Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea. Part II: Krill growth and survival

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Abstract

A time-dependent, size-structured, physiologically based krill growth model was used in conjunction with a circulation model to test the hypothesis that Antarctic krill (*Euphausia superba*) populations at South Georgia are sustained by import of individuals from upstream regions. Surface phytoplankton concentrations along the simulated drifter trajectories were extracted from historical Coastal Zone Color Scanner (CZCS) measurements and sea ice biota concentrations were calculated from sea ice concentration and extent extracted along drifter trajectories from Special Sensor Microwave/ Imager measurements. As additional food sources, a time series of heterotrophic food was constructed from historical data, and time series of detritus concentrations were calculated using phytoplankton concentrations extracted from CZCS measurements together with measured particulate organic carbon to chlorophyll *a* ratios. These food resources along specified drifter trajectories were then input to the krill growth model to determine the size and viability of krill during transport from the source region to South Georgia. The krill growth model simulations showed that no single food source can support continuous growth of krill during the 58–306 days needed for transport to South Georgia. However, under the current assumptions results indicate that combinations of food sources during the transport time enhanced krill survival, with heterotrophic food and detritus being particularly important during periods of low phytoplankton concentrations. The growth model simulations also showed that larval and juvenile krill originating along the western Antarctic Peninsula can grow to 1+ (14–36 mm) and 2+ (26–45 mm) age and size classes observed at South Georgia during the time needed for transport to this region. Krill originating in the Weddell Sea need 20 months for transport, which allows retention in a potentially high food environment, provided by sea ice, for almost 1 year. Krill then complete transport to South Georgia in the following year and larval and juvenile krill grow to 2+ (26–45 mm) and 3+ (35–60 mm) age and size classes during transport. The results of this study show that the successful transport of krill to South Georgia depends on a multitude of factors, such as the location of the spawning area and timing of spawning, food concentrations during transport, predation, and variations in the location of the Southern Antarctic Circumpolar Current Front (SACCF) and in sea ice extent.
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1. Introduction

Strong spatial and temporal variations in Antarctic krill (*Euphausia superba*) standing stock have been detected in surveys of several regions throughout the Southern Ocean (Everson, 1983; Hampton, 1985; Priddle et al., 1988; Miller and Hampton, 1989; Everson and Miller, 1994). Interannual variability of Antarctic krill around South Georgia is well recognized (Harmer, 1931; Kemp and Bennet, 1932; Mackintosh, 1972), with substantially greater catches of krill in colder years (Mackintosh, 1972). Analyses of historical data sets suggest that variability in Antarctic krill abundance within the South Georgia ecosystem may be the manifestation of periodic variations across the Scotia Sea and indeed the whole Southern Ocean (Priddle et al., 1988; Murphy et al., 1995; Fedoulov et al., 1996; Whitehouse et al., 1996; Atkinson et al., 2004). During the last 20 years, krill abundance around South Georgia was much reduced in at least 4 years (Priddle et al., 1988; Brierley et al., 1997), which affected many krill predators. Using hydro-acoustic estimates Brierley et al. (1999) showed that the magnitude of krill densities and between-year gradients of density between Elephant Island (for map, see Fach and Klinck, 2006; Fig. 1) and South Georgia mirrored each other for seven austral summers. They concluded that krill densities at both locations are linked and subject to the same gross physical and biological factors acting over similar temporal and spatial scales. These factors include key physical–biological interactions such as variations in upstream sea-ice extent and recruitment fluctuations in potential source populations off the west Antarctic Peninsula (Murphy et al., 1998).

Most Antarctic krill spawning throughout the Antarctic Peninsula, Weddell Sea, and Scotia Sea regions occurs between December and February (Ross and Quetin, 1986; Spiridonov, 1995). Chlorophyll concentrations in the Scotia Sea are typically low ($<0.6\,\mathrm{mg\,m^{-3}}$, Comiso et al., 1993) and transport during and subsequent to the spawning season places larval and juvenile krill in a low food environment during a time when their potential food supply is undergoing further decline. Thus, while transport of krill across the Scotia Sea to South Georgia is feasible (Hofmann et al., 1998; Murphy et al., 1998; Fach et al., 2002; Fach and Klinck, 2006), sufficient food during transport to ensure delivery of viable krill to South Georgia is

not guaranteed. Krill are omnivores and can feed upon phytoplankton, zooplankton (Kawaguchi et al., 1986; Daly, 1990; Nordhausen et al., 1992), on sea ice biota (Marschall, 1988; Daly and Macaulay, 1991), as well as detritus (Holm-Hansen and Huntley, 1984; Kawaguchi et al., 1986; Daly, 1990, 2004; Nordhausen et al., 1992), which provides a wide range of potential food.

Analyses of krill distributions from the Antarctic Peninsula suggest a developmental migration from inshore regions of Bransfield Strait to outer shelf break regions of the South Shetland Islands (Siegel, 1988; Brinton, 1991). Similarly, Siegel (1992) described migration off the west Antarctic Peninsula, with gravid females mostly found on the outer shelf and spent females found in inshore regions. This pattern, confirmed by later studies (Lascara et al., 1999; Siegel et al., 2002), suggested that spawning here occurs in the outer shelf regions. Consequently, currents, like those associated with the Antarctic Circumpolar Current (ACC), that flow close to the edge of the continental shelf in this area, can potentially entrain larval krill spawned at the shelf edge. Once entrained in high speed currents, these can rapidly be transported downstream. In open ocean regions advective transport dominates the movement of krill, so in general they will be passively transported in the ocean currents. However, as they grow krill become stronger swimmers and undertake diurnal vertical migrations (Murphy et al., 2004a). The spatial segregation of different age and size classes in shelf regions (Siegel, 1988; Nicol et al., 2000) and the formation of swarms (Watkins, 1986) indicate that behavior and swimming of larger individuals will modify local distribution (Murphy et al., 2004a,b). However, so far, it has only been possible to speculate on whether krill can undertake large-scale directed movement in open ocean regions (Nicol, 2003a,b).

To test the hypothesis that Antarctic krill populations at South Georgia are sustained by import of individuals from upstream regions, a modeling framework was developed. The framework couples physical and biological processes to investigate the transport and survival of larval, juvenile, and adult stages of krill under different environmental conditions (Fig. 1). A primitive equations model, the Harvard Ocean Prediction System (HOPS), was used to simulate the flow field and temperature and salinity distributions of the Scotia Sea which provided the environmental structure and characteristics (Fach and Klinck,
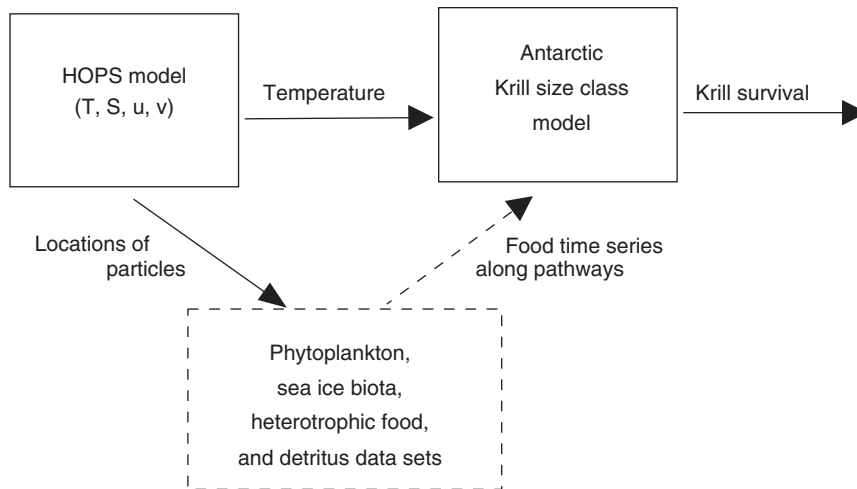
Fig. 1. Schematic of the physical–biological modeling framework. The solid-line boxes indicate the circulation (HOPS—Harvard Ocean Prediction System) and krill growth models and the dashed-line box indicates the data types that are input to the growth model. The solid arrows indicate outputs and inputs of the two models and the dashed arrow indicates the data sets input into the krill growth model.

2006). Drifters were released in the circulation model and tracked over time, providing transport pathways along which time series of food concentrations were constructed. A time-dependent, size-structured, physiologically based krill growth model (Hofmann and Lascara, 2000) was used to examine the growth dynamics of krill from 2 (Calyptopis I stage/larvae) to 60 mm (adults) presented with different time series of food concentration. Because the model is size structured, it incorporates ontogenic physiological changes that occur as the animals age. The circulation model results were combined with the krill model to provide simulations of krill growth and development during transport across the Scotia Sea (Fig. 1).

The goal of this research is to understand different environmental and biological factors that influence the successful transport and survival of krill across the Scotia Sea. Ultimately, the interpretation of transport mechanisms will lead to a better understanding of factors controlling krill distribution and production, which is needed for management of this commercially fished and vital "keystone" prey species.

2. Methods

2.1. Krill growth model

The biological model used to simulate krill growth and development is based on that described in Hofmann and Lascara (2000). This time-depen-dent, size-structured, physiologically based model incorporates a governing equation for the time-dependent (t) change in the number of krill individuals (N) in a given size class, j, of the form

$$\frac{dN_j}{dt} = -\alpha_j N_j - \beta_j N_j + \alpha_{j-1} N_{j-1} + \beta_{j+1} N_{j+1}, \qquad (1)$$

where each size class is defined by a length and carbon weight. The rate of transfer between size classes is given by the coefficients α and β, which are determined by changes in net production based on carbon weight. When net production is positive the gain in krill biomass (growth) effects a transfer to the next larger size class ($\alpha_j > 0$ and $\beta_j = 0$). For a negative net production the loss in krill biomass (shrinkage) is represented by a transfer of individuals to the next smaller size class ($\alpha_j = 0$ and $\beta_j < 0$). A detailed description of the model is given in Hofmann and Lascara (2000).

Krill are simultaneously presented with a variety of four food sources (phytoplankton, sea ice biota, heterotrophic food, and detritus) in the simulations and the food chosen is dependent on the life stage of krill (e.g. sea ice biota versus heterotrophic food). As sea ice biota become available, small krill (<18 mm) selectively feed on this and on detritus entrained in sea ice as their only food source (per Daly, 1990). Feeding upon heterotrophic food is possible only for krill larger than 18 mm, as shown by observations (Granéli et al., 1993; Huntley et al., 1994a). Therefore, all four food sources are available to only older krill.

This krill model incorporates modifications described in Fach et al. (2002), that include temperature dependence of krill growth and feeding on a heterotrophic food source. Ingestion of heterotrophic food (I_j^{hf}) by krill size class, j, is given by

$$I_j^{hf} = \gamma_j F_j^{cf} \, \text{HF}(t), \tag{2}$$

where F_j^{cf} is compression filtration, $\text{HF}(t)$ is the time series of available heterotrophic food, and γ_j is the time spent feeding.

To include detritus feeding, ingestion of detritus (I_j^{df}) filtered from the water column is formulated as

$$I_j^{df} = \gamma_j F_j^{cf} D(t), \tag{3}$$

with $D(t)$ representing a temporally varying detritus concentration. The relationship used to describe feeding on phytoplankton and sea ice biota, are similar to those given by Eqs. (2) and (3) and are described in Fach et al. (2002).

Food availability is dependent on the position of krill along simulated drifter trajectories (e.g. entrainment in an eddy, presence/absence of sea ice), and food choice is dependent on availability at a given location. Phytoplankton, sea ice biota, and heterotrophic sources are preferred foods relative to detritus and detrital feeding occurs only when these sources are scarce. When presented with multiple sources, feeding is proportional to the amount of each food present. Total ingestion (I) is then defined as

$$I = I_j^{fc} + I_j^{ig} + I_j^{hf} + I_j^{df}, \tag{4}$$

which is the sum of ingestion associated with each available food source. Assimilated ingestion is obtained using an assimilation efficiency of 80% for all size classes of krill feeding on phytoplankton, sea ice biota or heterotrophic food. This lies within the range of values observed by Kato et al. (1982) for krill feeding on a variety of food types. Unassimilated ingestion is lost as fecal pellets.

Because detritus is more refractory in nature, krill assimilation efficiency is lower than when feeding on living matter. Therefore, the assimilation rate for detritus feeding is set to 50%, which is at the lower end of the range reported by Schnack (1985). All size classes are allowed to feed on detritus in the simulations because larval (Daly, 1990, 2004), juvenile, and adult krill (Holm-Hansen and Huntley, 1984; Kawaguchi et al., 1986; Daly, 2004) have been observed feeding on this food source.

2.2. Specification of food sources

Food time series are the primary input to the krill growth model. Ship-based observations sufficient to construct food distributions across the Scotia Sea do not exist. Therefore, time series of food concentrations are extracted along particle trajectories produced by the HOPS circulation model (Fach and Klinck, 2006) in the same manner as described in Fach et al. (2002).

Surface phytoplankton concentrations are extracted from monthly chlorophyll distributions constructed from 8 year composites (1978–1986) of CZCS observations over the Scotia Sea (Feldman et al., 1989). Most of the chlorophyll signal detected by the satellite is from the upper 20% to 25% of the euphotic zone (Gordon and McCluney, 1975), which is defined as the 1% light level. Thus, chlorophyll present deeper than this could not be detected by the CZCS and therefore is not made available to krill in this model. In addition, sea ice concentrations along the particle trajectories are extracted from Special Sensor Microwave/Imager (SSM/I) measurements during 1988, which was a high-ice year.

Phytoplankton time series. The composite phytoplankton concentrations for all particles originating along the west Antarctic Peninsula (Fig. 2) show a wide range of spatial and temporal variability. Phytoplankton concentrations associated with two drifters originating along the west Antarctic Peninsula in austral summer (Fig. 2) illustrate food availability along the most prominent pathways. Differences in the end time of the food time series reflect the time drifters took to reach South Georgia and hence the end of the simulation.

Chlorophyll concentrations encountered along the two drifter trajectories released on the first day of December (Year Day 335, November spawning), are between 1 and $3 \, \text{mg chl m}^{-3}$ (Fig. 2A). The chlorophyll time series for particles released on the first day of January (Year Day 1, December spawning), show overall higher concentrations (Fig. 2B) with a one-time maximum concentration of $12 \, \text{mg chl m}^{-3}$. The chlorophyll time series for particles released on the first day of February (Year Day 32, January spawning), show concentrations similar to the December release (Fig. 2C). In all three release scenarios, phytoplankton concentrations decrease significantly after the end of April (Year Day 120) since Southern Ocean phytoplankton concentrations decrease as light becomes limiting with the onset of winter.
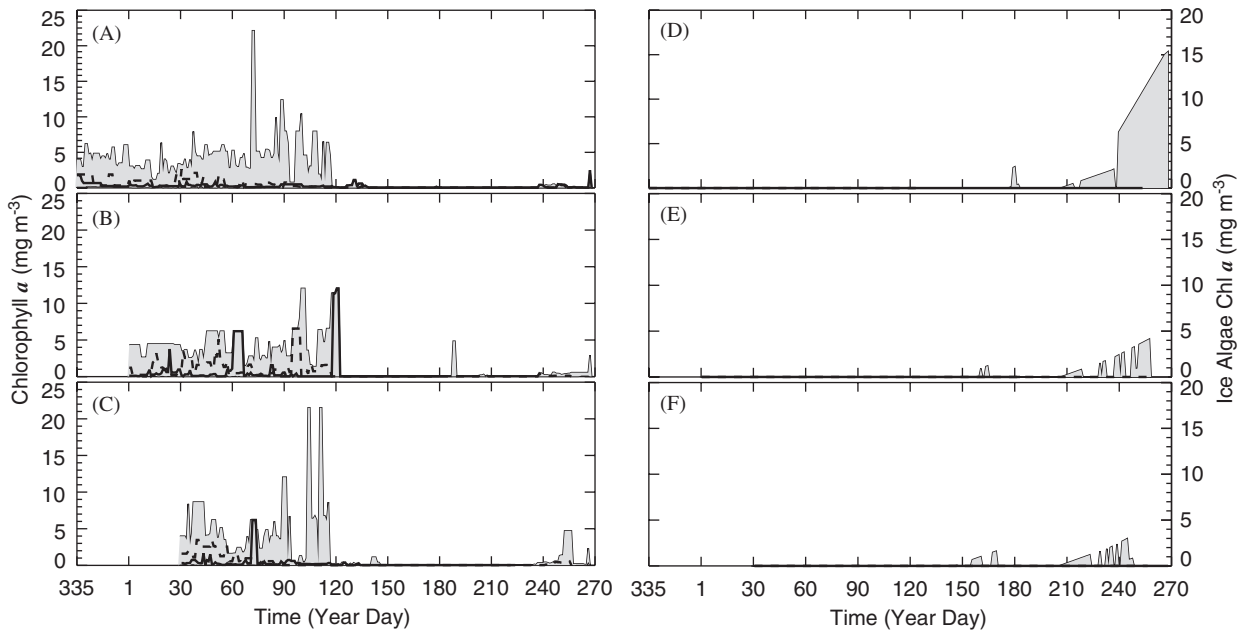
Fig. 2. Range of CZCS-derived time series of pigment concentration (mg m^{-3}) along trajectories of drifters originating at the west Antarctic Peninsula (region 1) starting in (A) December (Year Day 335), (B) January (Year Day 1), (C) February (Year Day 32), and along trajectories of drifters originating at the Weddell Sea (region 5) starting in (D) December (Year Day 335), (E) January (Year Day 1), (F) February (Year Day 32). The heavy solid line and dashed line indicate concentrations along two different particle trajectories within the range of concentrations, which is denoted by the gray shading.

The extracted phytoplankton time series illustrate large mesoscale variability in food supply encountered along trajectories which are not widely separated in space. The time particles spend in different phytoplankton concentrations coincides with entrainment of the drifter in eddies and is a measure of eddy variability. These entrainments last from 5–20 days. Also, considerable temporal variability in phytoplankton availability occurs depending on the time a particle leaves the Antarctic Peninsula. Drifters released in December are more likely to encounter high concentrations of phytoplankton food up to the end of April, approximately 5 months. A drifter released in February at the same location has only 3 months of potentially high phytoplankton concentrations. These general observations are true for drifters originating at the western and southwestern Antarctic Peninsula, the Weddell Sea (Figs. 3A–C), Bransfield Strait area (Fach, 2003), and Elephant Island/Scotia Sea region (Fach, 2003).

Sea ice-derived food time series. Sea ice biota concentrations encountered along trajectories of the same two drifters released along the western Antarctic Peninsula in December (Year Day 335),

January (Year Day 1), and February (Year Day 32) (Figs. 2D,E) are zero. However, the range of concentrations constructed from the other drifters shows that some do encounter sea ice food. Drifters originating in the southwestern Antarctic Peninsula and Scotia Sea/Elephant Island area and those moving through the open Scotia Sea do not encounter significant sea ice in austral fall and winter (Fach, 2003). Drifters originating in Bransfield Strait generally pass by pack ice forming off the Antarctic Peninsula during winter, and those originating in the Weddell Sea spend most of their transport time under sea ice (Figs. 3D,E).

Heterotrophic food. No continuous measurements of copepod concentrations across the Scotia Sea are available from which a time series of copepod concentrations along drifter paths could be extracted. Therefore, a time series (Fig. 4) was constructed using estimates of mean mesozooplankton biomass in the greater South Georgia region (Atkinson and Snÿder, 1997) as described in Fach et al. (2002). This time series assumes that krill encounter occasional patches of high mesozooplankton concentrations along with low background concentrations. The heterotrophic food
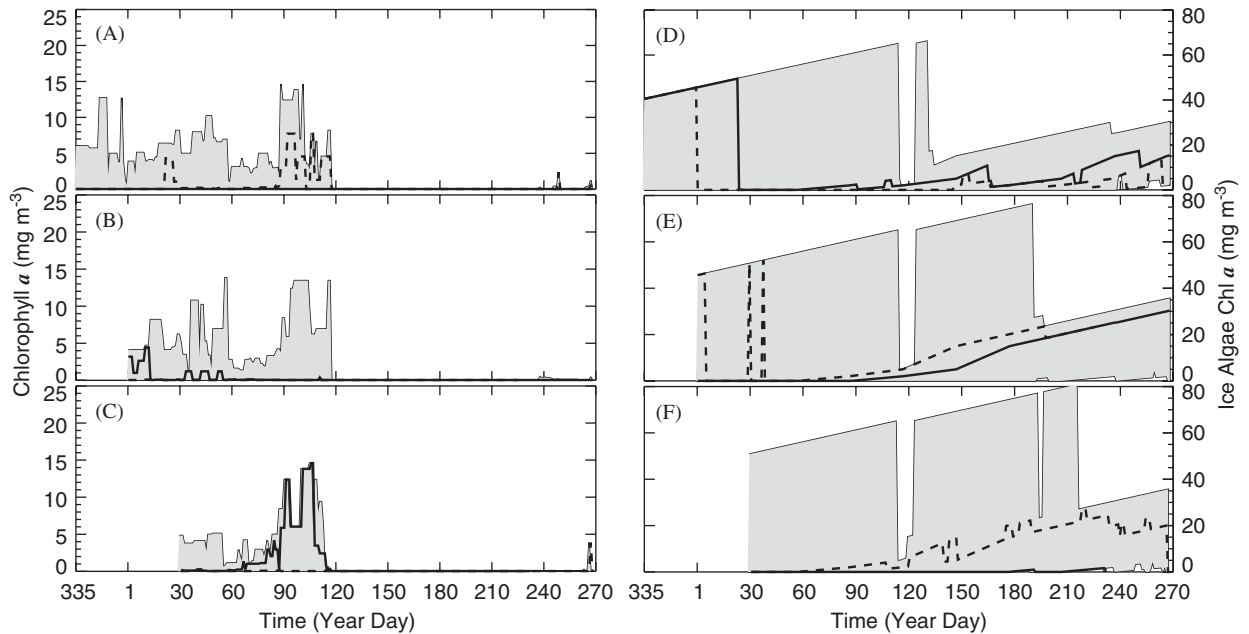
Fig. 3. Range of SSM/I-derived time series of sea ice biota concentration (mg m^{-3}) along trajectories of drifters originating at the west Antarctic Peninsula (region 1) starting in (A) December (Year Day 335), (B) January (Year Day 1), (C) February (Year Day 32), and along trajectories of drifters originating at the Weddell Sea (region 5) starting in (D) December (Year Day 335), (E) January (Year Day 1), (F) February (Year Day 32). The heavy solid line and dashed line indicate concentrations along two different particle trajectories within the range of concentrations, which is denoted by the gray shading.
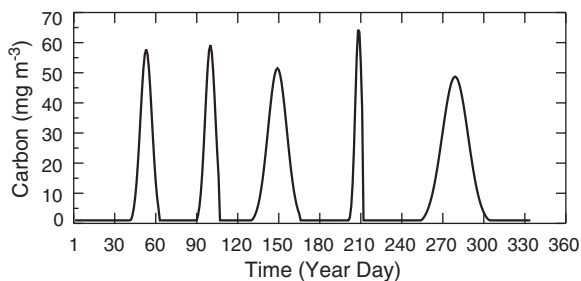

Fig. 4. Time series of heterotrophic food input to the krill growth model.

source (Fig. 4) is used for all drifter trajectories independent of origination site.

2.2.1. Detritus

Large scale or temporal data sets of detritus concentration in the Scotia Sea are also not available. Therefore, time series of this food source were constructed using the 8-year composites of CZCS observations to obtain a conservative estimate of chlorophyll *a* in the area (Figs. 2A–C, 3A–C), which was then converted to an estimate of detrital material.

Particulate organic carbon (POC) is generally considered to be part of the non-living component of sea water and is used here as a measure of detritus. A direct relationship between detritus and chlorophyll *a* has been reported in the form of POC:Chl*a* ratios (Fabiano et al., 1993, 1995). The POC concentrations are dependent on species composition and physiological state of the phytoplankton (Cota et al., 1992), factors that change with specific phytoplankton blooms and season. Therefore, a conversion from chlorophyll *a* concentrations is a somewhat crude and problematic approach for defining POC concentrations. This problem is well understood, but lacking other conversion factors and more specific data on POC concentrations, this method is used here.

Several measurements of POC:Chl*a* ratios have been made in the area of interest (Table 1). Chlorophyll *a* and POC concentrations measured along 6°W in October/November 1992 (Table 1; Dehairs et al., 1997) were used to calculate a linear regression (Fig. 5) that can be used to estimate POC. Pigment concentrations along simulated drifter paths were extracted from the CZCS distributions and converted to summer POC values

Table 1
Summary of particulate organic carbon to chlorophyll a (POC:Chl) ratios measured for Antarctic waters

POC:Chl	Season	Location	Reference
56–259	Nov–Dec 1980	Elephant Island	v. Bodungen et al. (1986)
260 ± 140 (euphotic zone)	Jan–Feb 1985	Weddell Sea	Nöthig (1988)
>300 (below 100 m)	Jan–Feb 1985	Weddell Sea	Nöthig (1988)
219	Oct–Dec 1986	55°S, 5°E	Scharek (1991)
189	Oct–Dec 1986	58°S, 2°E	Scharek (1991)
138	Jan–Feb 1983	Ross Sea	Cota et al. (1992)
32	Nov 1983	Weddell–Scotia Sea	Cota et al. (1992)
114	March 1986	Weddell Sea	Cota et al. (1992)
530	July–Aug 1988	Weddell–Scotia Sea	Cota et al. (1992)
60–739	Dec 1993	Bellinghausen Sea, 88°W	Kennedy and Robertson (1995)
40–171	Nov–Dec 1992	6°W	Dehairs et al. (1997)
242 (SD = 120) (<1.0 mg chl m^{-3})	Oct–Nov 1992	46–56°S, 6°W	Bathmann et al. (1997)
123 (SD = 53) (>1.0 mg chl m^{-3})	Oct–Nov 1992	46–56°S, 6°W	Bathmann et al. (1997)
29–597	April 2000	western Antarctic Peninsula shelf	Brichta and Bathmann (pers. comm.)

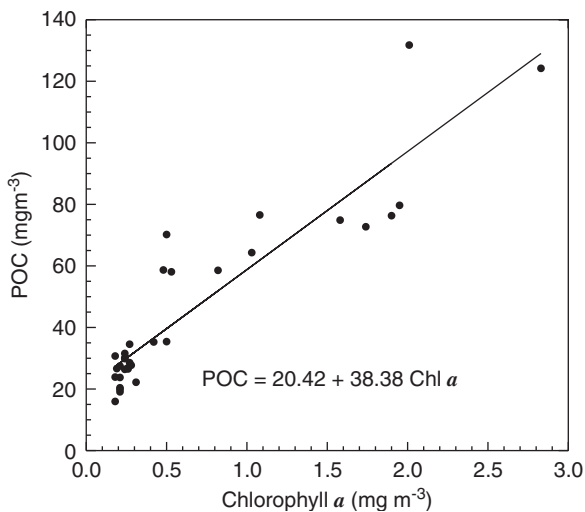For each, the season and location where the measurement was made is given, as well as the relevant reference.

Fig. 5. Measurements of POC and chlorophyll a concentration (●) from Dehairs et al. (1997). The linear regression between particulate organic carbon (POC) and chlorophyll a fit to these data (solid line) is shown. The units in the linear regression equation are mg C m^{-3} for POC and the intercept, mg chl m^{-3} for chlorophyll a, and mg C (mg chl)$^{-1}$ for the ratio 38.38.

(October–March) with the ratio of 38, the slope factor of the linear regression (Fig. 5). This value is representative of carbon in intact phytoplankton cells (Cota et al., 1992) and is a conservative estimate for a ratio in chlorophyll-rich environments. The calculated ratio of 38 is at the lower end of the previously reported values for the same area (i.e. 123 (SD = 53); Bathmann et al., 1997), but

agrees with the slope of 47.2 (±30.1) calculated by Cota et al. (1992).

For winter months (April–September) the average value of 233, calculated for the western Antarctic Peninsula continental shelf area (Table 1; Brichta and Bathmann, pers. comm.) was used to convert chlorophyll values extracted along simulated drifter paths to POC. However, most of the simulated drifter paths moved through open ocean (Fach and Klinck, 2006) and processes there differ greatly from the continental shelf. Nevertheless, this value is similar to the average POC:Chla ratio 242 (SD = 120) calculated for chlorophyll-poor open ocean regimes with less than 1.0 mg chl m^{-3} in summer time (Bathmann et al., 1997). The 233 value is close to this average value and therefore provides a useful estimate of the ratio in winter time, when chlorophyll a values are likely to be well below 1.0 mg chl m^{-3}. The estimated time series for detritus along drifter trajectories are similar to those obtained for chlorophyll (cf. Figs. 2A–C, 3A–C).

2.2.2. Simulations

Food time series constructed along simulated drifter trajectories obtained from the reference simulation for release sites in the five regions discussed in Fach and Klinck (2006) were input to the krill growth model. Krill growth and development were obtained until the end of the simulation. Krill growth model simulations produce length–frequency distributions of krill, which are then used

Table 2
Summary of the simulations done with different combinations of the food time series

Food assumption	Food time series	Results
P	Fig. 2	Tables 3–7, Figs. 7–11A
P + SIF + DF	Figs. 2, 3 and 5	Tables 3–7, Figs. 7–11B
P + SIF + DF + HF	Figs. 2–5	Tables 3–7, Figs. 7–11C
DF	Fig. 5	Tables 3–7, Figs. 7–11D

The figure showing each food time series is indicated as are the tables and figures showing the results of the individual simulations. The different food types are: P—phytoplankton, SIF—sea ice-derived food, DF—detritus food, and HF—heterotrophic food.

to test the effects of the physical environment and biological factors on survival of particular age groups of krill during transport. Those simulations are summarized in Table 2.

Krill growth is maintained by tracking animal size and different krill sizes are defined to correspond to certain age classes of krill after Siegel (1987). Larvae of sizes 2–15 mm are defined as 0+ krill, 1+ krill defines juveniles of 1–2 years and 14–36 mm, 2+ krill are subadults of 2–3 years and 26–45 mm, while 3+ krill describe 3–4 year old adults of 35–60 mm size.

2.3. Predation

Krill undoubtedly encounter predators during their transport to South Georgia. Estimates of predation rates on krill are limited. Boyd and Croxall (1996) calculated the demand for krill by Antarctic fur seals (*Arctocephalus gazella*) and macaroni penguins (*Eupdyptes chrysolophus*) at South Georgia, from a combination of physiological data and diet samples, to be 32,000 t fresh mass d^{-1}. These two species together consume >75% of the estimated total for all land-based predators here (Croxall et al., 1985). For the same two species, Atkinson et al. (2001) calculated a total food removal off the west coast of South Georgia of 0.94 g fresh mass $m^{-2} d^{-1}$, compared with a mean krill biomass of 30 g fresh mass m^{-2}. This area includes breeding and non-breeding populations of Antarctic fur seals and macaroni penguins. They conclude that the total removal of krill by land-

based predators here is on average approximately 3% d^{-1}.

These estimates are calculated for the productive waters around South Georgia which have a large predator species diversity and biomass (Croxall et al., 1984, 1988; Croxall and Prince, 1987; Hunt et al., 1992; Boyd et al., 1994) and are not representative for other regions supporting predator colonies or the open ocean, in which most of the transport time is spent. Therefore, 3% d^{-1} removal (Atkinson et al., 2001) is considered a maximum estimate for predation that cannot be applied to krill being enroute to South Georgia.

Murphy (1995) estimated the total land-based predator demand at South Georgia as a function of distance from land. Close to shore the annual impact was up to 250 t $km^{-2} year^{-1}$ while 350 km away the impact vanished. Assuming the predator demand at South Georgia is 3% d^{-1} (Atkinson et al., 2001), predator impact decreases to 2.4% d^{-1} at 75–130 km from shore to 0.45% d^{-1} at 200 km. Krill being transported to South Georgia spend most of the time >350 km away, which means predation by South Georgia-based predators is negligible. However, krill originating at the western Antarctic Peninsula are in proximity to predator colonies located there. Also, krill are constantly subject to predation by whales, fish and sea birds. Thus, a predation rate of 0.3% d^{-1} is assumed to be representative during transport. This value is within the predation estimates of 0% and 0.45% d^{-1} given by Murphy (1995).

The effect of predation during transport to South Georgia is estimated as

$$N(t) = N_0 e^{-dt}, \tag{5}$$

where $N(t)$ is the number of krill at a certain time, t, during transport, N_0 is the initial number of krill at the time of release (assumed to be 5000), and d is the rate of predation (0.3% d^{-1}). The number of krill chosen as N_0 is arbitrary and intended to represent a small krill swarm. The predation estimates are in terms of a non-dimensional ratio $(N(t)/N_0)$ that is between 0 and 1 and therefore does not change with different N_0 values.

3. Results

3.1. General characteristics of simulations

Larval krill with an initial size of 2 mm represent the current season's spawn. Krill of this size were

exposed to the different phytoplankton food time series (Fig. 2A) extracted along simulated drifter trajectories from the west Antarctic Peninsula (region 1 as defined in Fach and Klinck, 2006; Fig. 12). These krill begin feeding in December (Year Day 335) and grow over time to different sizes (Fig. 6) because of the different amounts of food available to them along a given trajectory. Of these larvae, 38% survive until the end of the simulation and 62% die because of insufficient food (Table 3). The maximum size reached by survivors at the end of the simulation is 13.1 mm and the smallest size when reaching South Georgia is 2.9 mm; the different length simulations are determined by the time it takes for a specific drifter to reach South Georgia. The 2.9 mm individual never encounters sufficient food to grow in size but has just enough food to fulfill its relatively low energy demand (Fig. 2A). The other surviving krill manage to grow over the time of transport (Table 3). Krill that grow fast during the first days of the simulation often die when less food is encountered later in development because energy demand increases with increasing size. Therefore, 62% of the krill die during the simulation, the smallest being 6.1 mm, the largest being 14.4 mm at the time of death.

The simulated growth of 22 mm krill (juveniles) develops differently than 2 mm krill and achieves a wide range of sizes at the end of the simulation (Fig. 6). The smallest surviving individual is 21.9 mm, the largest is 31.6 mm (Table 3). Of the
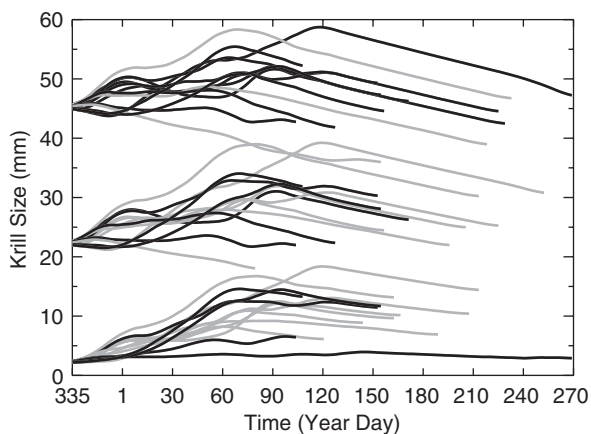

Fig. 6. Simulated growth of 2 mm krill (lower curves), 22 mm krill (middle curves), and 45 mm krill (upper curves) starting in December (Year Day 335) using phytoplankton food only. Krill that survive the time needed for transport to South Georgia are shown by black lines. Krill that die before reaching South Georgia are indicated by gray lines.

juveniles, 38% die during the simulation time and their sizes at death range from 17.9 to 30.6 mm. Juveniles grow slightly faster than do larvae because they can feed on higher daily rations. At the same time, their energy demand is higher. Therefore, juveniles shrink more rapidly than larvae, but can also survive longer periods of shrinking. Krill death is defined here as the loss of more than 45% of body wet weight, so larger krill can survive longer because they have higher initial wet weight (Hofmann and Lascara, 2000).

The pattern of growing and shrinking for 45 mm krill (adults) is similar to that of juveniles, except that shrinking periods are more pronounced and the 45 mm krill survive shrinking longer because of higher initial wet weight (Fig. 6). Of the adults, 77% survive the entire time of the simulations and are between 41.6 and 51.9 mm in size when reaching South Georgia (Table 3). The implication is that food encountered during transport was not sufficient for krill to grow much in size. Krill that died were between 35.9 and 46.6 mm. Adult krill simulations are included for comparison although they are not likely to be passive drifters.

3.1.1. Western Antarctic Peninsula

The drifters released in December along the western Antarctic Peninsula (region 1) need between 141 and 306 days to reach South Georgia (see Fach and Klinck, 2006). Phytoplankton alone (Fig. 2A) is not sufficient to sustain krill originating here and many of these, especially larvae, die during the time required to reach South Georgia (Fig. 7A, Table 3).

With the inclusion of sea ice biota (Fig. 3A) and detritus as additional food sources there is a significant improvement in krill growth and survival (Fig. 7B). Larval krill survival is more than doubled with additional food. The maximum size of krill at the time of arrival at South Georgia is 17.4 mm, which is significantly greater than with phytoplankton only. Juvenile krill also show enhanced survival over phytoplankton food only with 100% survival. The maximum size of survivors increases to 38.4 mm, but the minimum size decreases to 18.6 mm. Adult krill profit from the additional food as well with 100% surviving transport. The maximum size of adult survivors at the end of the simulation increases to 55.9 mm during the last days of the simulation. This improvement in growth and survival is mainly an effect of detritus being available, as most krill from this region do not encounter sea ice biota (Fig. 3A).

Table 3
Summary of krill growth simulations for different food types, initial sizes, and release times that are based on the food available along the trajectories of 13 drifters released in region 1, the west Antarctic Peninsula

Food type	Initial size (mm)	Release time (month)	% surviving	Final length (mm)	% dying	Length at death (mm)
P	2	Dec	38	2.9–13.1	62	6.1–14.4
		Jan	31	2.4–6.9	69	2.4–14.4
		Feb	31	2.4–5.1	69	1.9–8.9
	22	Dec	62	21.9–31.6	38	17.9–30.6
		Jan	31	21.9–27.9	69	17.1–31.6
		Feb	23	17.9–24.6	77	17.1–24.4
	45	Dec	77	41.6–51.9	23	35.9–46.6
		Jan	77	36.6–48.1	23	35.1–35.9
		Feb	77	36.9–44.9	23	35.1–42.4
PID	2	Dec	85	5.1–17.4	15	10.1–13.4
		Jan	85	2.9–14.9	15	2.9–10.9
		Feb	77	2.1–8.6	23	6.4–8.9
	22	Dec	100	18.6–38.4	0	NA
		Jan	69	19.1–36.4	31	17.1–18.1
		Feb	92	17.9–18.1	8	17.4
	45	Dec	100	38.1–55.9	0	NA
		Jan	100	35.9–54.1	0	NA
		Feb	100	38.6–47.9	0	NA
PIDH	2	Dec	85	5.1–21.9	15	10.1–13.1
		Jan	77	2.9–22.4	23	2.9–10.9
		Feb	77	2.1–6.4	23	6.4–8.9
	22	Dec	100	29.7–45.1	0	NA
		Jan	100	23.6–44.1	0	NA
		Feb	100	24.9–38.1	0	NA
	45	Dec	100	49.1–59.9	0	NA
		Jan	100	44.1–59.9	0	NA
		Feb	100	44.6–55.1	0	NA
D	2	Dec	69	2.1–4.4	31	1.9–5.6
		Jan	38	2.4–6.6	62	1.6–5.6
		Feb	8	2.4	92	1.6–3.4
	22	Dec	46	18.1–21.7	54	17.1–21.9
		Jan	15	17.6–26.1	85	17.1–23.4
		Feb	8	20.6	92	17.1–19.6
	45	Dec	69	36.1–42.4	31	35.1–36.4
		Jan	54	35.4–44.6	46	35.1–35.4
		Feb	31	37.1–40.6	69	35.1–37.4

The percent (%) and length of krill surviving and dying, at the end of each simulation is shown. Abbreviations used in the table are: P (phytoplankton), PID (phytoplankton, sea ice biota, and detritus), PIDH (phytoplankton, sea ice biota, detritus, and copepods), D (detritus), NA (not applicable).

Adding heterotrophic food (Fig. 4) to the food supply further improves growth and survival of juveniles and adults (Fig. 7C, Table 3). Larvae initially do not profit from this additional food source, but begin using this food as they reach lengths >18 mm. Therefore, while the number of survivors stays the same, the maximum size increases to 21.9 mm at the time of arrival at South Georgia. Post-larval krill can use the additional food supply and the effect is that juveniles grow to sizes between 29.7 and 45.1 mm and adults to 49.1 and 59.9 mm. Under these conditions all krill manage to grow above their starting size during the simulation time.

Feeding solely on detritus is not beneficial for krill originating from region 1 (Fig. 7D). Food
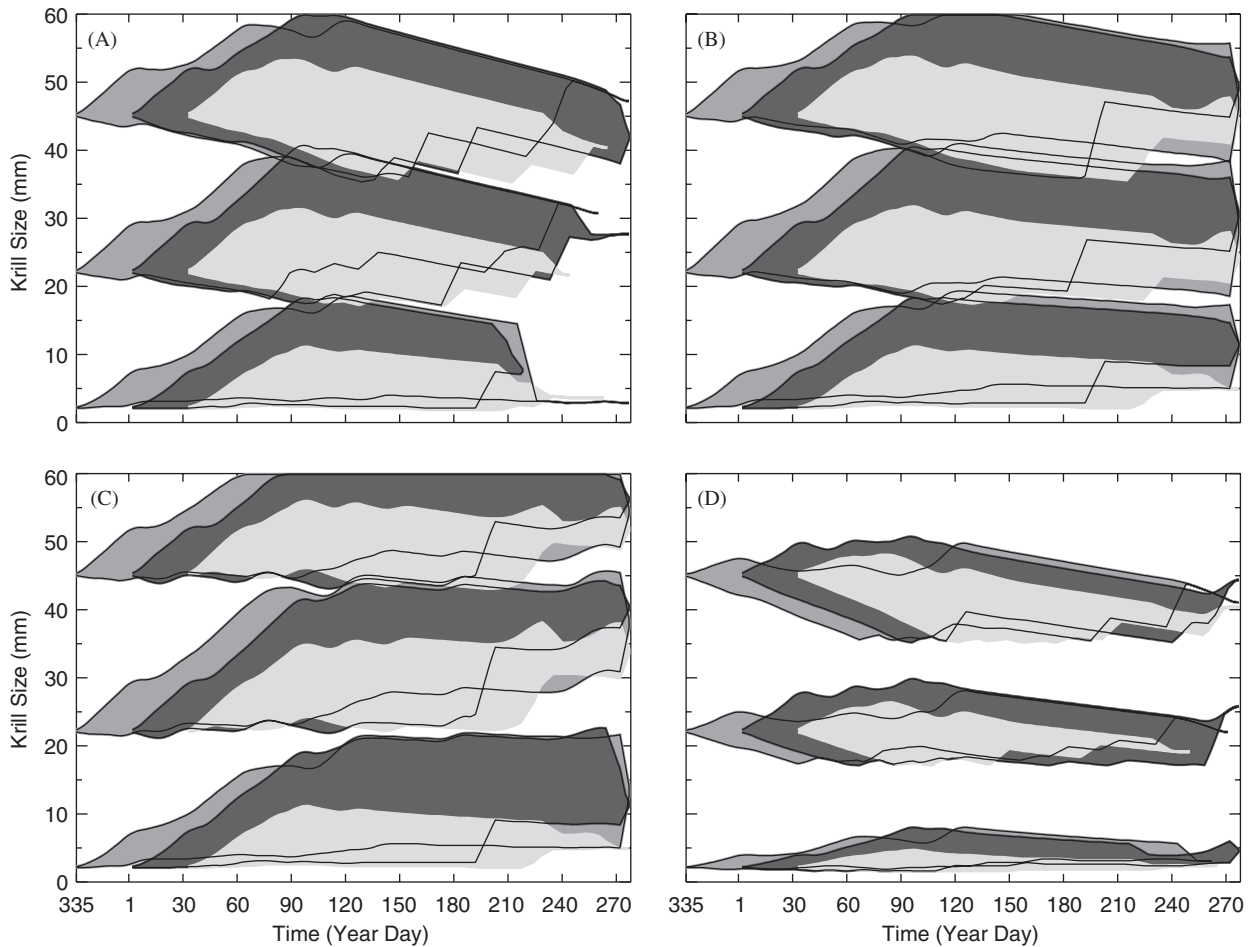
Fig. 7. Range of simulated growth of 2 mm krill (lower curves), 22 mm krill (middle curves), and 45 mm krill (upper curves) released in the west Antarctic Peninsula region in December (medium shading), January (dark shading), and February (light shading) obtained for Antarctic krill feeding on (A) phytoplankton only, (B) phytoplankton and sea ice biota with detritus, (C) phytoplankton, heterotrophs and sea ice biota with detritus, and (D) detritus only.

concentrations are highest during the first 5 months of the simulation but are still too low for krill to grow much in size. Detritus concentrations decrease during winter, so that all krill shrink from then on. Although 69% of the adults survive transport, they only grow to final sizes of 36.1–42.4 mm. Larval krill, with their lower energy needs, grow slightly more during the first 5 months of the simulation and 69% survive transport times. These grow to sizes of 3.1–4.4 mm over the simulation period. All three size classes grow to smaller lengths when feeding on detritus only versus phytoplankton only.

Results similar to those obtained from a December release are obtained for all other release times (Fig. 7). For krill originating at the western Antarctic Peninsula the combined phytoplankton,

sea ice biota, detritus, and heterotrophic food is the most favorable supply. In these simulations phytoplankton alone is sufficient for some krill to survive (Fig. 2A), but the addition of detritus provides sufficient food to improve survival of all krill sizes. Consistent supplies of detritus and heterotrophic food (Fig. 4) are the primary sources that support survival during times of low phytoplankton concentrations in these simulations.

3.1.2. Bransfield Strait

The drifter results (Fach and Klinck, 2006), indicate that krill originating in Bransfield Strait (region 2) in December require between 184 and 306 days to reach South Georgia. Phytoplankton alone is not sufficient and only 33% of the larvae

originating in this region survive the transport to South Georgia (Fig. 8A, Table 4). The survivors grow to sizes between 4.4 and 16.1 mm, which is larger overall than larvae originating in region 1. Only 22% of juveniles survive, growing to between 22.1 and 35.1 mm, while 78% of adults survive, reaching 35.9–59.9 mm.

The addition of sea ice biota and detritus further improve growth and survival (Fig. 8B) by more than doubling the number of larval and juvenile survivors, similar to what was found for krill originating in region 1. The survival rate for juveniles and adults is 100%, mainly because of the availability of detritus. Growth and survival further improves when heterotrophic food is added (Fig. 8C), with 89% of larvae surviving transport to South Georgia and growing to

16.4 mm. All juveniles and adults reach South Georgia and their sizes increase to between 33.4–46.1 mm and 48.6–59.9 mm, respectively.

Detritus as the only food source is not beneficial for juvenile and adult krill originating in region 2 (Fig. 8D, Table 4), and the simulated growth patterns are similar to those for region 1. Surviving krill of all sizes do not grow significantly in the total simulation time. Thus, for juveniles and adults originating in Bransfield Strait combined phytoplankton, sea ice biota, detritus, and heterotrophic food is the most favorable food supply. Few of these krill have access to sufficient sea ice biota, but the consistent supply of detritus and heterotrophic food (Fig. 4) allows them to survive times of low phytoplankton concentrations.

Fig. 8. Range of simulated growth of 2 mm krill (lower curves), 22 mm krill (middle curves), and 45 mm krill (upper curves) released in the Bransfield Strait region in December (medium shading), January (dark shading), and February (light shading) obtained for feeding on (A) phytoplankton only, (B) phytoplankton and sea ice biota with detritus, (C) phytoplankton, heterotrophs and sea ice biota with detritus, and (D) detritus only.

Table 4
Summary of krill growth simulations for different food types, initial sizes, and release times that are based on the food available along the trajectories of nine drifters released in region 2, the Bransfield Strait

Food type	Initial size (mm)	Release time (month)	% surviving	Final length (mm)	% dying	Length at death (mm)
P	2	Dec	33	4.4–16.1	67	7.9–13.4
		Jan	11	17.4	89	8.9–11.7
		Feb	11	10.9	89	6.4–9.9
	22	Dec	22	22.1–35.1	78	17.4–28.6
		Jan	22	25.1–40.6	78	22.1–28.6
		Feb	22	27.1–30.4	78	22.4–27.1
	45	Dec	78	35.9–59.9	22	40.9–41.6
		Jan	44	41.6–59.9	56	40.6–46.6
		Feb	44	42.9–50.4	56	39.6–43.9
PID	2	Dec	89	6.1–18.1	11	8.4
		Jan	33	12.1–17.4	67	6.9–11.4
		Feb	44	8.6–11.1	56	7.6–9.9
	22	Dec	100	21.1–39.6	0	NA
		Jan	100	23.9–40.6	0	NA
		Feb	100	23.9–32.1	0	NA
	45	Dec	100	41.6–59.9	0	NA
		Jan	100	43.1–59.9	0	NA
		Feb	100	44.1–52.1	0	NA
PIDH	2	Dec	89	6.1–16.4	11	8.4
		Jan	33	12.9–12.1	67	6.9–11.4
		Feb	44	7.6–11.1	56	7.6–9.9
	22	Dec	100	33.4–46.1	0	NA
		Jan	100	33.6–43.4	0	NA
		Feb	100	32.6–40.4	0	NA
	45	Dec	100	48.6–59.9	0	NA
		Jan	100	51.9–59.9	0	NA
		Feb	100	50.9–59.9	0	NA
D	2	Dec	34	2.9–3.1	66	1.9–6.1
		Jan	34	3.6–7.1	66	2.6–4.6
		Feb	34	2.6–3.9	66	2.6–3.9
	22	Dec	23	17.1–18.1	77	17.1–18.1
		Jan	34	19.9–20.9	66	17.1–26.1
		Feb	23	20.6–23.6	77	17.4–21.6
	45	Dec	78	35.4–46.1	22	35.1
		Jan	45	37.1–51.1	55	35.1–43.1
		Feb	56	37.1–44.6	44	35.1–38.1

The percent (%) and length of krill surviving and dying, at the end of each simulation is shown. Abbreviations are: P (phytoplankton), PID (phytoplankton, sea ice biota, and detritus), PIDH (phytoplankton, sea ice biota, detritus, and copepods), D (detritus), NA (not applicable).

3.1.3. Elephant Island/Scotia Sea

The simulated drifters released in the Elephant Island/Scotia Sea area (region 3) in December need between 58 and 277 days to reach South Georgia (Fach and Klinck, 2006), which is considerably less time than required for the other regions. Phytoplankton alone is sufficient to sustain krill originating here, as evidenced by 43% of larvae, 62% of juveniles, and 86% of adults surviving transport to South Georgia (Fig. 9A, Table 5).

The addition of sea ice biota and detritus improves growth and survival (Fig. 9B, Table 5) solely because of available detritus. These individuals encountered no sea ice because they precede the advancing winter ice. Addition of heterotrophic food increases growth and survival of juveniles
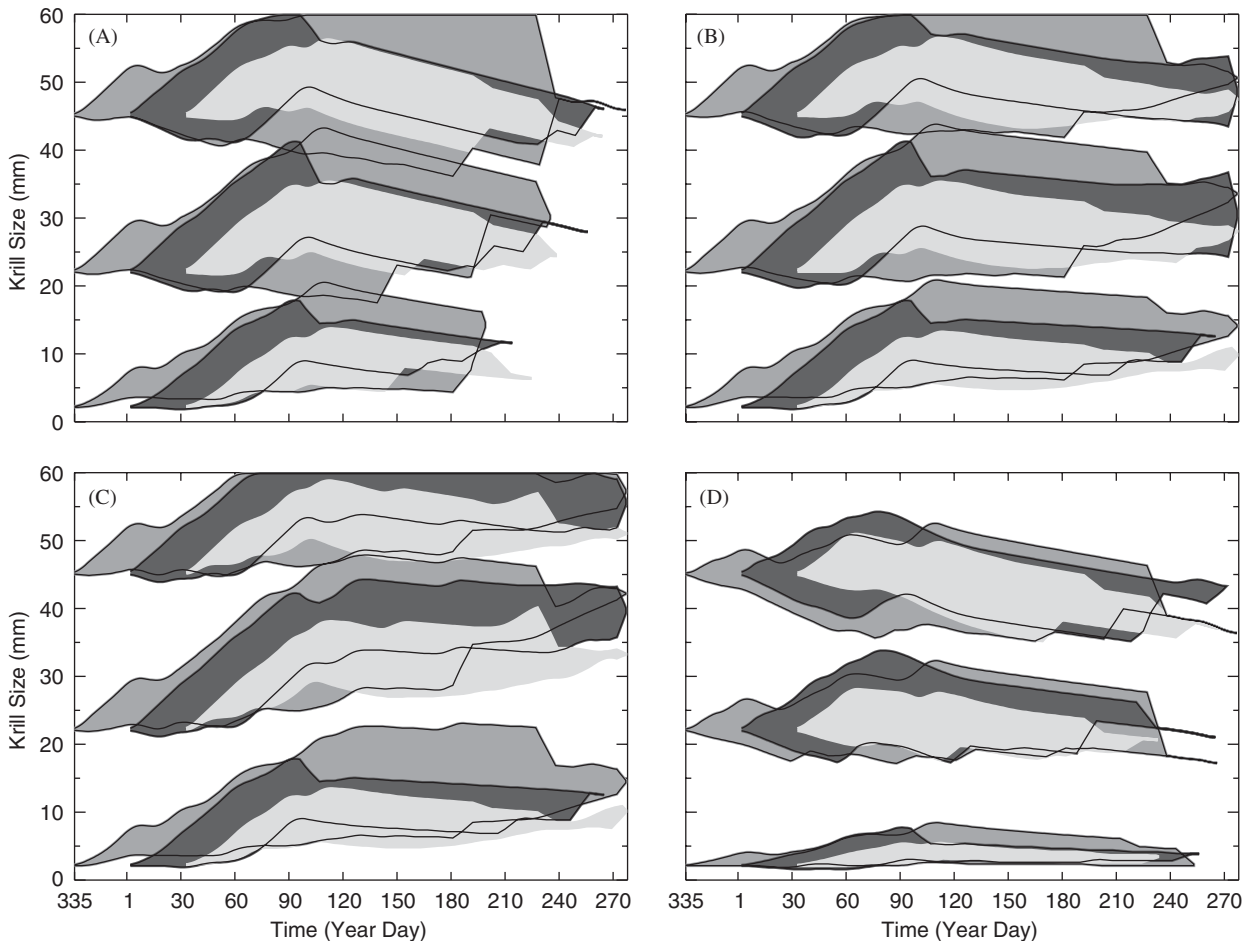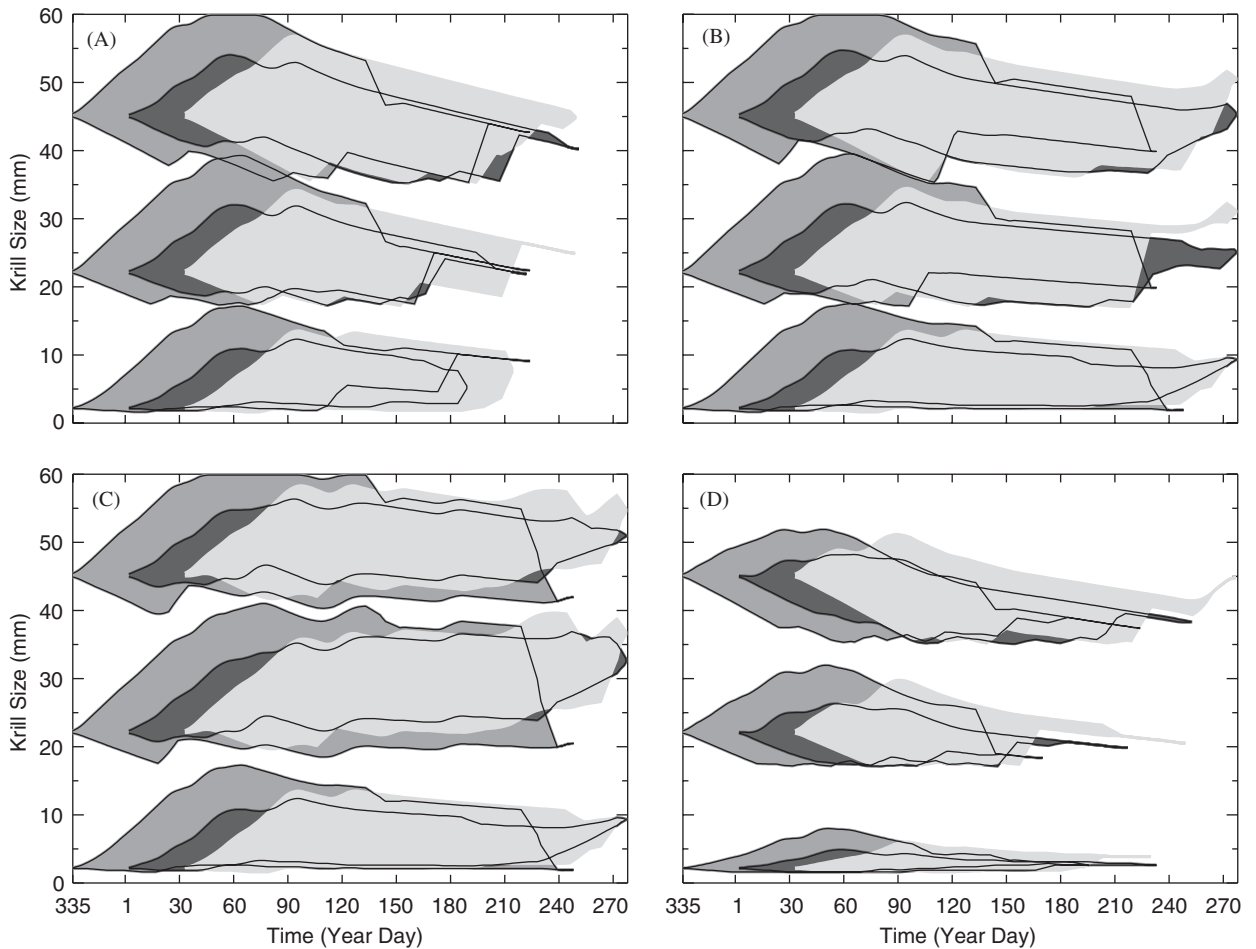
Fig. 9. Range of simulated growth of 2 mm krill (lower curves), 22 mm krill (middle curves), and 45 mm krill (upper curves) released in the Elephant Island/Scotia Sea region in December (medium shading), January (dark shading), and February (light shading) obtained for feeding on (A) phytoplankton only, (B) phytoplankton and sea ice biota with detritus, (C) phytoplankton, heterotrophs and sea ice biota with detritus, and (D) detritus only.

and adults (Fig. 9C) because more food is available during the simulation. Juvenile survival reaches 95%, and adult survival 100%. However, the same number of larvae (86%) survive as in the simulation with phytoplankton, sea ice biota and detritus.

During the first 5 months, detritus concentrations along the simulated drifter trajectories are high compared to other origination areas. As a result, all three sizes of krill grow slightly more during this time (Fig. 9D). However, subsequent detritus concentrations all greatly decrease and only 29% of juveniles, 48% of larvae, and 67% of adults reach South Georgia. None of the krill grow significantly compared to those feeding on phytoplankton.

3.1.4. Southwestern Antarctic Peninsula

Because of the great distance separating them, drifters originating at the southwestern Antarctic Peninsula (region 4) reach South Georgia in 211–306 days (Fach and Klinck, 2006). Feeding limited to phytoplankton only is deleterious (Fig. 10A, Table 6). Although sufficient food is available in the first 4 months to support growth, none of the krill survive the time needed to reach South Georgia. The long transit time and low phytoplankton concentrations from April onwards result in essentially no survival.

Augmentation with sea ice biota combined with detritus enables 83% of all krill to survive the necessary transport time (Fig. 10B, Table 6). This is

Table 5
Summary of krill growth simulations for different food types, initial sizes, and release times that are based on the food available along the trajectories of 21 drifters released in region 3, the Elephant Island/Scotia Sea area

Food type	Initial size (mm)	Release time (month)	% surviving	Final length (mm)	% dying	Length at death (mm)
P	2	Dec	43	3.1–10.6	57	1.9–13.4
		Jan	33	3.1–6.6	67	2.9–9.9
		Feb	33	17.9–36.6	67	1.9–10.9
	22	Dec	62	19.1–31.9	38	17.1–23.6
		Jan	43	18.9–24.4	57	17.1–24.9
		Feb	38	17.9–26.6	62	17.1–26.6
	45	Dec	86	35.6–52.9	14	35.1–39.6
		Jan	57	37.4–45.4	43	35.1– 40.4
		Feb	67	35.1–47.9	33	35.1–45.6
PID	2	Dec	86	2.1–14.1	14	1.6–10.1
		Jan	67	3.1–10.1	33	4.9–9.9
		Feb	71	2.4–9.1	29	1.6–10.9
	22	Dec	86	19.9–34.4	14	17.1
		Jan	86	17.9–27.6	14	17.1–20.9
		Feb	62	19.4–33.1	38	17.1–20.9
	45	Dec	95	37.4–55.4	5	35.1
		Jan	100	36.6–47.4	0	NA
		Feb	100	35.1–48.6	0	NA
PIDH	2	Dec	86	2.1–12.1	14	1.6–10.1
		Jan	67	3.1– 10.1	33	4.9–9.9
		Feb	71	2.4–9.1	29	1.6–10.6
	22	Dec	95	20.9–40.6	5	17.1
		Jan	100	23.9–37.6	0	NA
		Feb	100	19.9–33.9	0	NA
	45	Dec	100	40.4–59.9	0	NA
		Jan	100	40.1–54.1	0	NA
		Feb	100	41.7–57.6	0	NA
D	2	Dec	48	2.1–4.1	52	1.6–5.6
		Jan	24	1.9–2.4	76	1.6–3.4
		Feb	10	1.9–2.4	90	1.6–3.9
	22	Dec	29	18.4–25.4	71	17.1–21.6
		Jan	10	17.1–17.6	90	17.1–20.6
		Feb	14	20.4–20.9	86	17.1–21.6
	45	Dec	67	35.9–43.9	33	35.1–36.1
		Jan	43	35.9–39.1	57	35.1–38.1
		Feb	52	35.1–45.1	48	35.1–39.1

The percent (%) and length of krill surviving and dying, at the end of each simulation is shown. Abbreviations are: P (phytoplankton), PID (phytoplankton, sea ice biota, and detritus), PIDH (phytoplankton, sea ice biota, detritus, and copepods), D (detritus), NA (not applicable).

mostly because of the inclusion of detritus, as sea ice biota concentrations are low. Krill growth and survival improve even more with the addition of heterotrophic food (Fig. 10C, Table 6). All juveniles and adults survive the simulation time and develop to sizes of 26.6–42.1 mm and 46.4–57.9 mm, respectively. Detritus concentrations along trajectories

originating from this region are so low during the first months that all krill sizes relying on this sole food source die before the simulation ends (Fig. 10D, Table 6).

For all krill from the southwestern Antarctic Peninsula the combination of all four food sources is optimal. These krill do not encounter much sea
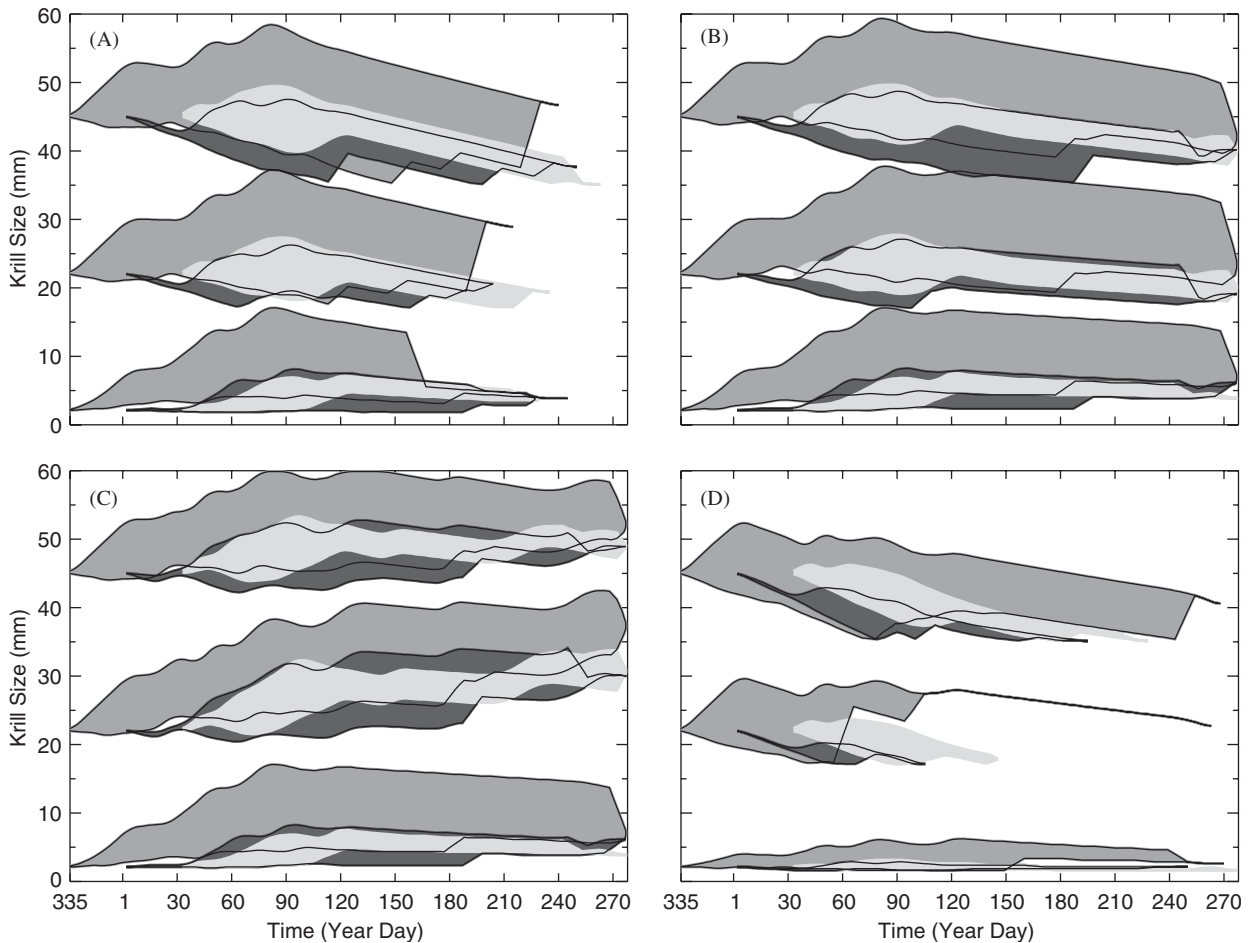
Fig. 10. Range of simulated growth of 2 mm krill (lower curves), 22 mm krill (middle curves), and 45 mm krill (upper curves) released in the southwest Antarctic Peninsula region in December (medium shading), January (dark shading), and February (light shading) obtained for feeding on (A) phytoplankton only, (B) phytoplankton and sea ice biota with detritus, (C) phytoplankton, heterotrophs and sea ice biota with detritus, and (D) detritus only.

ice but detritus and additional heterotrophic food increase their chances of survival during times of low phytoplankton concentrations.

3.1.5. Weddell Sea

The simulated growth for krill originating in the Weddell Sea continental shelf break area (region 5) differs from the other regions because most are transported to the Weddell–Scotia Confluence (WSC) and only few reach South Georgia. Phytoplankton alone is not sufficient to sustain these krill (Fig. 11A, Table 7) because most originate underneath sea ice where surface phytoplankton is scarce (Fig. 2D).

Sea ice biota (Fig. 3D) and detritus are abundant and their addition improves krill growth and survival (Fig. 11B, Table 7). All larval krill that

survive the simulation time (65%) along with juvenile and adult survivors (71% and 100%, respectively) grow to large sizes. While this growth is within the limit set in the model (maximum daily growth rate of $0.25 \, \text{mm} \, \text{d}^{-1}$) it is not realistic. Krill mortality here is attributed to the fact that individuals leave the sea ice covered area of the WSC at a time of low phytoplankton concentrations.

The addition of heterotrophic food (Fig. 4) improves the survival of juveniles and adults (Fig. 11C, Table 7) because it provides the resources when krill leave the ice-covered area. Again, the simulated growth rates are not realistic. Detritus concentrations along the drifter trajectories are high compared to trajectories from region 4, but lower than in all other areas. However, similar to results

Table 6
Summary of krill growth simulations for different food types, initial sizes, and release times that are based on the food available along the trajectories of six drifters released in region 4, the southwest Antarctic Peninsula

Food type	Initial size (mm)	Release time (month)	% surviving	Final length (mm)	% dying	Length at death (mm)
P	2	Dec	0	NA	100	3.1–13.4
	2	Jan	0	NA	100	1.9–5.9
		Feb	0	NA	100	3.6–5.1
	22	Dec	0	NA	100	17.4–28.9
		Jan	0	NA	100	17.1–20.6
	45	Feb	0	NA	100	17.1–21.1
		Dec	0	NA	100	35.1–46.6
		Jan	17	37.6	83	35.1–36.1
		Feb	17	35.4	83	35.1–39.1
PID	2	Dec	83	4.1–13.4	17	8.4
		Jan	100	2.4–6.4	0	NA
		Feb	67	3.9–6.1	33	4.1–4.9
	22	Dec	83	19.4–31.9	17	24.9
		Jan	83	17.1–23.6	17	17.1
		Feb	83	17.9–22.9	17	20.1
	45	Dec	83	38.9–49.4	17	42.9
		Jan	100	35.4–43.1	0	NA
		Feb	100	37.9–43.1	0	NA
PIDH	2	Dec	83	4.1–13.4	17	8.9
		Jan	100	2.4–6.7	0	NA
		Feb	67	3.9–6.1	33	4.1–4.9
	22	Dec	100	26.6–42.1	0	NA
		Jan	100	23.1–35.1	0	NA
		Feb	100	27.9–33.9	0	NA
	45	Dec	100	46.4–57.9	0	NA
		Jan	100	44.4–51.6	0	NA
		Feb	100	47.1–52.1	0	NA
D	2	Dec	0	NA	100	1.6–4.6
		Jan	0	NA	100	1.6–2.1
		Feb	0	NA	100	1.6–2.4
	22	Dec	0	NA	100	17.1–18.1
		Jan	0	NA	100	17.13
		Feb	0	NA	100	17.1–18.4
	45	Dec	0	NA	100	35.1–41.8
		Jan	0	NA	100	35.1
		Feb	0	NA	100	35.1–36.6

The percent (%) and length of krill surviving and dying, at the end of each simulation is shown. Abbreviations are: P (phytoplankton), PID (phytoplankton, sea ice biota, and detritus), PIDH (phytoplankton, sea ice biota, detritus, and copepods), D (detritus), NA (not applicable).

from other simulations this sole food source is not beneficial with only 12% larvae, 18% juveniles and 24% adults surviving (Fig. 11D).

Due to the release location sea ice biota is the dominant food source; addition of heterotrophic food increases the chances of survival for larger krill. These drifters need an additional 10 months of transport to reach South Georgia, as discussed in Fach and Klinck (2006), which places them at South Georgia in October to December of the following year.

3.2. Effect of different spawning times

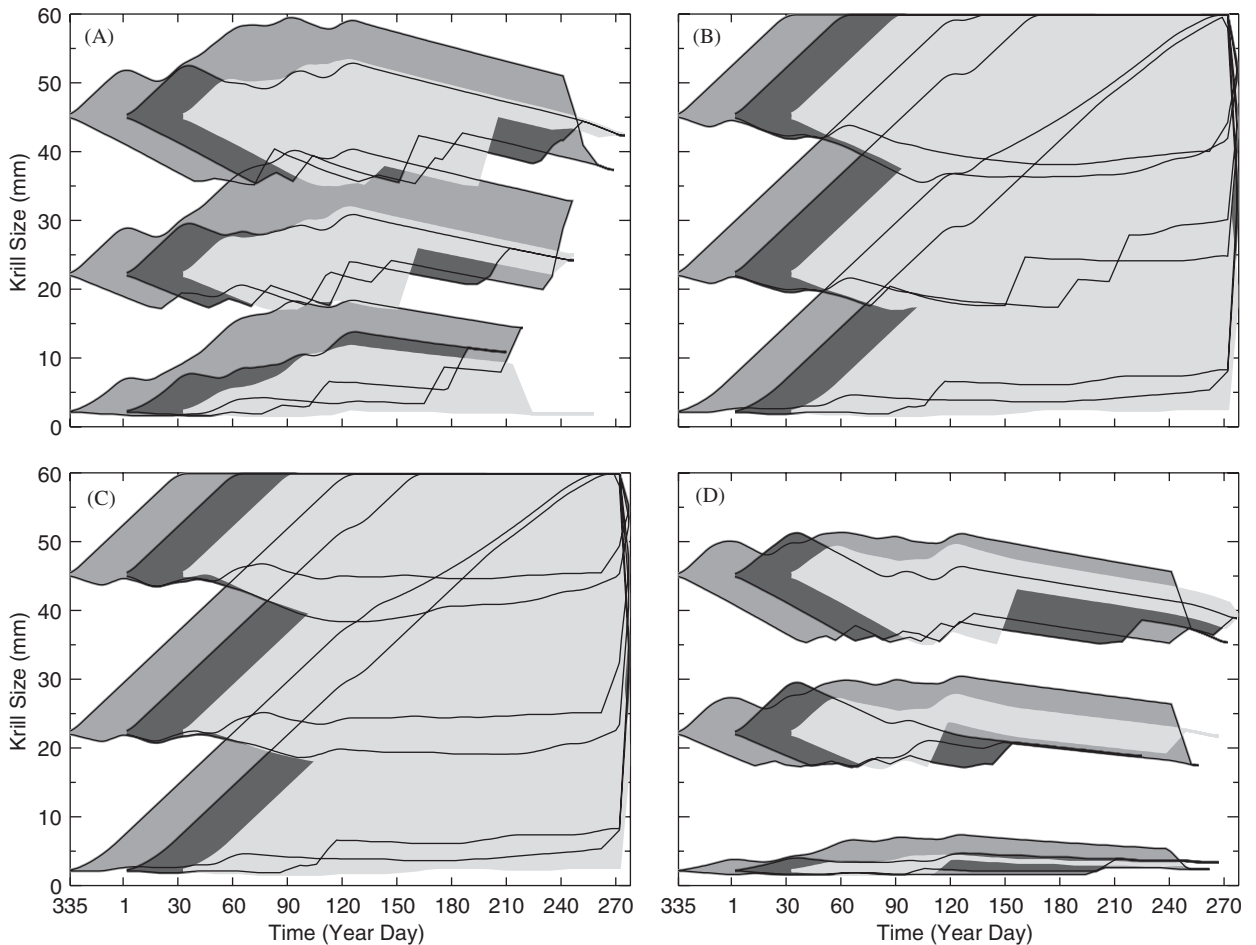The range of growth rates obtained for drifters originating at the west Antarctic Peninsula

Fig. 11. Range of simulated growth of 2 mm krill (lower curves), 22 mm krill (middle curves), and 45 mm krill (upper curves) released in the Weddell Sea region in December (medium shading), January (dark shading), and February (light shading) obtained for feeding on (A) phytoplankton only, (B) phytoplankton and sea ice biota with detritus, (C) phytoplankton, heterotrophs and sea ice biota with detritus, and (D) detritus only.

(region 1) during January is larger for the different food time series, except detritus, than those from December and February simulations (Figs. 7A–C). However, the important results from the simulations are krill survival and growth rates over the time required for the drifter to reach South Georgia. The length of time during which high phytoplankton concentrations are encountered decreases significantly with later spawning times (Fig. 2). This is apparent in the simulation results for the three initial krill sizes and the first three feeding simulations (Figs. 7A–C), wherein the number and maximum size of survivors decrease between December and February releases. This also applies when detritus is the primary food source (Fig. 7D) and the survival rate is highest for krill released in December.

December release (i.e. early spawning) is optimal for survival and growth of krill transported to South Georgia from the western Antarctic Peninsula. This is particularly true for larval krill which is the size class most likely to get transported to South Georgia. For juveniles and adults the difference in growth and survival for the different spawning times is small when they are able to exploit a combination of all food sources.

The effects of different spawning times for krill originating in Bransfield Strait (region 2) (Fig. 8, Table 4) are similar to those from region 1. December release is optimal for feeding on all food types except detritus. The results for feeding on detritus only are also similar to those obtained for region 1 except that January is the best start time in

Table 7

Summary of krill growth simulations for different food types, initial sizes, and release times that are based on the food available along the trajectories of 17 drifters released in region 5, the Weddell Sea

Food type	Initial size (mm)	Release time (month)	% surviving	Final length (mm)	% dying	Length at death (mm)
P	2	Dec	0	NA	100	1.6–14.4
		Jan	0	NA	100	1.6–10.9
		Feb	0	NA	100	1.6–8.8
	22	Dec	12	24.9–32.6	88	17.1–24.1
		Jan	0	NA	100	17.1–24.1
		Feb	6	22.1	94	17.1–24.9
	45	Dec	18	43.9–50.6	82	35.1–41.6
		Jan	0	NA	100	35.1–42.1
		Feb	6	43.1	94	35.1–42.4
PID	2	Dec	65	5.4–59.9	35	6.1–15.1
		Jan	47	8.1–59.9	53	1.9–8.1
		Feb	59	2.6–53.4	41	1.6–8.6
	22	Dec	71	29.4–59.9	29	17.4–27.6
		Jan	65	18.1–59.9	35	17.1–21.6
		Feb	59	25.9–59.9	41	17.1
	45	Dec	100	40.1–59.9	0	NA
		Jan	82	42.1–59.9	18	36.4–40.6
		Feb	82	36.9–59.9	18	35.1
PIDH	2	Dec	65	5.4–59.9	35	6.1–15.1
		Jan	47	8.1–59.9	53	1.9–8.4
		Feb	59	2.6–53.1	41	1.6–8.6
	22	Dec	94	25.1–59.9	6	27.9
		Jan	82	23.1–59.9	18	18.4–21.9
		Feb	94	22.4–59.9	6	17.6
	45	Dec	100	45.4–59.9	0	NA
		Jan	100	45.4–59.9	0	NA
		Feb	100	43.6–59.9	0	NA
D	2	Dec	12	3.6–4.9	88	1.6–5.4
		Jan	0	NA	100	1.6–3.4
		Feb	6	2.9	94	1.6–3.1
	22	Dec	18	10.1–26.1	82	17.1–19.9
		Jan	0	NA	100	17.1–23.1
		Feb	6	19.9	94	17.1–21.6
	45	Dec	24	35.1–45.4	76	35.1–37.4
		Jan	6	38.6	94	35.1–40.9
		Feb	18	37.1–40.6	82	35.1

The percent (%) and length of krill surviving and dying, at the end of each simulation is shown. Abbreviations are: P (phytoplankton), PID (phytoplankton, sea ice biota, and detritus), PIDH (phytoplankton, sea ice biota, detritus, and copepods), D (detritus), NA (not applicable).

this simulation (Fig. 8D, Table 4). For krill originating in the Elephant Island/Scotia Sea area (region 3), the southwest Antarctic Peninsula (region 4), and the Weddell Sea (region 5) December release is most favorable for krill feeding on all four food sources although differences in growth between release times are small.

3.3. Krill growth rates

Daily growth rates of krill being transported from the west Antarctic Peninsula along a particular drifter path were examined to assess the effect of different food sources on krill growth and survival. Transport begins in January and growth rates
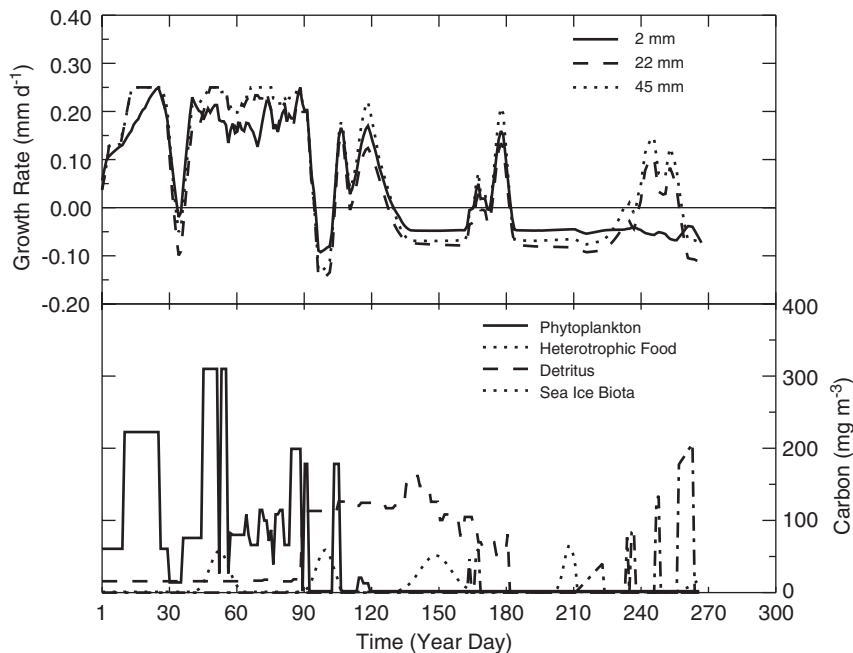
Fig. 12. Simulated daily growth rates of 2, 22 and 45 mm krill feeding on all food sources combined when starting transport from the west Antarctic Peninsula in January. The time series of phytoplankton, sea ice biota, heterotrophic food and detritus are shown.

associated with 2 mm krill feeding on combined four food sources (Fig. 12) range from −0.1 to 0.25 mm d^{-1}. Growth rates of 22 and 45 mm krill are between −0.13–0.25 mm d^{-1} and −0.15–0.25 mm d^{-1}, respectively. Periods of shrinking occur in all size groups, but more so for 45 mm krill because of the higher energy demand. Shrinking rates decrease between 45, 22, and 2 mm krill due to decreasing size related metabolic rates. The simulated values are within the range of observed growth rates, 0.101–0.179 mm d^{-1} (Rosenberg et al., 1986) and 0.33 mm d^{-1} (Clarke and Morris, 1983) summarized in Siegel and Nicol (2000).

Different food sources have different effects on the daily growth rates (Fig. 12). At the beginning of transport phytoplankton concentrations are low but increase rapidly after 10 days. This causes an increase in the larval growth rate over the time of high phytoplankton supply. Their growth rate does not increase quickly because food uptake is limited by their small size (Hofmann and Lascara, 2000; Fach et al., 2002). Juvenile and adult krill growth rates increase more rapidly because of the ability to feed on heterotrophic food in conjunction with a larger food ration. A sudden decrease in phytoplankton food causes negative growth rates (shrinking) in all size classes. Until day 90 growth rates are closely tied to available phytoplankton concentra-

tions. Constant high phytoplankton concentrations, such as occur between day 40 and day 50, indicate that krill encountered an eddy which maintained a bloom for a period of time.

After day 90, other food sources gain more importance (Fig. 12). The combination of heterotrophic and phytoplankton food sources promote increased growth rates for all size classes around day 115, after which shrinkage starts because of insufficient food. Larval krill attain sizes > 18 mm at this time and are therefore able to utilize the heterotrophic food. Detritus as the only food source is available after day 110, but because of its low quality the amount available is not enough to sustain growth in this simulation. Krill encounter four patches of sea ice biota after day 210. Larval krill have shrunk below 18 mm by this time and show a decreased growth rate, indicating that low concentrations of sea ice biota as a sole food source have a negative effect on krill growth. The energy needed to feed on sea ice biota exceeds that gained from this food. This is also observed for juveniles and adults.

In the field, growth may be slowed for older krill during maturation in summer because of the energy needed for this process. Growth parameters calculated by Rosenberg et al. (1986) using the von-Bertalanffy growth function indicate that maximum
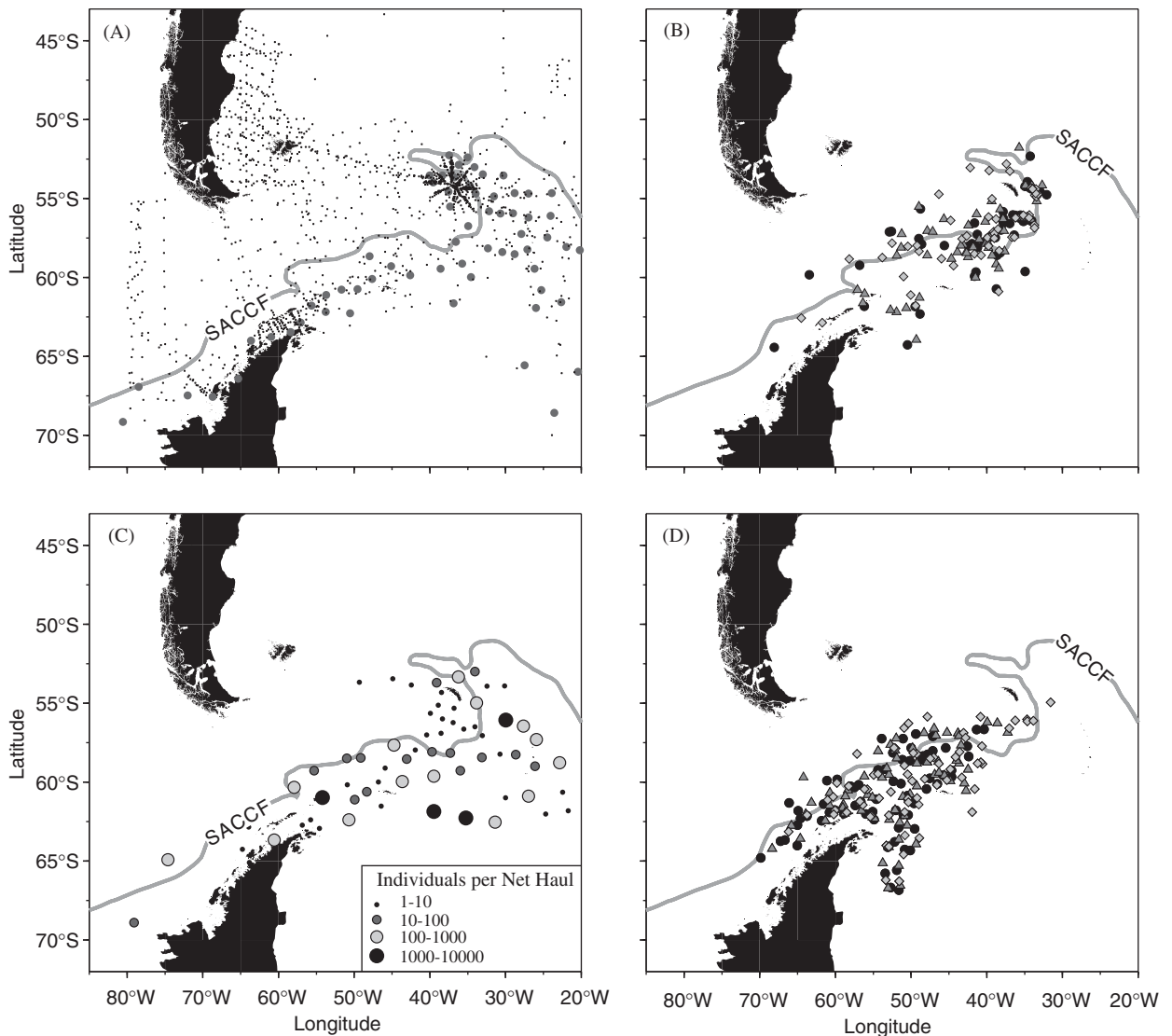
Fig. 13. Distribution of Antarctic krill: (A) surface larvae and (C) older krill (>20 mm) in summer (January–March) across the study region extracted from net haul observations obtained during the *Discovery* investigations, 1926–1940 (Marr, 1962). Simulated distribution of (B) larval krill across the study area for individuals that were released in December (●), January (▲), and February (◆) and (D) simulated distribution of older krill (>20 mm) released in January at the end of January (●), February (▲), and March (◆). The small dots in (A) indicate the distribution of the sampling locations. The heavy line shows the Southern Antarctic Circumpolar Current Front (SACCF) as given in Orsi et al. (1995).

growth occurs over about 3 months, which is in agreement with Mauchline (1980) who calculated a maximum growth period of 90 days. Similar conclusions were derived by Siegel (1982) in that krill growth at the Antarctic Peninsula may be confined to the period from late October to end of January/early February. In this model the growth period is dependent solely on food supply, which results in maximum growth rates during summer only (Fig. 12), consistent with above calculations.

3.4. Distribution of krill across the Scotia Sea

Krill size distributions obtained from simulations along trajectories can be compared with observed krill length–frequency distributions from the *Discovery* data (Marr, 1962) (Figs. 13A,C). The distribution of larval krill at the end of the simulation in which combined phytoplankton, sea ice biota, detritus and heterotrophic food are available (Fig. 13B) shows that they are distributed

along the path of the Southern Antarctic Circumpolar Current Front (SACCF) from the Antarctic Peninsula to South Georgia with most located in the southeastern Scotia Sea. Large numbers of larvae are also found at the eastern and northern sides of South Georgia. This distribution compares well with *Discovery* observations (Fig. 13A) which show abundant krill larvae distributed along the western Antarctic Peninsula, across the Scotia Sea south of the SACCF, and around South Georgia. However, the simulated distributions show larvae north of the SACCF west of 43°W which is not observed in the measured larval distribution.

The simulated length–frequency distributions obtained for >20 mm krill feeding on combined food sources (Fig. 13D) can be compared to distributions of similar sizes reported in summer (January–March) (Fig. 13C). These comparisons show that the earlier the simulation starts, the further the krill spread across the Scotia Sea by the end of January, February, or March. The *Discovery* data indicate older krill distributed across the whole Scotia Sea along the path of the SACCF. The simulated krill distributions also show larval and older krill transported to the western Weddell Sea, an area not sampled during the *Discovery* cruises (cf. (Fig. 13A).

4. Discussion

4.1. Krill transport and survival

Krill are not just passive particles in the ocean currents around the Antarctic Continent (Murphy et al. 2004a,b). Behavior and swimming ability of adult krill may allow more selection of location or retention in an area than the passive drifter approach used in this study (Murphy et al., 2004a). However, it has been shown that advection by ocean currents is a major factor in determining the large-scale distribution (Marr, 1962; Murphy et al., 1998). Although Nicol (2003a) suggests the concept of krill flux around the Antarctic Continent is faulty, there have only been few studies of the potential affects of behavior in analyses of large-scale distribution (Murphy et al., 2004a). This modeling study, therefore, is best regarded as a first-order description of what may influence krill distribution and survival in the Scotia Sea and environs. It clearly demonstrates that krill transport across the Scotia Sea is possible and that there are

sufficient food resources available to krill to survive such transport.

The population structure of many species can be considered as an array of local populations linked by variable degrees of gene flow (Wade and McCauley, 1988). In such a metapopulation concept, migrants are not only an integral part of the structure but are essential for the survival, persistence, and expansion of the metapopulation (McQuinn, 1997). Migrants abandon their local population and cannot be selected for at that level. However, these migrants can be selected for in the environment to which they emigrate and are therefore advantageous by ensuring survival of the resident population. This may be the case for krill transported from the Antarctic Peninsula and Weddell Sea to South Georgia. South Georgia krill is assumed to be a "sink population" within the metapopulation of the greater Antarctic Peninsula/ Scotia Sea region. However, recent studies indicate that there may be downstream connections of the South Georgia population back into the wider population of krill further south and east (Murphy et al., 2004a). Krill populations found along the Antarctic Peninsula and in the Weddell Sea are assumed to be the source of South Georgia krill. The survival of the South Georgia population and their predators is therefore dependent on input of viable krill from areas along the western Antarctic Peninsula and the Weddell Sea.

Observations suggest that 1+ krill and, to a greater extent 2+ krill, arrive at South Georgia mainly from the east (Murphy et al., 1998; Watkins et al., 1999). The SACCF bounds the east side of South Georgia and most krill (91%) in the simulations are transported to this side of the island. Larvae released along the west Antarctic Peninsula, Bransfield Strait, Elephant Island/Scotia Sea area and southwest Antarctic Peninsula grow to 1+ sizes during the average time needed for drifters to reach South Georgia, while juveniles grow to 2+ sizes. However, krill originating at the southwest Antarctic Peninsula attain smaller sizes than those from other areas because of long transport times and low food supply. Thus, larvae produced in the main spawning area along the Antarctic Peninsula can be transported to South Georgia and arrive at sizes comparable to those observed for the local population. However, individuals spawned further south along the western Antarctic Peninsula are not likely to reach South Georgia at these sizes after 10 months. The same is true for the individuals

spawned in the far east Scotia Sea, because krill originating there are transported eastward and never reach South Georgia (Fach and Klinck, 2006). Drifters located further north in Drake Passage can be transported to South Georgia but krill are not typically found in this offshore area (Fig. 13A). Moreover, any drifters positioned in the Scotia Sea along the path of the SACCF will be transported to South Georgia.

4.1.1. Weddell Sea

Fach and Klinck (2006) show that an average transport time of 263 days places krill near the WSC from where advection to South Georgia is possible. During transport from the Weddell Sea shelf break to the WSC, larvae and juveniles do not encounter significant periods of low food supply. As a result, when reaching the WSC, these stages have reached 2+ to 4+ sizes, respectively, and continue transport from there.

Additional simulations starting in the WSC in November (after arrival there in October) showed that krill require on average 10 additional months from different areas there to reach South Georgia (Fach and Klinck, 2006). Thus, krill arrive at South Georgia after a transport time of approximately 20 months. Concentrations of all four food sources along the simulated drifter paths originating in the WSC, as defined in this study, are sufficient to sustain krill during this additional transport.
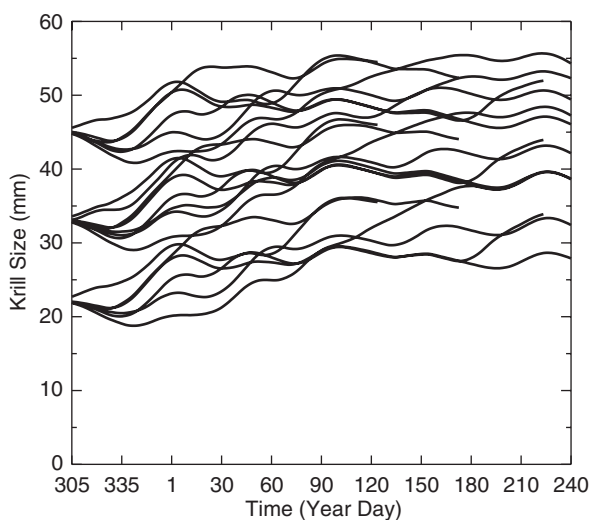

Fig. 14. Simulated growth of 22 mm krill (lower curves), 33 mm krill (middle curves), and 45 mm krill (upper curves) released in November (Year Day 305) in the Weddell–Scotia Confluence.

Simulations using the krill size-class model suggest that all classes starting from the WSC survive and grow during transport to South Georgia (Fig. 14). Juvenile krill (22 mm) grow to between 28 and 39 mm, subadult krill (33 mm) grow to between 39 and 46 mm, while adult krill (45 mm) measure 45–55 mm. Therefore, krill originating in the Weddell Sea can be transported to South Georgia in approximately 20 months, thereby contributing 2+, 3+ and older krill to the population there.

4.1.2. Effect of different spawning times on transport

Krill are believed to spawn during 3 or more years of their life span (Siegel, 1987; Nicol et al., 1995). It has been suggested that they spawn multiple times during 1 year (Ross and Quetin, 1983), but laboratory studies were only able to demonstrate a single spawning event (Harrington and Ikeda, 1986). Nicol et al. (1995) argued that multiple spawning would require above average phytoplankton concentrations and filtration rates in order for krill to fulfill the necessary energy input, and thus may not be likely. Spiridonov (1995) showed that there is considerable variation in the start, peak and duration of krill spawning along the Antarctic Peninsula. Spawning may start early (late November) and be extended (3–3.5 months) or start early and last for a short time. Variable starting times have also been observed.

The simulations of krill growth suggest that early spawning is most beneficial to ensure survival and transport to South Georgia, especially from the main spawning areas off the western Antarctic Peninsula, Bransfield Strait and Weddell Sea. In contrast, later spawning increases the possibility for krill originating further north in Drake Passage to reach South Georgia. Thus, a single spawn early in the season, rather than prolonged multiple spawns, may result in a greater krill supply to South Georgia. However, the timing of a single spawn is crucial because of variability in food supply and circulation characteristics. The timing of spawning relative to environmental characteristics may contribute to the year-to-year fluctuations in krill biomass observed at South Georgia.

4.1.3. Effect of environmental changes

The Antarctic Circumpolar Wave (ACW) causes anomalous sea surface temperatures (SST) and sea ice anomalies to propagate eastward around Antarctica (White and Peterson, 1996). Atmospheric response to changes in SST then produces a positive

feedback to the ocean which is eastward displacement of the anomalous SST and thereby eastward propagation of the ACW. Although Antarctic sea ice is predominantly annual, interannual variability does occur (Murphy et al., 1995). Zwally et al. (1983) showed that the position of anomalies in maximum sea ice extent proceeds around the Antarctic Continent with a period of approximately 7–9 years.

Timing of the advance and retreat of the sea ice edge determines irradiance and hence potential light available for photosynthesis in the biologically active marginal ice zone. Total irradiance may vary by as much as 50% depending on timing along the seasonal ice edge (Murphy et al., 1995) affecting primary production and higher trophic levels.

Propagation of high sea ice extent around the continent imposes interannual changes on the Southern Ocean ecosystem. High concentration and long duration of sea ice is important for overwintering krill, especially larvae (Daly, 1990), and also provides sufficient food to promote early spawning. Two consecutive years of high sea ice concentration are necessary for successful krill recruitment (Siegel and Loeb, 1995; Loeb et al., 1997). Because of the periodic dynamics of the ACW, sea ice extent shifts around Antarctica with fluctuations between low and high sea ice years. Years of low sea ice result in less krill recruitment and a decline in krill biomass that occurs with an observed periodicity. At the same time, juvenile krill originating along the west Antarctic Peninsula continental shelf are selected for by biological and environmental factors to successfully complete transport to South Georgia. Variable sea ice extent because of the ACW therefore potentially has a large effect on the supply and successful transport of krill from this source population. However, because of the distance between the Antarctic Peninsula and South Georgia and dynamics of the progressing ACW, a winter of low sea ice extent at the Peninsula might not necessarily be so at South Georgia. This variability may be a contributing factor to the out-of-phase fluctuations in krill biomass in the west Antarctic Peninsula and South Georgia regions.

The effects of the ACW on krill populations is only now being recognized. Additional, multi-year observational studies are needed in order to investigate the teleconnections between periodic changes in sea ice extent and concentration and krill abundance at the Antarctic Peninsula and South Georgia.

4.2. Food supply

Spawning between December and February at the four main regions along the Antarctic Peninsula places krill in an environment in which surface chlorophyll concentrations are not always sufficient to support growth over the 58–306 days needed for transport to South Georgia. Sea ice biota do not provide a viable alternative food source because sea ice extent and concentration tends to be low here. Possible additional food may be available to krill through the deep chlorophyll maxima, which is not included in this study because of limited data availability. Spawning in December with early transport results in more successful growth than does later spawning because of summer food availability prior to the rapid decline in phytoplankton concentrations during fall.

The implication of these simulations is that all size classes, but particularly larvae, rely on additional food sources during transport across the Scotia Sea, especially in winter, as has been suggested by Fach et al. (2002). This food source, apart from additional phytoplankton available at depth that is not included in this model set-up, may be detritus (Kawaguchi et al., 1986; Holm-Hansen and Huntley, 1984; Daly, 1990, 2004). The addition of detritus has a positive influence on krill growth and survival, especially larvae (Daly, 1990), and is most needed during winter. Under the current assumptions for food sources results show that growth and survival during transport from the Antarctic Peninsula to South Georgia is most successful when krill feeds on a combination of phytoplankton, sea ice biota, detritus and heterotrophs.

Krill growth rates are influenced by temperature (Poleck and Denys, 1982) with increased temperatures resulting in a higher growth rate. Krill in the Scotia Sea experience temperatures from $-1.8\,^{\circ}\text{C}$ in winter to $4\,^{\circ}\text{C}$ in summer. The simulated krill growth rates increase in response to increased temperature only in conjunction with high food concentrations (Fach et al., 2002). However, the changes in growth rate due to temperature alone are small relative to those produced by changes in food concentration (see Fach et al., 2002). Therefore, enhancements due to increased temperature are not sufficient to compensate for a low food environment.

The food time series used in this study represent specific assumptions about how food is distributed

across the Scotia Sea and, once defined, food availability and type does not evolve along a given trajectory. Polar phytoplankton growth is mainly influenced by temperature, the presence or absence of sea ice, nutrient supply and seasonal variations in available light (Smith and Sakshaug, 1990). Changes in water temperature, sea ice cover, and wind stress that may result in increased or decreased water column mixing will have a strong effect on phytoplankton growth and species composition, as well as location and magnitude of deep chlorophyll maxima. Also, POC concentrations are dependent on phytoplankton species composition and physiological state (Cota et al., 1992).

Environmental changes thus propagate throughout the food web and are important factors determining the food supply available to krill during transport. Inclusion of the effects of environmental changes on krill food supply requires development of lower trophic level models that allow autotrophic and heterotrophic food distributions to evolve over time in response to environmental conditions. Such a model will then be able to translate the repercussions of climate change discussed in Fach and Klinck (2006) into the overall food web and allow testing of these effects on food availability and krill.

4.2.1. Deep chlorophyll maximum

High phytoplankton concentrations ($> 1.0 \, \mathrm{mg \, m^{-3}}$) are found below 60 m in the study area (El-Sayed and Weber, 1982; Bianchi et al., 1992; Tréguer and Jacques, 1992; Smith et al., 1996; Whitehouse et al., 1996). Deep chlorophyll maxima have been observed mostly in the summer/fall in the Scotia Sea (El-Sayed and Weber, 1982), western Antarctic Peninsula (Bianchi et al., 1992; Tréguer and Jacques, 1992; Smith et al., 1996) and near South Georgia (Whitehouse et al., 1996); they are not observed during winter/spring (El-Sayed and Weber, 1982; Smith et al., 1996). Due to limited data this feature was not included in this modeling approach, although it may well be one additional food source available to krill in summer. Therefore, the presented results should be interpreted as first-order scenarios, with the provision that there may be more phytoplankton available to krill during transport.

To exploit this food source krill must be able to reach depths of 80–100 m. Krill exhibit a distinct diel vertical migration pattern (Marr, 1962; Nast, 1979; Kalinowski and Witek, 1980; Everson and Ward, 1980; Godlewska, 1996) with no difference between female and male behavior (Nast, 1979). However, there is a connection between krill size and the amplitude and period of migration (Nast, 1979; Godlewska, 1996; Everson and Ward, 1980) with a 24-h period and larger vertical migration distance (to 100 m) associated with older krill and a 12-h period, and a smaller range of vertical migration associated with younger krill (Everson and Ward, 1980; Godlewska, 1996). This difference is believed to result from passive krill sinking following feeding (Pavlov, 1969; Everson and Ward, 1980). After digestion, krill actively ascend to the surface where high chlorophyll a concentrations occur. Because small and large krill need different periods of time for feeding and digestion, size separation occurs with larger krill located above or below smaller krill (Everson and Ward, 1980). Godlewska (1996) shows that the amount of phytoplankton available for feeding is a main factor influencing krill migration. High phytoplankton abundance will cause krill to migrate with a maximum amplitude and longer period, while low food supply will cause krill to migrate less and over a shorter period. Krill are therefore found at average depths of 50–70 m (Godlewska, 1996). There are seasonal changes in vertical migration patterns due to phytoplankton availability (Godlewska, 1996), with greatest migrations in January.

Migration and feeding behavior are not included in the modeling framework used in this study. The drifters in the simulated circulation fields remain at a fixed depth of 50 m and the HOPS model, as it was implemented here, does not allow for vertical migration (Fach and Klinck, 2006). Vertical migration must be included in future studies because concentrations of chlorophyll at depth may be an important additional food source for krill. Also, vertical migration positions krill at levels with different flow speeds that may influence overall transport times (Murphy et al., 2004a). The inclusion of behavior requires parameterization of corresponding energy requirements in the krill growth model linking energy demand to behavior. However, data on the energy expenditures associated with swimming activity are limited (Kils, 1982) and not adequate for application. Thus, additional measurements of energy expenditure during swimming and vertical migration are needed.

4.2.2. Selection of age group?

The simulated drifter results (Fach and Klinck, 2006) showed that there are four regions from which

krill can be transported to South Georgia in $\leqslant 10$ months and that it is possible for larval krill to be transported from these regions to South Georgia and grow to 1+ sizes during transport using food sources as defined in this study. In addition, juveniles from all four regions survive transport to South Georgia and can grow to sizes of 2+ and 3+ krill.

Larvae and juveniles from the southwestern Antarctic Peninsula survive transport to South Georgia but individuals that arrive at South Georgia are relatively small (4.1–13.4 mm and 26.6–42.1 mm) compared to those originating from the other three regions. The transport pathways originating at the southwestern Antarctic Peninsula show that drifters spend up to 4–5 months in transit toward the tip of the Antarctic Peninsula. Thus, larvae and juveniles originating here may not be the primary source for krill at South Georgia. More likely, they supply 1+ and 2+ animals to the west Antarctic Peninsula and Elephant Island/Scotia Sea regions which are located along their paths.

All krill sizes originating in the Weddell Sea are likely to survive transport to South Georgia due to their access to large amounts of sea ice biota and detritus during the first 10 months of transport. No size class selection was observed for krill originating here. Krill arriving at South Georgia after 20 months reach sizes of 2+, 3+ and older classes.

In summary, food availability and the length of time needed for transport together favor juveniles as the stage most able to survive transport to South Georgia from regions 1–4. This implies that given the assumptions for food sources in this study regions 1–4 supply mainly 2+ animals while 2+ and 3+ animals at South Georgia are derived from the Weddell Sea. These results agree with studies that show that 2+ typically is the youngest dominant size class at South Georgia while only occasionally the 1+ size class is dominant (Mackintosh, 1972; Murphy et al., 1998).

4.2.3. Estimates of krill food demand

Recent estimations of krill densities for the Scotia Sea and environs (Hewitt et al., 2004), made from acoustic and net sampling, gave a mean density in the Scotia Sea of $24.54\,\mathrm{g\,m^{-2}}$, at the Antarctic Peninsula of $11.24\,\mathrm{g\,m^{-2}}$, and $39.30\,\mathrm{g\,m^{-2}}$ at South Georgia. All estimates represent krill fresh weight and are integrated over the upper 200 m (Hewitt et al., 2004).

The amount of food necessary to sustain such large summer krill densities was estimated from the metabolic needs of different-sized krill. Field-derived krill growth rates show that daily growth rates decrease with age (Siegel and Nicol, 2000). Larvae grow fastest at 0.13–$0.16\,\mathrm{mm\,d^{-1}}$, 1+ krill at 0.12–$0.148\,\mathrm{mm\,d^{-1}}$, and older stages may only grow 0.025–$0.07\,\mathrm{mm\,d^{-1}}$ (Siegel and Nicol, 2000). However, there have also been observations of 30 mm krill growing at $0.33\,\mathrm{mm\,d^{-1}}$ (Clarke and Morris, 1983).

Assuming a mean growth rate of $0.148\,\mathrm{mm\,d^{-1}}$, the parameterizations used for ingestion and respiration in the krill growth model (Hofmann and Lascara, 2000) suggest that larval krill (2 mm) gain $0.0027\,\mathrm{mg\,C\,d^{-1}}$ body weight. Assuming further that summer food sources are phytoplankton, detritus and heterotrophs and that feeding on sea ice biota is unlikely because of reduced or no sea ice at the specified locations, a total of $76.21\,\mathrm{mg\,C\,d^{-1}}$ food intake is needed by larvae to grow $0.15\,\mathrm{mm\,d^{-1}}$. The required food intake reflects what is needed to cover high larval respiration costs and provide energy for positive growth. These high rates may be due to the feeding parameterization for 2 mm krill which is extrapolated from observations of larger krill (Hofmann and Lascara, 2000) and may overestimate larval metabolic needs.

A 22 mm juvenile requires an increase of $0.161\,\mathrm{mg\,C\,d^{-1}}$ body weight to grow $0.15\,\mathrm{mm\,d^{-1}}$ which translates into a total of $67.24\,\mathrm{mg\,C\,d^{-1}}$ food intake per individual. A 45 mm adult needs to gain $0.84\,\mathrm{mg\,C\,d^{-1}}$ to grow the same amount. This requires a total of $73.85\,\mathrm{mg\,C\,d^{-1}}$ food intake.

Using the above krill density estimates for the Scotia Sea, Antarctic Peninsula, and South Georgia and assuming that larvae, juveniles and adults are present in equal numbers in each of the areas the amount of food necessary to sustain this biomass can be calculated. Weights of the different krill sizes are calculated from equations used in the growth model (Hofmann and Lascara, 2000): 0.23 mg for larvae, 83.22 mg for juveniles, and 162.01 mg for adults. The resulting food demand for South Georgia krill is $34.77\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$. The Scotia Sea area would need to supply $21.71\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$ to feed $24.54\,\mathrm{g\,m^{-2}}$ of krill and at the west Antarctic Peninsula $11.24\,\mathrm{g\,m^{-2}}$ is needed to satisfy a krill demand of $9.95\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$.

The values at South Georgia seem realistic for summer conditions, where high average phytoplankton concentrations of $5.1\,\mathrm{mg\,chl\,m^{-3}}$ have

been measured and ocean color distributions show intense phytoplankton blooms of >10 mg chlorophyll a m^{-3} over the shelf (for review, see Atkinson et al., 2001). Other studies in this region estimate mean phytoplankton biomass of 132 mg chl m^{-2} $(6.6$ g C m$^{-2})$ to 625 mg chl m^{-2} $(31.25$ g C m$^{-2})$ (Ward et al., 1995; Atkinson et al., 1996) for the surface mixed layer over the shelf in summer. In addition, mean summer time mesozooplankton biomass of 5.85 g C m^{-2} and 5.54 g C m^{-2} were calculated by Ward et al. (1995) and Atkinson et al. (1996), respectively. These values provide an average range of 12.45–36.47 mg C m^{-2} for both sources. When detritus concentrations are included (POC:Chl ratio of 38 in summer) a total of 17.47–60.54 g C m^{-2} may be available for krill to meet the demand of 58.28 g C m^{-2} d^{-1}. It should be noted that the observed values used here are averages of individual patches representing a wide range of biomass. In addition, biomass estimates vary widely between studies (Atkinson and Snÿder, 1997).

January phytoplankton abundance in the west Antarctic Peninsula region derived from Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) cruise data (Priddle et al., 1994) ranges from 0.45 to 1334.5 mg chlorophyll a m^{-2} integrated over the upper 50 m. High phytoplankton concentrations here were reported by Holm-Hansen and Mitchell (1991) who observed biomass exceeding >700 mg chl m^{-2} at some continental shelf stations. Mean phytoplankton biomass in the upper 50 m was 291 mg chl m^{-2} in December 1986 and 176 mg chl m^{-2} in January 1987 (Mitchell and Holm-Hansen, 1991a,b). These biomass levels are more than what is needed to sustain high krill densities observed in this region. Including detritus concentrations derived from POC:Chl ratios, a total of 52.02 g C m^{-2} may be available.

Data available for heterotroph concentrations at the west Antarctic Peninsula are sparse. Schnack-Schiel and Mujica (1994) provide abundance estimates of the two dominant copepods species *Calanoides acutus* and *Metridia gerlachi* of 2000 and 20,000 per 1000 m^3, respectively. For Gerlache Strait at the northern tip of the Antarctic Peninsula, Huntley et al. (1994b) reported *Calnoides acutus* numbers of 1086 m^{-2} at the end of October 1989, which declined to 244 m^{-2} by the end of November 1989. Again, these calculations show that it may be patches of high food concentrations that krill depend on for growth and survival.

4.3. Effect of variability

4.3.1. Variability of food sources

The Scotia Sea is a variable environment and CZCS-based phytoplankton concentrations along drifter trajectories that are not widely separated in space and time show marked differences in concentration (Fig. 2). Similarly, the sea ice (Fig. 3) and detritus time series calculated from CZCS data suggest environmental variability occurring at a large number of scales. Circulation across the Scotia Sea is affected by variability in location of the ACC fronts and is characterized by mesoscale eddies (Brandon et al., 1999). Mesoscale variability is evident in the simulated circulation fields and formation of mesoscale eddies is a component of the circulation distribution (Fach and Klinck, 2006; Fig. 2). Maxima and minima in the food time series along drifter trajectories correlate with trajectories moving through mesoscale eddies which may be located in high or low food environments. Fach et al. (2002) imposed this kind of variability on a time series of chlorophyll concentrations using characteristics of mesoscale features seen in World Ocean Circulation Experiment (WOCE) drifter trajectories. Simulations in the present study which include mesoscale flow variability show that more krill survive and grow to larger sizes when feeding on phytoplankton only (Figs. 7–11A) when compared to the earlier study that included variability in an ad hoc manner (Fach et al., 2002; Fig. 8). This shows that variability in food supply resulting from mesoscale variability in the simulated circulation field plays a major role in the survival of krill during transport.

4.3.2. Variations in krill biomass at South Georgia

The results from this study show a strong connection between krill at South Georgia and along the western Antarctic Peninsula, which potentially represent sink and source populations, respectively, within the metapopulation. Transport times are relatively short, with 163–306 days required to cover the 1500 km distance between the two regions. Thus, biomass changes at the western Antarctic Peninsula may influence South Georgia biomass in the same year with a relatively short lag time.

Oscillations in krill biomass at Elephant Island and South Georgia have been shown to coincide (Brierley et al., 1999) although Nicol (2003a) points out that comparisons of krill density in vastly

different areas should be viewed with caution. Brierley et al. (1999) showed that changes in krill density apparent at Elephant Island in any particular year (of a total of 6 years) seemed to be manifested at South Georgia in the same season, with no apparent time lag between locations. These results support the idea that environmental influences, recruitment success in different regions (Ried et al., 2002), and sea ice extent may similarly effect both populations and that teleconnections may transmit environmental-mediated changes in density across the Scotia Sea. Variations in krill biomass at South Georgia can be attributed to variations in krill populations at the upstream source in the Antarctic Peninsula, Weddell Sea and local populations at South Georgia, as suggested by the simulations.

4.3.3. Estimates of predation

Predation effects on krill survival as calculated with Eq. (5) vary depending on origination area, or total transport time (Fig. 15). Krill originating in the Elephant Island/Scotia Sea region have a better chance of surviving transport to South Georgia than do those from the Weddell Sea because of the shorter transport times. However, krill from the Weddell Sea spend most of the transport time away from land and land-based predators and for these

Table 8
Summary of the total times (days) necessary for different percentages (%) of krill to be removed by different rates of predation (% d^{-1})

Krill removal (%)	Predation rate (% d^{-1})			
	0.2	0.3	1	2
1	5	3.4	1	0.5
10	53	35	10	5
50	347	231	69	35
90	1157	767	230	115

individuals a predation rate of 0.3% d^{-1} may be too high.

Calculations of the total time needed to remove 50% of krill transported to South Georgia ($N(t)/N_0 = 0.5$) yield a wide range of values depending on different predation rates (Fig. 15, Table 8). Assuming a 0.3% d^{-1} predation rate krill originating at the Elephant Island/Scotia Sea region and west Antarctic Peninsula are able to reach South Georgia before 50% are removed. Krill originating in Bransfield Strait and the southwest Antarctic Peninsula take longer to reach South Georgia, which allows >50% of the population to be removed by predation. At the same time, 82% of the Weddell Sea krill are removed before reaching South Georgia.

The above analysis indicates that predation can have a considerable effect on the successful transport of krill to South Georgia and that its potential impact on krill biomass there cannot be neglected. Thus, the effect of predation needs to be explicitly included in future studies on krill transport. This requires detailed estimates of predation rates on krill as a function of the different predators and geographical regions.

5. Conclusions

This study used a modeling framework that couples physical and biological processes to characterize the transport and survival of larval, juvenile, and adult krill under different environmental conditions. Krill survival during transport is dependent on food availability along transport paths and the krill growth model simulations showed that no single food source (surface phytoplankton, detritus, sea ice biota or zooplankton) can support continuous growth during the time needed for transport to South Georgia. However, under the
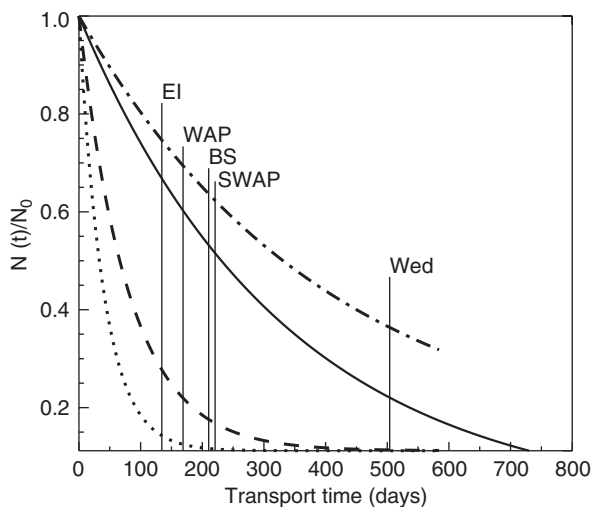

Fig. 15. Estimates of krill loss due to different rates of predation. The vertical lines indicate average simulated transport times from different source regions: Elephant Island (EI), west Antarctic Peninsula (WAP), Bransfield Strait (BS), southwest Antarctic Peninsula (SWAP), and Weddell Sea (Wed).

current assumptions results indicate that combinations of food sources enhanced krill survival during transport, with zooplankton and detritus being particularly important during periods of low phytoplankton concentrations. It was shown that mesoscale patches of high food concentrations may be important to sustain krill in a variable food environment.

At the west Antarctic Peninsula combined environmental and biological factors favor juveniles as the age group that successfully completes transport. For krill originating in the Weddell Sea no such selection was observed. The implication is that for best transport success the source krill population along the Antarctic Peninsula needs to provide large numbers of juveniles. However, it has been shown in previous studies that recruitment success depends on the occurrence of two consecutive years of high sea ice extent (Siegel and Loeb, 1995; Loeb et al., 1997). This implies that interannual changes in sea ice extent, such as driven by the ACW, potentially have a large effect on krill supply from this source population. Therefore years of low sea ice extent may result in a substantial reduction of krill numbers supplied to South Georgia.

Observed episodic variations in krill biomass at South Georgia result from a combination of variations on the source populations during transport and on site. Simulation results show that successful transport of krill to South Georgia depends on multiple factors, including location and time of spawning, food concentrations during transport and predation. It also depends on recruitment success of the source population. This implies that Antarctic krill are well adapted to the variable environment in which they live. However, the many factors that need to converge to produce successful krill supply to the sink population at South Georgia makes that population susceptible to climate variations and human impact.

The fact that krill at South Georgia, the west Antarctic Peninsula and Weddell Sea belong to the same metapopulation has wide reaching implications for fisheries management strategies of this commercially harvested species. Catch limits need to take into account that separate fisheries at South Georgia and Antarctic Peninsula are exploiting the same population, and not separately contained populations as previously believed (Mackintosh, 1973; Makaraov, 1973; Lubimova et al., 1982). This may ensure survival of the metapopulation while sustaining the existing fishery.

This study provides insight into which biological and environmental factors control successful transport of krill across the Scotia Sea, and with this further insight into krill distribution and production in the Scotia Sea. Future modeling efforts on krill growth and survival will require inclusion of krill vertical migration and corresponding energy dynamics. In addition, inclusion of a lower trophic level ecosystem model is essential to better account for dynamically changing krill food sources and allow for testing the influence of environmental changes on krill growth and survival. Furthermore, inclusion of estimates of predation upon krill is important because this may constitute a major source of mortality during transport.

Additional, multi-year observational studies are needed to investigate teleconnections between periodic changes in sea ice extent and krill abundance at the Antarctic Peninsula and South Georgia. It is also necessary to more closely investigate transport and retention mechanisms for krill around South Georgia, to assess their importance for the local population and to understand krill distribution patterns around the Island. Subsequent studies are needed to investigate the fate of krill transported further downstream from South Georgia, looking at the teleconnections of krill populations around Antarctica. It is only with such a holistic approach that the dynamics of these krill populations can be understood.

Acknowledgments

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