Modelling the pathways of transport of krill in the Scotia Sea: spatial and environmental connections generating the seasonal distribution of krill

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Abstract

A coupled physical-biological model analysis was undertaken to examine the seasonal development of the distribution of Antarctic krill (Euphausia superba Dana) in the Scotia Sea. The origin and fate of krill observed during the CCAMLR 2000 Synoptic Survey was studied using output from the Ocean Circulation and Climate Advanced Modelling Project (OCCAM) model. Lagrangian particle tracking for the period prior to the survey showed the expected dominance of the west to east flow of material associated with the Antarctic Circumpolar Current (ACC), but there was no simple association of particle transport with any one of the fronts of the ACC. Consideration of the pathways of krill transport with satellite derived sea-ice distributions showed that particles that were present in the high krill biomass regions in January would have come from areas that were covered by sea-ice during late winter/early spring (September-October). The results of Eulerian grid-based simulations of the development of the biomass distribution after the survey period showed transport of particles around South Georgia, probably in association with the Southern Antarctic Circumpolar Current Front (SACCF), however, a lot of the krill encountered in the east of the Scotia Sea would have exited towards the east, passing north of the South Sandwich Islands, probably in association with the Southern Boundary of the Antarctic Circumpolar Current (SB). Simulations of particle tracks that included diurnal vertical migration showed that krill behaviour could modify the pathway of transport, although the current flows will dominate the movement of krill in open ocean regions.

The study has shown that the summer distribution of krill in the Scotia Sea is connected to the winter sea-ice distribution and probably the pattern and rate of the spring retreat. Much of the krill in the Synoptic Survey region in the summer of 1999/2000 came out from under the sea-ice regions in the eastern Scotia Sea, the southern Scotia Arc and the northern Weddell Sea. This highlights that the spatial association of the sea-ice with the frontal regions of the ACC during winter and spring will be crucial in determining the summer krill distribution. Variation in the extent and timing of sea-ice retreat, and fluctuations in the Scotia Sea flow, will change the pathways of transport resulting in large changes in the distribution of the krill during the summer.

Introduction

The Scotia Sea contains the most extensive regions of high biomass of Antarctic krill (Euphausia superba Dana) in the Southern Ocean (Marr, 1962), it encompasses many of the major predator colonies of the Southern Ocean (Croxall et al., 1988) and is the area where krill fishing has been concentrated (Murphy et al., 1997; Murphy et al., 1998). The main sites in the Scotia Sea (Figure 1) where it is considered that viable krill spawning occurs are in the coastal areas of the Antarctic Peninsula even though the distribution of krill extends far to the north in the Scotia Sea (Marr, 1962). The krill population in the northern Scotia Sea is not self-sustaining, relying on input from areas further south for it to be maintained (Ward et al., 1990). The krill are a key component of the regional food-web, being the major prey item of many of the key predators such as the fur-seals and macaroni penguins that occur in such large numbers in the Scotia Sea (Croxall et al., 1985). Longterm observations of krill abundance and availability to predators have shown that there is large interannual variability in the abundance of krill in the Scotia Sea region that is associated with major changes in the ecosystem (Atkinson et al., 2001; Murphy et al., 1998). Although krill are such a key component of the regional ecosystem and we know a lot of the krill are brought into the northern Scotia Sea from west and south, we do not know what the major routes for transport are for krill in the Scotia Sea, how these routes relate to winter sea-ice cover or where the krill are transported to during the late summer period (Hofmann et al., 1998; Murphy et al., 1998).

A range of studies have considered the physical and biological factors that may be important in generating the observed variation in krill abundance in the Scotia Sea (Murphy and Reid, 2001; Murphy et al., 1998; Priddle et al., 1988). Early studies of the large-scale distribution of krill showed that the surface circulation in association with the ACC was important in generating the observed distribution of krill in the Scotia Sea (Marr, 1962). Priddle and co-workers (Priddle et al., 1988) discussed how fluctuations in ocean frontal positions as a result of changes in atmospheric circulation patterns could influence the distribution and transport of krill. Subsequently, the

fluctuations in krill abundance were related to coherent changes in the coupled atmosphere-ice-ocean systems of the Southern Ocean (Fedulov et al., 1996; Murphy et al., 1995). More recently, as our understanding of the dynamics of krill populations has increased, Murphy and Reid (2001) showed that fluctuations in year class strength of krill are also an important component of the observed variation. Understanding the geographical, winter-summer, connections in the development of krill distributions in the Scotia Sea will be fundamental to determining what generates the observed variation and predicting the response of these systems to change.

Marr (1962) and Mackintosh (1973) considered that krill could enter the Scotia Sea in two ways, through Drake Passage past the Antarctic Peninsula in the ACC or from the Weddell Sea associated with the surface outflow of Weddell waters in the Weddell-Scotia Confluence. Thus, krill at South Georgia could come from these 2 sources and there have been suggestions that the different types of krill observed in the area have their origin in these different regions (Mackintosh, 1973; Watkins et al., 1999). Recent studies of the potential pathways of transport of krill in the Scotia Sea have shown that the fronts of the ACC can have an important role (Hofmann et al., 1998; Murphy et al., 1998). As these fronts are routes of enhanced current speeds it is suggested that flows from the Antarctic Peninsula region will be the main route for bringing krill into the Scotia Sea.

Much of the study of distribution of krill has been based on data collected during summer months when most of the region is free of sea-ice, so there is a tendency to concentrate on the ocean flows and connections to frontal regions when considering the major factors influencing the distribution (Hofmann et al., 1998; Murphy et al., 1998). The sea-ice environment is known to be crucial to krill in the Scotia Sea, Marr (1962) and Mackintosh (1973) emphasized that the broad scale distribution of krill during summer was related to the sea-ice retreating in spring and it has long been known that the marginal ice regions are areas of high krill abundance. Much of the harvesting of the great whales occurred in the marginal ice regions where they were observed to be feeding on krill. Murphy et al.

(1998) discussed the potential for variability in sea-ice extent (Murphy et al., 1995) to change the interaction of the sea-ice with the flow field during spring to modify the summer krill distribution. Recently, Fach et al. (2002) have also shown how interaction with sea-ice may be a key aspect in the survival during transport of krill in the Scotia Sea.

It has also been suggested that active movement of krill may be important in the development of the large-scale distribution. In coastal regions of the Antarctic Peninsula active migration has been identified as a likely mechanism for the movement of krill from shallow to deeper waters (Siegel, 1988; Trathan et al., 1993) and in such areas active krill movement may be important in the horizontal transport of krill. However, in more open-ocean regions where the flow rates are consistent and high compared to the maximum swimming speeds of krill it is difficult to envisage a situation in which such active migration will be important (Marr, 1962). To be significant this would require a consistently directed migration in deep-water areas and there is no evidence to support this speculation. Vertical migration is a different matter and may have an effect depending on the vertical shear structure of the flow field (Hardy, 1967). Again, in coastal regions these effects will be more important than in more open ocean regions where major current flows will dominate. However, differential movement of surface or deeper currents may be important and may allow vertical migration effects to produce differences in the pathways of transport (Murphy et al., submitted; Tarling et al., 2000).

Most of the studies of spatial connection in the Scotia Sea have been based on general observations of occurrence of krill in the southern Scotia Sea and at South Georgia and not on the broader distribution. The only real large-scale view available came from the *Discovery* expeditions during the first half of the 20th century (Marr, 1962). The CCAMLR 2000 Synoptic Survey data therefore provide the most comprehensive and up to date view available of the large-scale distribution of krill in the Scotia Sea over a short period of time. The data provide a unique opportunity to consider the

development and fate of the krill in ocean currents in the Scotia Sea. Until now there have been limited particle tracking analyses based on climatological analyses of flow fields or using a mean field analysis from a General Circulation Model for the region (Hofmann et al., 1998; Murphy et al., 1998). Model output is now becoming available that was generated using real wind fields making it possible to consider the particular flow conditions during the period of field observations. The current models do not include realistic simulations of sea-ice dynamics, however, the availability of detailed satellite data means that seasonal variations in sea-ice extent can be analysed in conjunction with the modelled flow fields. This availability of a combination of realistic time varying sea-ice fields with modelled ocean flow fields for the same period, coupled with the large-scale view of the krill distribution gives the potential to develop analyses of the seasonal, geographical and environmental connections controlling the dynamics of krill distributions.

Here we report on a modelling analysis of the potential pathways of transport and development of the krill distribution in the Scotia Sea. The aims of this study were to: (i) develop Lagrangian particle track analyses of the pathways of transport during the austral spring (September-December) of krill that were observed in the high biomass regions during January, (ii) develop an Eulerian simulation of the dynamic development of the krill biomass field in the period following the survey (January to April) to investigate the fate of the krill, and (iii) to examine the potential for behavioural vertical migration effects to modify the pathways of transport of krill.

Methods, Models and Data

Krill biomass distribution

The depth-integrated krill biomass field generated during the CCAMLR Synoptic Survey 2000 (Hewitt et al., submitted) is used to analyse the effects of current flow (Figure 2). The krill biomass data were 0.5° latitude by 1° longitude resolution and were regridded at 0.25° resolution for coupled analyses with the velocity data.

Model Velocity Fields

Output from the 6-hourly wind forced run of the Ocean Circulation and Climate Advanced Modelling Project (OCCAM) model (Fox et al., 2000a; Fox et al., 2000b; Saunders and Ghil, 2001; Webb et al., 1998) is used to provide the velocity fields for the particle tracking and grid-based models (Figure 3). OCCAM is a global, eddy-permitting *z* level primitive equation model of the Bryan-Cox-Semtner type and includes a free surface (Killworth et al., 1991). It has a horizontal resolution of 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 bathymetry is derived from the DBDB5 dataset (Anonymous, 1983) with manual checking and correction where necessary of key sills (Thompson, 1995). The model has been run over the period 1992—2000, forced with the European Centre for Medium-Range Weather Forecasts (ECMWF) 6 hourly reanalysed wind dataset and relaxed to climatological (Levitus and Boyer, 1994; Levitus et al., 1994) temperature and salinity values to provide the surface heat and freshwater forcing. Monthly mean velocity fields are used in this work to eliminate aliasing of inertial oscillations that occur when models are forced with high frequency wind stress and the output is sampled as snapshots (Jayne and Tokmakian, 1997).

Particle tracking

To assess the likely origins of the regions of high krill biomass in the Synoptic Survey data, we employ a Lagrangian particle tracking method. Transport of passive drifters released on a regular grid covering the Scotia Sea (Figure 4) is simulated using a two dimensional Runge-Kutta advection scheme. The position of a particle at timestep n+1 [$x_{n+1} = (x_{n+1}, y_{n+1})$] is given by

$$\mathbf{x}_{n+1} = \mathbf{x}_n + \mathbf{v}_{n+1/2} \Delta t$$
, (1)

where $x_n = (x_n, y_n)$ represents the position of the particle at the previous timestep n, Δt is the timestep and $v_{n+\frac{1}{2}} = (u_{n+\frac{1}{2}}, v_{n+\frac{1}{2}})$ is the advective component of motion derived from modified monthly mean OCCAM velocity fields at time $t + \frac{1}{2}\Delta t$. To satisfy stability criteria, a timestep, Δt , of 0.1 days is used in the scheme and thus requires interpolation between the monthly mean velocity fields. Prior to interpolation, the mean monthly velocity fields are modified following the method of Killworth (1996) to avoid errors associated with straightforward linear interpolation between monthly means. Depth-weighted mean fields are calculated over the relevant upper levels of the model and the consecutive fields used in the particle tracking. A no-slip condition is in place at land areas and once particles have left the model domain they take no further part in the simulation.

Grid-based model

To simulate the temporal development of the krill biomass field determined by Hewitt et al. (submitted), we use an Eulerian advection-diffusion model which again employs the modified mean monthly velocity fields from the 6-hourly wind forced run of OCCAM. Use of an advection-diffusion method allows concentration (mass) to be defined at every model grid point rather than limited to particle locations and hence, smaller-scale detail of the distribution can be predicted. The numerical scheme is based on the method of Smolarkiewicz (1983), extended by Smolarkiewicz and Clark (1986) to include diffusion. The simplified advective form of the equation may be written as

$$\partial C/\partial t + \partial/\partial x [(u + w_x)C] + \partial/\partial y [(v + w_y)C] = 0,$$
⁽²⁾

where *C* is the nondiffusive scalar quantity (mass in grams in this case), and *u* and *v* are the depth-mean velocity components in the x- and y-directions respectively. w_x , w_y are diffusive fluxes both set to 0 m² s⁻¹ in this model. Use of positive values for the diffusive fluxes results in the same patterns in the evolution of the krill biomass field although it is more smoothed.

Equation (2) can be solved using an anti-diffusive iterative process and to satisfy the stability criteria for this model $\Delta t = 1/12$ day. The biomass distribution is assumed to be representative of mid-January and is then developed over time using the advection-diffusion scheme with the consecutive modified mean monthly velocity fields linearly interpolated in time. A no-slip condition is set for land areas so that there is no flux onto land. Fluxes out of the model domain take no further part in the simulations and there is no influx to the model.

Results

Lagrangian particle tracking

The krill biomass distribution across the Scotia Sea during the Synoptic Survey was highly heterogeneous, with more than 50% of the biomass concentrated into 6 mesoscale (~400 to 700 km²) areas of high biomass (> 100 g m⁻²). Here we focus the particle tracking analyses on the transport of the krill into these 6 high biomass regions. These regions of high biomass occurred in the vicinity of the South Shetland Islands from on the shelf northwards towards deeper waters, around the shelf region of the South Orkney Islands, across the central Scotia Sea at about 30-40°W, and north and west of South Georgia (Figure 2 and are generally outlined for modelling purposes by coloured boxes in Figure 4). Analyses of a gridded set of releases starting in October 1999 showed those particles that would have passed through the high biomass regions during January 2000 (Figure 4). Analyses based on depth-weighted mean velocity fields for the upper 116, 182 and 323 m (model levels 1-5, 1-7 & 1-10 respectively) showed very similar results (Figure 5).

The simulations show that particles in the high biomass regions during January were generally moved from the west in the main flow of the ACC (Figures 2, 3 and 4). Examination of the transport pathway analyses with data on the monthly sea-ice extent from September shows that except for the most northern regions, west of South Georgia, the particles transported into the areas of high krill biomass would have been in areas covered by sea-ice approximately 2-3 months before the survey

(Figure 4 and 5). Particles in the southeastern regions of the Scotia Sea and around the South Orkney islands were in areas covered by sea-ice as late as November or December (Figure 4 and 5). The simulations indicate that particles in the high biomass regions around the Antarctic Peninsula $(60^{\circ} \text{ to } 62^{\circ}\text{W})$ were brought into the region in the ACC from the west (Figure 4 and 5).

To the east of the Antarctic Peninsula in the Scotia Sea the circulation field connects the main high biomass regions (Figures 3 and 4). Particles in the region of the South Shetland Islands, to the west of 60°W that were exposed by the retreating sea-ice in about October –November were transported east and reach the South Orkney Islands by about January (Figures 4 and 5, pale blue lines and symbols). Right across this region, from the Antarctic Peninsula at 60°W to about 40°W particles were transported to the east to pass through the high biomass regions in the eastern Scotia Sea during January (Figures 4 and 5, green lines and symbols). Particles further east of about 60°W in about October were transported more rapidly to the east reaching the central Scotia Sea around 35°W by about January (Figures 4 and 5, dark blue lines and symbols). Particles in the central Scotia Sea during October were transported north to occur around the western end of South Georgia during January (Figures 4 and 5, black lines). One or two months previously, during June or July, these particles would have been in the vicinity of the ice edge to the west of the South Orkney Islands (Figures 4 and 5). These flow routes along the north side of the Scotia Arc and across the Scotia Sea reflect the major pathway of flow of the ACC where the SACCF and SB occur close together (Figures 2, 4 and 5). The eastward and northward trajectories of transport of particles were broadly associated with these frontal regions but it is not possible to distinguish a dominance of one of the fronts in the transport of krill with this analysis.

Particles present in the more southern regions of the Scotia Sea at about 60°S and 35°W and on the southern shelf at the South Orkneys would have been under the ice until late November or December and would have been transported along the southern side of the Scotia Arc through the Jane Basin

(Figures 1, 4 and 5; dark blue symbols and lines). This indicates that krill in these areas were not being transported in the main flow routes of the ACC but were more influenced by flows from the Weddell Sea.

Larval krill distribution

Most of the larval krill observed across a large area of the Scotia Sea north of about 60°S were calytopsis stages 1 & 2 (> 70%; Siegel et al., submitted) and about 30 - 45 days old (Siegel et al., submitted; Ward et al., submitted). During the development phase these larvae would have gone through a descent-ascent cycle associated with egg sinking and larval ascent over about 1000m (Capella et al., 1992). While not modelled explicitly the short duration of the vertical cycle (about 10-20 days) and the general consistency of flow direction between about 100 and 1000m means that upper water column (<250 m) particle tracking will give a reasonable representation of the general flow direction although distances may be overestimated. Particle tracking indicates that the larvae were transported into the region where they were observed in January from the west in association with the ACC (Figures 2 and 6). Thus the krill larvae in these more northern regions were probably from areas on the northern side of the Scotia Arc associated with the ACC, probably flowing through Drake Passage from the Antarctic Peninsula region. These were areas where sea-ice occurred 2-3 months prior to the survey so the larvae were probably produced during November-December in open waters revealed by the retreating ice edge between about 65°W and 55°W (Figure 6). On the basis of the particle tracking, some of the krill larvae in the more eastern regions will have come from areas further south in the Scotia Sea that were covered by ice through until late October or into November (Figure 6) while some were probably never under the ice. However, the Lagrangian analyses indicate that the krill larvae that were observed in the most southerly regions during January (south of 60°S) were under the ice in the northern Weddell Sea through until late November or December (Figure 6).

Forward projections of the biomass distribution

Eulerian projections of the krill biomass field showed that much of the krill in the shelf regions near the South Shetland Islands, the South Orkney Islands and to a lesser extent around South Georgia were retained for extended periods in these areas because of low flow rates. The results from the simulations show that tracers in these more inshore areas were relatively static during the 3 months after the survey (Figure 7).

The simulations show krill from the high biomass regions streaming away downstream as the projection progresses (Figure 7). Krill biomass can be transported from the South Shetland Islands to the South Orkneys in about 2-3 months. By about the end of March, when the sea-ice was advancing northwards, the krill from the Antarctic Peninsula would have reached the South Orkney Islands. Krill from the northern side of the South Orkney Islands were transported across the Scotia Sea, reaching the central Scotia Sea in about 3 months (Figure 7). These flows from the Peninsula and the South Orkney Islands will have been associated with the major route of flow of the ACC and in particular the SACCF and SB frontal zones. However, it is not possible to distinguish whether there is one main route of krill transport associated with a particular front in this area using these model runs. This is a complex zone where the fronts are close together, are not well defined in the surface waters and are highly dynamic so there will be a lot of mixing. This is illustrated in the simulations, which show that flow routes in the eastern part of the Scotia Sea are very sensitive to the initial positions of the krill (Figure 7). Krill further west ($\sim 35^{\circ}$ W between $\sim 55^{\circ}$ and 58° S, e.g. blue marker Figure 7) were transported along the route of the SACCF to the north and then west around South Georgia. Krill just to the east of this region (e.g. red marker Figure 7) were entrained in the main flow associated with the SB and were taken to the north and then east around the north of the South Sandwich Islands at about 28°W and between 55° and 56°S. Much of the krill biomass was present in these more eastern regions of the Scotia Sea at the time of the Synoptic Survey (Figure 7a), suggesting that a lot of the krill biomass would, in time, have exited the Scotia Sea to the north-east.

In the simulations these flows are seen as waves of biomass that drift east, starting as a coherent stream along 35° W that extends from about 55° to 60° S, before taking a northward route around the South Sandwich Islands at about 30° W (Figure 7e).

The krill around South Georgia were generally moved slowly to the west with the main flow of the ACC associated with the SACCF (Figures 2 and 7). The krill were moved along and around the coast of South Georgia before being deflected north out to the west of the island. At different periods in the simulation a plume of high krill biomass formed away from the island that streamed out along the main route of the SACCF, being deflected north and then east with the main flow of the ACC. Krill encountered further to the west during the January survey were taken north and then east along this northern route of the SACCF. Krill close to the island are retained inshore although there is a general east to west flow. Krill in the vicinity of Bird Island (NW of South Georgia) were retained for the full 3-month period of the simulations.

Modifying effects of vertical migration

Lagrangian particle tracking shows the strong northward transport of particles in the very surface, wind-driven layer of the Scotia Sea (Figure 8). Particles released in the surface layer (~10 m) in the Antarctic Peninsula – Elephant Island regions were carried rapidly northwards across the ACC frontal zones and potentially out of the Southern Ocean over the Polar Front well to the west of South Georgia (Figure 8a-b). Particles in deeper layers (to 245 m) were moved to the east with the general flow of the ACC associated with the SACCF and SB on the northern side of the Scotia Arc. The deepest particles entered the northern Weddell Sea by this route flowing around the southern side of the South Orkney Islands (Figure 8a). The difference between the drift trajectories of particles released in the surface and deep layers further east around the South Orkney Islands (Figure 8c-d) did not result in such a marked divergence in flow as for those areas further west but the difference was still marked. Again the surface particles would have a more northward component which can take

material to the west of South Georgia while the deeper particles pick up a more eastward flow which takes particles to the east of South Georgia. Particles that are in the depth-weighted mean field of the upper 245 m show trajectories intermediate between the surface and deep drifters but are more similar to the deep flow routes reflecting the dominance of deeper flows in the mean field. The vertical migration scenario used, in which particles moved sinusoidally through the upper 245m of the water column during a 24 hour period, produced similar trajectories to the mean field flow routes, although they were further north and tended to be generally slower as shown by the shorter trajectories.

Discussion

Development of the krill distribution in the Scotia Sea during spring and early summer

The northward spread of krill in the Scotia Sea during spring is a crucial process in the operation of the regional ecosystem (Murphy et al., 1998). The large-scale dispersal of krill from southern shelf regions around the Antarctic Peninsula and the southern Scotia Arc makes the krill available to a wide range of predators whose foraging is constrained to more northern regions during the breeding season (Croxall et al., 1988). Understanding what determines the abundance of krill and the extent of the seasonal dispersal is crucial in attempts to examine the response of such large-scale ecosystems to change (Murphy et al., 1998). A question that continues to be asked in this regard is where do the krill come from that reach the northern Scotia Sea in areas such as South Georgia?

The particle tracking analyses reported in the current study support the view that the ACC is important in moving krill from west to east and northwards across the Scotia Sea towards South Georgia during the spring (Hofmann et al., 1998; Murphy et al., 1998). So the question of the origin of the krill in the Scotia Sea looks simple, the main track for moving krill is from the West Antarctic Peninsula region towards the east in association with the main flow route of the ACC. This simple

picture is complicated by krill arriving from south of the South Orkney Islands out of the northern Weddell Sea but even this track is associated with some flows from the west so the krill could still have come from the Antarctic Peninsula region. However, tracking the krill in the high biomass regions back to spring shows that at this time many were associated with the sea-ice. To track where the krill came from we must take account not only of the ocean model, but also the interaction of krill with the drifting sea-ice.

The study has revealed the direct seasonal link between the pelagic krill distribution during summer and the sea-ice environment during the previous winter and spring (Murphy et al., submitted). The analyses indicate that the majority of the krill observed during the Synoptic Survey would have been in sea-ice covered regions 2 to 3 months previously. Only the krill encountered in the northern Scotia Sea around South Georgia would have been outside the sea-ice zone at that time. Even the krill at South Georgia could have been in sea-ice covered regions 4-6 months previously during the early winter period of July-August. These analyses support the view that much of the krill population observed in the Scotia Sea during summer is released into the Scotia Sea current flows during spring retreat of the sea-ice zone (Mackintosh, 1972; Mackintosh, 1973; Marr, 1962). This highlights that the krill-sea-ice interaction during the spring period will be crucial in determining the summer distribution of krill, and hence the large-scale availability to their predators.

Unfortunately there is little information available about how krill interact with the sea-ice-ocean environment in these areas, but the available evidence about how krill utilise the sea-ice habitat indicates there will be variation associated with the sea-ice characteristics (Quetin and Ross, 1991). The sea-ice provides a highly structured environment that shows marked variation in time and space (Eicken, 1992), so in some areas, such as the Weddell Sea, the occurrence of both annual and multi-year ice generate an environment that can be highly spatially structured. Elsewhere, such as in the Antarctic Peninsula region, annual ice that tends to be smooth can predominate making a more

homogeneous environment. As a strategy for obtaining food and for predator avoidance in multiyear sea-ice regions krill often occur in close association with the ice, in brine channels and grazing on sea-ice algae growing on the sub-surface of ice floes (Marschall, 1988; Quetin and Ross, 1991; Siegel et al., 1990). Krill swarms are also found in the water column below the sea ice (Brierley et al., 2002; Quetin and Ross, 1991; Sprong and Schalk, 1992), while in shelf areas that are sea-ice covered the krill may also be associated with bottom substrates and the benthic communities (Gutt and Siegel, 1994).

The above discussion emphasizes that krill interactions with the sea-ice habitats are likely to be complex and variable through the season and between regions. This means that gaining a general understanding of the winter-spring-summer transition processes for krill emergence from under the ice will be difficult. This is further complicated by the lack of understanding of how the sea-ice and surface ocean interact in these regions. The sea-ice will modify the surface ocean characteristics in terms of temperature and salinity gradients such that the surface current fields will be very different to those expected when sea-ice is not present (Timmermann et al., 2002). This is likely to lead to enhanced current velocities along the ice-edge in areas where the sea-ice drift is likely to be greatest (Timmermann et al., 2002). These processes will form a crucial component determining the development of the summer krill distribution. A strong association of the krill with the sea-ice habitat would mean that the krill should show a predominantly ice associated drift. Model based analyses indicate that the mean direction of the ice drift in the southern Scotia Sea is to the north-east out of the northern Weddell Sea south of the South Orkney islands, across the Scotia Sea towards the northern tip of the South Sandwich Islands (Timmermann et al., 2002, see their Figure 8). So krill associated with the ice in winter and spring would have come from the northern Weddell Sea. The general pattern of sea-ice drift in the Weddell Sea further indicates that krill associated with the seaice will have come from further south within the Weddell Sea, being moved north and east along the eastern side of the AP. Such a view highlights the interconnected nature of the krill populations of the Southern Ocean with potentially multiple centres and regional connections (Marr, 1962). The Weddell Sea krill may be an important component of the large-scale krill population with adult krill that are moved out of the area in spring returning to the central population regions during winter. This may be through interactions with the regional circulation in areas where there is a southward flow or with the sea-ice during periods of formation and retreat. To address this issue we need information on the detailed physical interactions between the ocean and sea-ice, and the krill interactions within and between these regimes. This should help develop a much better understanding of how krill respond to changing sea-ice cover during periods of ice-retreat and formation.

In such a view of the system, with a dynamic ice cover fluctuating over the ocean current flows it becomes clear why simple associations of the large-scale distribution of krill with regional ocean fronts should not be expected. Release of the krill into the pelagic regime during the spring period of sea-ice retreat means that their distribution in spring and summer will be a function not only of the flow field but also of the historical association with the retreating ice-edge. This historical aspect to the development of the distribution, combined with the importance of mesoscale variability, means that it will not be simple to specify that the krill are associated with a particular frontal system. The complicated interaction between the krill distribution and the physical environment is further illustrated by the model tracking which indicates that some particles are carried across the frontal boundaries as defined from field data (c.f. Figures 2 and 4). This result may in part be due to differences in the field and model frontal positions. However, there are areas of convergence and enhanced current flow in the model fields that act to aggregate and rapidly move particles across the central Scotia Sea (see also Hofmann et al., 1998).

Much of the krill observed during the Synoptic Survey in more southern regions in areas that would have been covered by winter sea-ice were in continental shelf regions. In these shallow regions complex physical and biological interactions will greatly affect the development of the krill distribution during spring and summer. In such areas retention rates (Murphy, 1995) may be much greater than those indicated by the particle tracking with the broad resolution current data from the OCCAM model. The OCCAM model data cannot resolve the horizontal and vertical structure that will be present in these areas. In such shallow regions the fine scale ocean interactions of the circulation with the topography and local tidal effects will be important.

One of the key findings from the biological analyses of the krill distribution obtained during the Synoptic Survey was the occurrence of a high biomass of small (20-30 mm) krill in the eastern Scotia Sea (Siegel et al., submitted, see their Figure 5). The distribution of these small krill did not extend continuously back to the Antarctic Peninsula region, rather the distribution of small krill extended to the south back into the northern Weddell Sea. The particle tracking analyses undertaken in this study indicate that these small krill in the more southern regions would have emerged from under the ice in the southern-central-Scotia Sea to the east of the South Orkney Islands, and may well have come out of the northern Weddell Sea associated with the main sea ice drift in the area. This would suggest that the strong recruitment of these krill was not generated in the Antarctic Peninsula region but was generated in the southern Scotia Sea around the Scotia Arc or in the Weddell Sea. However, the simulations show that some of these small krill in the more northern regions (green and dark blue squares in Figure 4) could have been transported from the area north of the Antarctic Peninsula. The proposal that the year class originated in the Weddell Sea sector is consistent with the observation that recruitment indices in the Antarctic Peninsula region for the 1998/99 season, when these krill were probably produced, were low indicating poor recruitment (Hewitt et al., submitted). Thus, these krill may have been produced from spawnings to the east of the Antarctic Peninsula, possibly in the Weddell Sea or associated with the southern Scotia Arc to the east and west of the South Orkneys Islands. This would indicate that krill stocks of the Antarctic Peninsula, Scotia Sea and Weddell Sea form a single population. In different years the main centre(s) of production of krill larvae and

juveniles may vary across the region as a function of the regional environmental conditions. The model analyses indicated that during 1999/2000 much of the krill exited out to the east of the Scotia Sea away from South Georgia. These different routes of transport may indicate that South Georgia is generally more dependent on recruitment from the Antarctic Peninsula region, which may be why length frequency analyses indicate that krill year class strength tends to be similar in the Antarctic Peninsula and South Georgia regions (Reid et al., 2002).

The data available on the distribution of larval krill observed during the Synoptic Survey (Siegel et al., submitted; Ward et al., submitted) do not allow definitive statements about the region where spawning occurred. Lagrangian analyses indicate that krill larvae observed in the most southerly regions during January (south of 60°S) could have come out from under the ice close to where they were observed or could have emerged from under the ice in the northern Weddell Sea as late as November or December. Larvae observed in more northern areas of the Scotia Sea may have been produced in a similar area around the South Orkney Islands in association with the retreating iceedge. Such a scenario would be likely to occur if the early krill developmental stages spend a significant part of the day in the very surface layers (<50 m) where the currents will have a strong northward component associated with the wind driven layer. Alternatively, the krill larvae in the more northern regions may have been generated in areas further west closer to the Antarctic Peninsula region in areas of retreating sea-ice during spring and then been moved east in association with the ACC. The potential also exists for enhanced eastward transport rates near the ice edge as a result of the occurrence of ice-edge current jets, which could generate movement over relatively large distances.

Development of the krill distribution in the Scotia Sea during summer

A key question in relation to the krill distribution in the Scotia Sea is what are the exit routes for krill during the summer? This will be important in understanding whether there is the potential for the krill to return back into the main spawning regions to contribute to future generations in the area. This in turn will be crucial in the dynamics of the regional population; any feedbacks will have a major effect on the long-term dynamics.

The Eulerian runs indicate that during the 1999/2000 season a lot of the krill found in the Scotia Sea during the Synoptic Survey will have been transported out of the region around the north of the South Sandwich Islands. Some of these krill may become entrained in these island regions due to mesoscale shelf effects and behavioural interactions, but the model runs indicate that this may have been a major flow route during this season. These regions are known to be areas of large predator colonies and such a flow route may help explain how the colonies are maintained (Convey et al., 1999). Much of the flow would have been associated with the SB. Such a flow around the South Sandwich Islands will tend to be deflected south in the main flow to the east of the islands and provides a route for potential connection back into the eastern Weddell Sea region.

The model analyses indicate a strong sensitivity in the particle flow tracks in the central Scotia Sea with some of the krill being transported to South Georgia while krill slightly further east would be moved eastward to pass to the north of the South Sandwich Islands. To what extent this is a general or an annual effect generated by the wind and circulation conditions in the 1999/2000 season is unclear at present. The strong eastward flow observed during 1999/2000 may have been the result of the particular conditions observed during the season. Such a view would support suggestions that the wind and ocean circulation conditions may be a strong determinant of the major flow routes in different years and hence crucial in generating the observed regional interannual variation (Fedulov et al., 1996; Mackintosh, 1972; Mackintosh, 1973; Murphy et al., 1998; Priddle et al., 1988). The potential for physical driven interannual variability in transport of krill to determine large-scale changes in the distribution will be a valuable focus for further model studies (Thorpe et al., 2002).

Krill as passive tracers, the importance of behaviour and swimming

An assumption of the modelling analysis is that at least in the main open ocean regions the krill are transported largely passively in the main flow field. While maximum swim speeds of 8 body lengths per second (~25-48 cm s⁻¹) have been measured (Kils, 1979), a sustainable swimming speed is thought to be much lower at about 13 cm s⁻¹ (Kils, 1981). In areas where the current velocities are strong and consistent, horizontally and vertically, and in open ocean regions the assumption of passive transport will be reasonable. In areas where the current velocities are low and variable, or in regions of marked vertical shear, then krill swimming is likely to be an important aspect of the development of the krill distribution. However, there is little evidence of any marked spatial migratory behaviour in areas away from the shelf regions. Some studies have apparently noted directed swimming migrations of krill, as opposed to localised movement (Kanda et al., 1982; Sprong and Schalk, 1992). However, detecting such directed movement of krill aggregations in areas where there is marked mesoscale variation in the current field, such as at ice-edges, requires simultaneous measurements of the krill movement and the current field over sufficiently long time periods to show differential and directed movement. Any seasonal migratory behaviour, such as a southward migration during late summer, could have a major impact on distribution but there is no evidence of any such behaviour. Therefore, the simplest view of distribution changes at this stage can only consider local behavioural responses that may have a larger scale impact such as vertical migration.

The analysis in this study shows that krill behaviourally driven diurnal vertical migration will produce very different drift trajectories and will be important in the Scotia Sea. The crucial aspect will be the amount of time the krill spends in the very surface waters, which have a strong northward velocity component. The results show that the horizontal and vertical positions of krill in the central Scotia Sea generate very different outcomes in terms of flow routes. The area of the central Scotia Sea seems to be a particularly sensitive region for determining the krill trajectories. Depending on the geographical location and the vertical position, krill can be transported to the west of South

Georgia, can be moved around the east and along the north coast of the island or can be transported east, out of the Scotia Sea, missing South Georgia completely. The OCCAM model data do not allow further resolution of such an effect because the main wind driven impacts will be largely confined to the surface (10 m) layer so the simulations will give an unrealistic view of the importance of the surface northward layer.

The simulations cannot account for a directed cross-shelf migration of the form that krill are thought to undertake in the Antarctic Peninsula region (e.g. Trathan et al., 1993). Krill that occur in inshore regions of the Antarctic Peninsula and then migrate across the shelf and the main direction of flow would produce very different trajectories. These krill may also exploit the strong vertical structure in these regions, possibly vertically migrating to depth into the upwelling Circumpolar Deep Water regions which will have an on shelf direction to the flow and would return the adults back towards more inshore regions. Given the potential for strong behavioural effects due to directed swimming, horizontally or vertically, the krill could be retained over very long periods in such habitats where primary production may be high and thus may be favourable for krill growth and development (Siegel, 1988).

It is interesting to note from the Eulerian simulations that flow interaction with the krill distribution generates plumes of high krill biomass away from the island groups at certain times. This highlights that passive tracers in the flow field can appear to generate enhanced levels of plankton as plumes downstream of the island groups. This is likely to be important in generating the large-scale distributions of other plankton, including phytoplankton, which also show rapid population growth.

Future developments

Developing coupled model analyses of krill growth and development with the environment are already underway (Fach et al., 2002). The current study has highlighted that for analyses of the population and distribution development the environment will need to include the physical characteristics (current speeds, directions and temperature), food availability based on ocean colour imagery from CZCS and SeaWiFS but also the time-varying sea-ice distribution as determined from satellite data. The emphasis of future studies will need to be on understanding the controls on spawning, recruitment success and earlier life-history, understanding how populations are maintained, including the importance of local retention and to what extent krill transported away from the southern Scotia Sea can produce viable offspring and are brought back into the main regions where spawning is thought to occur and so contribute to the future generations.

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Figure Legends

Figure 1. Bathymetry of the study region. Areas shallower than 3000 m are shaded grey and the 1000 m isobath is shown. Abbreviations marked are SShI – South Shetland Islands, SSIA – South Sandwich Island Arc, SOI – South Orkney Islands.

Figure 2. The distribution of integrated krill biomass (g m⁻²) generated by the CCAMLR 2000 Synoptic Survey (Hewitt et al., submitted). The positions of the major ocean-fronts are also shown as identified by (Brandon et al., submitted) from the CCAMLR 2000 Synoptic Survey data.

Figure 3. Mean velocity field for upper 182m (levels 1 to 7) in the Scotia Sea from the OCCAM model for the period October 1999 to March 2000. Colours show magnitude, arrows show direction (not scaled and not plotted on every grid point).

Figure 4. Lagrangian tracks of particles released at the beginning of October 1999 that passed through the high krill biomass areas during January 2000. Based on releases in a 0.5° latitude by 2° longitude grid in the depth-weighted mean velocity field over the upper 182m (levels 1 to 7). Different colours relate to different regions of high biomass and the associated particle tracks. The September to January ice-edge (15% concentration) positions are also shown (Sept 1999 thin grey line; Oct 1999 — ; Nov 1999 ……; Dec 1999 — ; Jan 2000 thick grey line).

Figure 5. Starting positions in a 0.5° latitude by 2° longitude grid for passive particles released at the start of October 1999 that pass through the main areas of high biomass observed during the CCAMLR Synoptic Survey during January 2000. Panels show particles released in the depth-weighted mean velocity field for (a) the upper 116 m (levels 1 to 5), (b) the upper 182 m (levels 1 to 7) and (c) the upper 323 m levels (1 to 10). The September to January ice-edge (15% concentration)

positions are also shown (Sept 1999 thin grey line; Oct 1999 — ; Nov 1999 …… ; Dec 1999 — ; Jan 2000 thick grey line).

Figure 6. Starting positions in a 0.5° latitude by 2° longitude for passive particles released at the start of November and December 1999 that pass through the regions where krill larvae were observed during the CCAMLR Synoptic Survey during January 2000. All plots were based on the depthweighted mean velocity field for the upper 116 m at the start of: (a) November and (b) December. Ice-edge positions as Figure 5.

Figure 7. The time-evolving krill biomass distribution based on the CCAMLR 2000 Synoptic Survey krill field (Hewitt et al., submitted) with the OCCAM velocity fields (mean 182 m) for the 3 month period following the survey in January. The krill biomass (g m⁻²) field is shown for day: (a) 0 (original grid), (b) 10, (c) 30, (d) 60 and (e) 90. The coloured points show the position of passive tracers released on the 16th January 2000 at each of the time steps. Thick black lines mark the mean ice edge (15%) for each month. The circular pie chart shows the proportion of the original krill biomass remaining in the grid area.

Figure 8. Lagrangian particle tracks for particles released on the first of October 1999 in 4 different localities in the survey region. Tracks are shown for single level drifters in the surface (~10 m— —) and at depth (~245 m ·······) along with the track of drifter through the depth-weighted mean field for the upper 245 m (solid line). The thick dark line shows the track of a vertically migrating particle that migrates over 245 m over 24 hours following a simple sinusoidal track.

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