allow more realistic simulation of the transport of the various life stages. The krill growth models in turn need to be coupled to models that simulate the distribution and variability of the lower trophic levels, including microbial processes. This will allow better simulation of time variation in potential food sources. Moreover, recent developments in modelling organism growth in terms of lipid, carbohydrate and protein metabolism (e.g. Bochenek *et al*. 2001) should be incorporated into models of the growth of Antarctic krill. This allows food quality as well as food quantity to affect growth processes. Models of higher predator populations that can interface with circulation, lower trophic level and Antarctic krill growth models are needed in order to understand the full energy flow in Antarctic marine ecosystems. This would be of particular use for studies of a system like South Georgia, where the predator population dynamics are a function of local and regional processes in which advection is crucial.

The large scale connected nature of the Antarctic circumpolar system requires a basin-scale view even when the focus is on regional or local dynamics. Making connections between advective processes at such a range of scales requires high resolution models of shelf and coastal circulation that can be coupled to regional and larger scale ocean circulation models. Moreover, the circulation models need to be coupled to realistic sea ice, atmospheric, and climate models. Along with the development of models for the physical environment there is the need to develop and maintain long-term monitoring studies in order to obtain the measurements that are needed to calibrate and verify the models, as well as provide basic information that can be used to understand and characterize environmental variability.

A combined modelling and observational program directed at understanding advective transport in the Southern Ocean would of necessity be a coordinated multinational effort. Such a program would include multidisciplinary focused field studies in specific regions that would be linked to provide a circumpolar view of processes controlling the population distribution of Antarctic krill.

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