Diel vertical migration of Antarctic krill (*Euphausia superba*) is flexible during advection across the Scotia Sea

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We model a summer snapshot of the behavior of Antarctic krill (*Euphausia superba*) during advection across the Scotia Sea. Individual krill respond to a changing landscape of predation risk and food availability by migrating vertically in the water column and choosing an average distance to their nearest neighbor (swarm density). We determine the optimal behavior of 30, 40 and 50 mm krill using a state-dependent life history model where individuals move along 30-day segments of hypothetical journey tracks in three different regions of the Scotia Sea, with the tracks extracted from a combination of circulation models and surface drifter data. Food availability is based on satellite data for surface Chl a with additional heterotrophic and detritus food components, and mortality is parameterized with respect to distance from shore, daylight and krill swarming-behavior. We predict that proximity to predator colonies has a distinct effect on behavior, particularly on depth choice when food-availability is low. Observations made during an acoustic survey of the region found swarms to be deeper at the Antarctic Peninsula compared with South Georgia, in line with model predictions. Our predictions are also consistent with observations that swarm density changes little on a logarithmic scale across the region. We show that being able to change behavior on short time scales has distinct advantages to krill.

INTRODUCTION

The Scotia Sea, in the southwest Atlantic sector of the Southern Ocean, is a crucial habitat for Antarctic krill *Euphausia superba*. Some of the highest abundances of krill occur between the Antarctic Peninsula and South Georgia (Marr, 1962; Mackintosh, 1973; Hewitt et al., 2004a), often coinciding with some of the highest levels of primary production in the Southern Ocean (Korb et al., 2004). The distribution of krill biomass is patchy at a number of scales (Murphy et al., 1998) and krill predator colonies tend to occur adjacent to the high biomass regions. These are also areas that are targeted by the krill fishery (Hewitt et al., 2004b), bringing into focus the need to manage the exploitation of this resource in a manner that minimizes the impact on the wider ecosystem.

Considerable movement of krill has been hypothesized between different regions of the Scotia Sea, particularly from the southwest around the Antarctic Peninsula to the northeast as far as South Georgia (Murphy et al., 2004). Other researchers have noted the importance of quantifying the movement of krill biomass by the use of drifters and passive transport models (Hofmann et al., 1998; Murphy et al., 2004; Thorpe et al., 2004), some including krill growth along the journey (Hofmann and Lascara, 2000; Fach et al.,...
2002; Fach et al., 2006). These studies help in determining how much movement detail should be included in management models. We complement these models in the present study with a focus on a shorter time scale, 6 h time segments over 30 days, to obtain a snapshot of how krill are predicted to respond behaviorally to varying conditions of predation and mortality as they journey across the Scotia Sea. The behavior of krill in the different regions can affect their growth and survival across the Scotia Sea and influence their availability to land-based predators on a local scale. These factors have not been included in previous models.

Krill can respond to a changing landscape of predation risk and food availability by migrating vertically in the water column (Russell, 1927) and by swarming (Ritz, 1994). Going deeper reduces both predation risk and food intake (De Robertis, 2002; Burrows and Tarling, 2004). Likewise, increased swarm density is believed to result in lower predation risk, due to group avoidance strategies and increased vigilance (O’Brien, 1987; Ritz, 2000) but also lower food intake, due to intraspecific interference and competition (Morris et al., 1983; Hamner and Hamner, 2000; Ritz, 2000).

Despite strong evidence for diel vertical migration (DVM) in the Southern Ocean (Marr, 1962; Miller and Hampton, 1989; Demer and Hewitt, 1995; Godlew ska, 1996), there are not many direct studies on the diel depth of krill across the Scotia Sea, with most work being carried out on general abundance, distribution and growth of krill (Atkinson et al., 2008). Studies that have noted patterns in depth distribution and DVM show that there is considerable variability depending on the environment and time of year. In a study around South Georgia, Everso n (Everson, 1983) found that diel movements of krill differed between on-shelf and off-shelf environments, with off-shelf krill showing a movement from depth to the surface at night while on-shelf krill moved from a daytime position above 75 m to spread through almost the whole 200 m water column at night. Nevertheless, according to Kalinowski and Witek (Kalinowski and Witek, 1983), such a pattern is atypical for the wider West Atlantic sector of the Southern Ocean, where a movement to the surface at night has been commonly observed. The FIBEX surveys carried out in a number of different sectors within the Southern Ocean (Anon., 1986) found likewise. Across seasons, a study by Lascara et al. (1999) around the Western Antarctic Peninsula (WAP) found that krill were mainly found below 70 m in the winter and above 50 m in the summer. Godlew ska (Godlew ska, 1996) considered that krill had the largest vertical migration range during the summer and the smallest during spring and autumn (winter was not considered).

Assessing the density of swarms through direct observations in the field is problematic (Hamner and Hamner, 2000) and, in the laboratory, krill show limited schooling behavior (Strand and Hamner, 1990; Hofmann et al., 2004; Swadling et al., 2005) although some recent advances in incubation techniques are remedying this issue (Kawaguchi, personal communication). Acoustics is most widely used to measure swarm density, although adjustments to krill target strength (TS) measurements over the years make absolute comparisons between studies difficult. Kalinowski and Witek (Kalinowski and Witek, 1983) drew up a classification scheme of swarms based on acoustic data, in which there were order of magnitude differences in krill densities between different swarm types. For instance, “superswarmas” contain densities in excess of 1000 g m⁻³ (660 ind. m⁻³ assuming a population consisting of 45 mm krill) and “standard” swarms 10⁻¹⁰0 g m⁻³ (6–60 ind. m⁻³). Around the WAP, Lascara et al. (1999) found that high density swarms (>100 ind. m⁻³) were particularly common in summer but, by winter, the most common swarms were an order of magnitude lower in density. Such trends may differ between regions, with Miller et al. (Miller et al., 1993) reporting that aggregations in the Indian Ocean sector of the Southern Ocean were smaller and further away from the surface than in the Atlantic sector.

These studies indicate that the behavior of Antarctic krill is responsive to environmental conditions (Ross et al., 2000), and that the nature of vertical migration and swarming density is dependent on location and time of year. However, the temporal and spatial scales over which these changes take place are less clear. For instance, whether krill are able to respond in terms of DVM and swarming behavior to conditions that are changing daily or weekly is unknown. Studying these behavioral responses in relation to the varying impact of predator colonies and food patchiness is a good way to determine the stability of DVM as a strategy for organisms faced with constantly changing conditions.

We use a state-dependent life history model, implemented by a stochastic dynamic programming model to examine a snapshot behavioral response of krill to changing conditions of food and predation across the Scotia Sea. Our work is unique in that we examine the small-scale behavior of krill as they move in varying proximity to predator colonies and through patches of food, with a more complex mortality function than previous models and a robust growth function in the form of accumulated energy. Individual krill in the model move along 30-day sections of surface drifter...
tracks in three different regions of the Scotia Sea, representing segments of a hypothetical journey from the Antarctic Peninsula to South Georgia. Along this track, conditions are determined from SeaWiFS/MODIS derived Chl a concentrations and calculated nearest distance to land. We run the model separately for small (30 mm), medium (40 mm) and large (50 mm) krill representative of the main size classes present in the Scotia Sea during January 2003 (Atkinson et al., 2006; Tarling et al., 2006). We analyze the results for small krill at the Antarctic Peninsula, medium-sized krill in the open ocean region and large krill in the South Georgia region as an approximation of the dominant size classes in each of the respective environments (Atkinson et al., 2006). At any time, krill can choose a depth and average nearest-neighbor distance (NND), representing local swarm-density, with the model documenting the choices made with regards to both of these behaviors and overall energy accumulated. We compare predictions with observations of krill swarms made during a summertime krill survey using acoustics and nets across a large section of the Atlantic sector of the Southern Ocean, encompassing the Antarctic Peninsula, the open Scotia Sea and waters around South Georgia.

### Table I: Parameters used in the model

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$W_{Me,t,z}$</td>
<td>Expected fitness from accumulated energy between $t$ and $T$ of an individual krill of size $l$ in zone $z$ between $t$ and $T$</td>
<td>0 to 200</td>
<td>–</td>
</tr>
<tr>
<td>$i$</td>
<td>Behavioral decisions made by individual krill at each time step</td>
<td>1 to 18</td>
<td>–</td>
</tr>
<tr>
<td>$T$</td>
<td>Final time step</td>
<td>360</td>
<td>6 h</td>
</tr>
<tr>
<td>$t$</td>
<td>Time step</td>
<td>6</td>
<td>h</td>
</tr>
<tr>
<td>$L$</td>
<td>Light intensity, calculated from $t$</td>
<td>0 night, 1 day</td>
<td>–</td>
</tr>
<tr>
<td>$a$</td>
<td>Krill depth</td>
<td>1 surface-layer or 2 deep</td>
<td>–</td>
</tr>
<tr>
<td>$s$</td>
<td>Nearest neighbor distance, high to low, representing local swarm density, low to high</td>
<td>1 to 3</td>
<td>–</td>
</tr>
<tr>
<td>$z$</td>
<td>Zone, from closest distance to shore</td>
<td>1 to 4</td>
<td>–</td>
</tr>
<tr>
<td>$e$</td>
<td>Accumulated energy</td>
<td>0 to 200</td>
<td>mg C</td>
</tr>
<tr>
<td>$l$</td>
<td>Size class based on total length (TL)</td>
<td>small 30, med 40, large 50</td>
<td>mm</td>
</tr>
<tr>
<td>$j$</td>
<td>Categories for chlorophyll concentration</td>
<td>0 to 20</td>
<td>–</td>
</tr>
<tr>
<td>$P_j$</td>
<td>Probability of chlorophyll of concentration $j$</td>
<td>0 to 0.4</td>
<td>–</td>
</tr>
<tr>
<td>$C_{C_j}$</td>
<td>Carbon from chlorophyll</td>
<td>0 to 150</td>
<td>mg C</td>
</tr>
<tr>
<td>$C_n$</td>
<td>Carbon from heterotrophic food</td>
<td>0 to 73.5</td>
<td>mg C</td>
</tr>
<tr>
<td>$C_{d,s}$</td>
<td>Carbon from detritus</td>
<td>0 to 135</td>
<td>mg C</td>
</tr>
<tr>
<td>$\gamma_l$</td>
<td>Target accumulated energy</td>
<td>Small, 53.1, large, 51.3</td>
<td>mg C</td>
</tr>
<tr>
<td>$w_l$</td>
<td>Dry mass, based on TL</td>
<td>Small, 45, large, 226</td>
<td>mg</td>
</tr>
<tr>
<td>$c_l$</td>
<td>Carbon weight, based on TL</td>
<td>Small, 19, large, 101</td>
<td>mg</td>
</tr>
<tr>
<td>$g_{sl}$</td>
<td>Filtration reduced by factor with krill density</td>
<td>0.1 to 1</td>
<td>–</td>
</tr>
<tr>
<td>$k_{sl}(\delta)$</td>
<td>Assimilated ingested energy</td>
<td>–</td>
<td>mg C h$^{-1}$</td>
</tr>
<tr>
<td>$R_{sl}^i$</td>
<td>Respiration rate</td>
<td>0.01 $R_{sl}^i(\delta)&lt;0.05$</td>
<td>mg C h$^{-1}$</td>
</tr>
<tr>
<td>$R_{dl}$</td>
<td>Respiration decreases by factor with density</td>
<td>1 to 0.8</td>
<td>–</td>
</tr>
<tr>
<td>$R_{l}$</td>
<td>Respiration increases by factor with ingestion</td>
<td>1 to 2</td>
<td>–</td>
</tr>
<tr>
<td>$M_2(d,s,z,L)$</td>
<td>Mortality risk close to an island</td>
<td>$1 \times 10^{-6} &lt; M_2(d,s,z,L) &lt; 0.67$</td>
<td>$P_{(death)}$</td>
</tr>
<tr>
<td>$M_2(d,s,L)$</td>
<td>Mortality risk in the open ocean</td>
<td>$1.6 \times 10^{-8} &lt; M_2(d,s,L) &lt; 0.2$</td>
<td>$P_{(death)}$</td>
</tr>
</tbody>
</table>

### METHOD

In this section, we describe the state variables and their dynamics, the calculation of fitness in the model and the dynamic programming algorithm. We list all model parameters in Table I.

#### The behavioral model

Each time step, individual krill in the model choose a depth: surface $<60$ m, or deep $60–150$ m. These choices are based on the average diving range of the major land-based predators at Bird Island, South Georgia (Boyd and Croxall, 1992; Croxall et al., 1993; Green et al., 2003). Each krill also chooses to maintain an average NND that is low, medium or high, relating to swarm densities of $>1000$ krill m$^{-3}$, 100–1000 krill m$^{-3}$ and $<100$ krill m$^{-3}$, respectively (Hamner and Hamner, 2000). There are thus $i=1$ to 6 possible decisions, which are (i) surface with low NND, (ii) surface with medium NND, (iii) surface with high NND, (iv) deep with low NND, (v) deep with medium NND and (vi) deep with high NND. We assume that krill are always in a swarm in the sense that the above categories cover a broad spectrum...
from loose feeding aggregations to tightly packed schools (Hamner and Hamner, 2000). In the model, the density of the swarm varies depending on the choice of NND. For example, the choice of a closer distance to the nearest-neighbor will affect the immediate surroundings of a krill in a swarm, making swimming more streamlined thus decreasing respiration, but also reducing food availability through increased competition. We also assume that a closer distance to the nearest neighbor will decrease the risk of predation.

The timeframe of the model is 360 time steps of 6 h, approximately 3 months. However, we analyze the results only from the middle month, time step 121 to 240, to find stable strategies and minimize effects of transients (Mangel and Clark, 1988). Parameter estimates are based on the month of January, when penguins and seals remain close to land for the breeding season (Williams and Croxall, 1991; Barlow et al., 2002; Barlow and Croxall, 2002; Green et al., 2002). At this time of year, the approximate day length is 18 h (www.exptech.com/sunrise.html), with light intensity $L$ valued at 0 for night and 1 for daylight hours.

**The environment**

We determine the optimal policy in the backward run of the model for average conditions across the Scotia Sea and then apply this to individual krill along specific pathways from the Antarctic Peninsula across the Scotia Sea to South Georgia. The tracks of krill across the Scotia Sea are taken from data from mixed layer World Ocean Circulation Experiment (WOCE) drifters and a varying forced run of a global ocean circulation model (Parallel Ocean Climate Model; POCM_4C) (Thorpe et al., 2004). We extract the latitude and longitude positions from 30-day sections of 10 of these tracks, a much shorter timescale than the models of Fach et al. (Fach et al., 2006) and Hofmann and Lascara (Hofmann and Lascara, 2000), with an equal number of model and drifter predictions shown in Fig. 1. We use the same flow field for shallow and deep in the model for the following reasons. First, the tracks that we use to predict krill movement are representative of the large-scale mean flow field, but include variability introduced by mesoscale eddies. The flow structure in the upper 150 m of the Antarctic Circumpolar Current (i.e. the depth range which we are modeling over) shows only small vertical shear on average. Mean current

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**Fig. 1.** Chlorophyll-a concentrations (mg m$^{-3}$) derived from MODIS, representing the mean of all chlorophyll data acquired in January for the years 2003–2005. White patches represent no data, where cloud or ice cover obscured the sea. We show segments from observed drifters and model-predicted pathways (Thorpe et al., 2004) in the near-surface of the ocean (upper 25 m), which we assume are representative of the advection routes krill will follow. Although exact pathways vary, all generally move from southwest to northeast, and there are three tracks in each of the regions compared in the model: the Antarctic Peninsula region; the open ocean region and the South Georgia region.
speeds across the Scotia Sea from ADCP data collected onboard the RRS James Clark Ross in Jan/Feb 2003 (cruise JR82) are 0.22 m s$^{-1}$ for the upper 60 m, and 0.2 ms$^{-1}$ for 60–150 m. Our selected pathways can therefore be considered representative for both the depth intervals used in our model. Second, Murphy et al. (Murphy et al., 2004) showed that a horizontal trajectory of krill migrating vertically produced similar trajectories to mean field flow routes for krill moving across the Scotia Sea even over a much larger time scale, around 120 days. It is to be noted that the overall aim of the model is not to predict the horizontal movement of krill, but to determine their depth and density behavior given local conditions of food and mortality.

We obtained data on chlorophyll, for summer conditions, from the MODIS instrument on board the Aqua satellite (operated by NASA), giving a mean of all global chlorophyll data acquired in January for the years 2003–2005 (Andrew Fleming, unpublished results, British Antarctic Survey) (Fig. 1). In further sensitivity analyses, we double and halve these values to simulate a year of high and low productivity, respectively. From this data set, we also extracted the distribution of chlorophyll concentration $C_l$ in mg Chl $a$ m$^{-3}$ (Fig. 2).

The three regions in the model are the Antarctic Peninsula region, the open ocean region of the Scotia Sea, and the South Georgia region. We selected the timescale such that krill did not pass from one region to another in the model period of interest, so that we could compare a summer-snapshot of krill behavior in the different regions. These regions differ in terms of average chlorophyll concentrations and expected krill mortality from land-based predators, as mortality is scaled with distance to shore.

We define a krill’s zone $z$ by distance from shore according to:

\[ z = 1 : \text{distance to shore} \leq 50\,\text{km} \]
\[ z = 2 : 50\,\text{km} < \text{distance to shore} \leq 100\,\text{km} \]
\[ z = 3 : 100\,\text{km} < \text{distance to shore} \leq 200\,\text{km} \]
\[ z = 4 : \text{distance to shore} > 200\,\text{km} \]

**State variables**

Accumulated energy is the simplest way of examining an energetic response to changing conditions, without using complex growth functions as parameterized in Hofmann and Lascara (Hofmann and Lascara, 2000) and Fach et al. (Fach et al., 2006). Thus, we define

\[ E(t) = \text{the accumulated energy of an individual krill at time } t \]

The energy accumulated by an individual krill in one time step $E(t+1)$, measured in mg C, depends on energy ingested $I(s, l, d)$ and energy respired $R(l, s)$. The energy ingested varies according to the distance to nearest neighbor $s$, length of the individual $l$ and depth $d$. Similarly, respiration $R(l, s)$ varies according to $l$ and $s$. The total energy accumulated cannot exceed $E_{\text{max}}$ at any time, where we calculate $E_{\text{max}}$ from the maximum clearance rate of 200 mg C m$^{-3}$ (Atkinson and Snyder, 1997). The maximum clearance rate represents the saturation level for filtration plus ingestion rate. Thus, the dynamics of energy are

\[ E(t+1) = \begin{cases} E(t) + I(s, l, d) - R(l, s) \\ 0 & \text{if } E(t+1) > E_{\text{max}} \\ E_{\text{max}} & \text{if } 0 \leq E(t+1) \leq E_{\text{max}} \\ & \text{and } (E(t+1) - R(l, s)) - E(t) < 0 \end{cases} \]

Hofmann and Lascara (Hofmann and Lascara, 2000) give conversions between wet, dry and carbon weights, and equations for filtration and respiration. Filtration rate $F(s, l)$ depends on dry mass $w(l)$ and swarm density $s$. We scale filtration by a scaling factor $g(s)$ based on Morris et al. (Morris et al., 1983), where $g(1)=1$ for a low-density swarm, $g(2)=0.5$ for a medium-density swarm and $g(3)=0.1$ for a high-density swarm. Thus, the filtration rate function...
described in Hofmann and Lascara to include changes with swarm density $s$ is

$$F(s, l) = 0.00858 \cdot (\omega(l))^{0.514} \cdot g(s) \quad (4)$$

Assuming an assimilation rate of 80% (Clarke and Morris, 1983), total carbon assimilated $I(s, l, d)$ from chlorophyll $C_c$, heterotrophic food $C_h$, and detritus $C_d$.

$$I(s, l, d) = F(s, l) \cdot (C_c + C_h + C_d) \cdot 0.8 \quad (5)$$

where we assume that the feeding of krill does not result in resource depletion. The total respiration cost for each size class is standard metabolism $R(l, s)$ plus an increase due to feeding $R_f$ and a decrease with increasing swarm density $q(s)$, where $q(1)=1$ for a low-density swarm, $q(2)=0.9$ for a medium-density swarm and $q(3)=0.8$ for a high-density swarm. $R_f$ increases linearly from 0 up to 1 for a percent daily ration (mg C) from 0 to 10%, remaining at 1 for a daily ration $>10\%$ (Hofmann and Lascara, 2000). Thus the total respiration is

$$R(s, l) = 0.00272 \cdot (\omega(l))^{0.85} \cdot g(s) \cdot (1 + R_f) \quad (6)$$

Fitness

We define fitness by

$$W(e, t|z, l)$$

maximum Expected fitness from accumulated energy between $t$ and $T$ of an individual krill of size $l$ in zone $z$ between $t$ and $T$, given that $E(t) = e$. 

$$W(e, t|z, l) = e; \quad 0 < e < E_{max} \quad (7)$$

We examine two cases for the terminal reward function, to examine their importance to model outputs.

Case 1

If we assume that fitness is proportional to accumulated energy, the end condition (terminal reward) is as follows

$$W(e, t|z, l) = e; \quad 0 < e < E_{max} \quad (8)$$

Case 2

In the second case for the terminal reward, krill were set a target level of accumulated energy to reach in order to gain positive fitness at $T$. We base the target level on observed growth rates of krill during summer in the Scotia Sea of $0.162 \pm 0.129$ mm day$^{-1}$ and $0.0224 \pm 0.036$ mm day$^{-1}$ for small (30 mm) and large (50 mm) krill, respectively (Atkinson et al., 2006). A target growth level of $0.092$ mm day$^{-1}$ for small krill, $0.036$ mm day$^{-1}$ for medium krill and $0.045$ mg C day$^{-1}$ for medium krill and $0.108$ mg C day$^{-1}$ for large krill. If an individual does not acquire the required amount of energy by the final time $T$, fitness is 0, otherwise fitness is equal to the total amount of carbon assimilated by time $T$.

$$W(e, T|z, l) = \begin{cases} 0; & e < 50 + 30\gamma(l) \\ e; & e \geq 50 + 30\gamma(l) \end{cases} \quad (9)$$

In both of these cases, for times $t<T$, we find $W(e, t|z, l)$ from the dynamic programming algorithm as follows

$$W(e, t|z, l) = \max_i (1 - \beta_i) \times \sum_{j=0}^{20} P_j \cdot W(e_j, t+1|z, l) \quad (10)$$

where $e_j$ is $e$ at time $t+1$, see equation (6).

Model implementation

We assume deep chlorophyll concentrations are 5% of surface concentrations based on in situ measurements of chlorophyll with depth from the RRS James Clark Ross (R. Korb unpublished results) from a range of sites to the northwest of South Georgia (53.5 to 53°S, 37 to 38°W). We used a carbon to chlorophyll ratio of 50 for $C_c$ (Atkinson, 1996).

Chlorophyll concentrations are typically low in the Scotia Sea (Korb et al., 2005), meaning that krill need food other than pelagic phytoplankton to sustain growth rates observed in transport across the Scotia Sea from the Antarctic Peninsula to South Georgia. There have been a number of attempts to characterize the components of the diet of Antarctic krill (Boyd et al., 1984; Clarke, 1984; Froneman et al., 1996; Atkinson and Snyder, 1997), with the variety of approaches and diversity of functions reflecting the difficulty of the task. Here, we use the approach outlined in Fach et al. (Fach et al., 2006) with three components to the diet: carbon from phytoplankton $C_c$, carbon from heterotrophs $C_h$ and carbon from detritus $C_d$.

We estimate a relationship between heterotrophic food and chlorophyll by combining a linear relationship
between chlorophyll concentration and the number of ciliates and protozoa in the water column (Atkinson et al., 2006) with data sets from Atkinson and Snyder (Atkinson and Snyder, 1997) comparing Longhurst–Hardy Plankton Recorder samples to concurrent chlorophyll a profiles. This approach is different to the approach used by Fach et al. (Fach et al., 2006) with a time-varying concentration for heterotrophic carbon. In the current model, heterotrophic carbon relates linearly to chlorophyll, with a background level of heterotrophic food present when chlorophyll is near absent according to

$$C_h = 0.09C_c + 60$$

with units in mg C. Carbon from detritus $C_p(d)$ [the particulate organic carbon (POC) content in seawater] also contributes to energy accumulated. We use a relationship derived from measurements of POC and chlorophyll a concentrations over several Antarctic cruises (Fach et al., 2002) as follows

$$C_p(d) = 20.42 + 0.77C_c$$

Estimates for both heterotrophic and detritus carbon are taken from surface measurements, so it is likely that the background level of carbon may also change with depth. Since the relationship between carbon and depth is unknown, from both heterotrophic and detritic sources, we assume the background level at depth is 5% of the surface background level, as for $C_c$ values.

**Mortality**

We separate mortality close to an island $M(d, s, z, L)$ [if $z \leq 3$, or distance from shore <200 km] from mortality in the open ocean $M(d, s, L)$ [if $z = 4$, or distance from shore >200 km], similar to the approach used in Fach et al. (Fach et al., 2006). Mortality in our model, however, is more complex because we further partition different zones of near-land mortality, we include diel variation in mortality and we allow behavior to influence mortality.

Close to an island, four factors contribute to mortality: krill depth $d$, nearest-neighbor distance $s$, distance from shore in zone $z$ and light intensity $L$. Further from shore, the zone $z$ does not change and therefore does not affect mortality. Murphy and Reid (2001) derived average mortality, which gives the probability of death per 6 h time step, or $M = 0.00085$ close to land and $M = 0.00035$ in the open ocean, from net hauls taken in the vicinity of South Georgia. To parameterize mortality, we assume that krill experience average mortality in a medium density swarm ($s = 2$), in the shelf-break zone if <200 km from shore ($z = 2$), with a consistent DVM. The consistent DVM places krill in a deep habitat for the illuminated three-quarters of the 24 h day ($L = 1$) and throughout the water column at night ($L = 0$).

Previous studies during summer at Bird Island, South Georgia, show a decrease in the density of both fur seals and macaroni penguins with increasing distance from the island (Hunt et al., 1992; Perissinotto and McQuaid, 1992), as would be expected from central place foragers (Houston and McNamara, 1985). The results from Hunt et al. (Hunt et al., 1992) indicate that predators are 10 times more concentrated on-shelf compared with off-shelf, so we use this estimation for the best estimate parameterization of the model. We also test a smaller and larger effect of zone habitat on mortality in the sensitivity analysis.

We assume that krill in higher density swarms reduce their risk of mortality through increased vigilance and group avoidance strategies, plus evasion and dilution factors once under attack (Hamilton, 1971; Ritz, 2000). These strategies are effective against visual predators that predate krill individually, such as penguins and seals. Sensitivity analyses test the influence of swarming factors on mortality risk and krill behavior.

We use the method of Fiksen and Giske (1995) to calculate mortality for different habitats depending on depth and light intensity. This method is described in Cresswell et al. (Cresswell et al., 2007). Using this method, we calculate predator density in the open ocean and close to an island.

To describe mortality close to an island, we introduce $\bar{\alpha}_1$ by the logistic transformation.

$$\bar{\alpha}_1 = \log_{10}\left[\frac{\bar{M}_1}{1 - \bar{M}_1}\right]$$

At any particular depth, zone, light intensity and swarm density, we linearly change $\bar{\alpha}_1$ to

$$\alpha_1(d, s, z, L) = \bar{\alpha}_1 + \alpha_{d,L} + \alpha_s + \alpha_z$$

where $\alpha_{d,L}$, $\alpha_s$, and $\alpha_z$ are defined in Table II. Then inshore mortality $M_1(d, s, z, L)$ is

$$M_1(d, s, z, L) = \frac{10^{\alpha_1(d, s, z, L)}}{1 + 10^{\alpha_1(d, s, z, L)}}$$


To calculate mortality in the open ocean $M_O(d, s, L)$ given $M_O$ we set

$$
\alpha_O = \log_{10} \left[ \frac{M_O}{1 - M_O} \right] \quad (16)
$$

and then introduce $\alpha_O(d, s, L)$.

$$
\alpha_O(d, s, L) = \alpha_O + \alpha_{d, L} + \alpha_s \quad (17)
$$

where $\alpha_{d, L}$ and $\alpha_s$ are defined in Table II. Finally, mortality in the open ocean is

$$
M_O(d, s, L) = \frac{10^{\alpha_{O}(d, s, L)}}{1 + 10^{\alpha_{O}(d, s, L)}}. \quad (18)
$$

Running the model

The dynamic programming algorithm works backward in time to calculate the optimal policy for each level of the state variables for the individual at each time step (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). It specifies an action that maximizes fitness for each $d, s$ and $z_c$ for different size classes of krill at each time. In the forward iteration, an individual with an initial set of state parameters effectively has a map of optimal action to take at each time step, which will further affect its state and fitness and therefore the decision chosen at the following time step. We run the model forward for one small, medium and large krill per track, taking results for small krill in the Antarctic Peninsula region, medium krill in the open ocean region and large krill in the South Georgia region following the observed field situation (Atkinson et al., 2006). We also look at results for all three sizes in each region to separate the effect of size and region. Conditions were extracted for each of the tracks.

We run the model with best estimates for parameters then conduct a sensitivity test for the form of the terminal reward [see equations (11)–(14)] and for three of the parameters. First, we test the effect of food availability, because conditions can vary considerably from year to year in the Scotia Sea (Korb et al., 2004; Korb et al., 2005). Second, we vary the background level of heterotrophic carbon, because this is difficult to parameterize and poorly understood (Atkinson et al., 2006). Third, we test the effect of the maximum clearance rate, because this is hard to determine in the laboratory. Finally, we fix the vertical location of krill to see how this affects their final accumulated energy.

Empirical data

We examined empirical patterns in diel vertical distribution through re-analyzing data from an acoustic survey carried out aboard the RRS James Clark Ross (cruise JR82) between 9 January and 16 February 2003. The cruise consisted of eight transects within the regions $65^\circ–50^\circ$S and $30^\circ–55^\circ$W, encompassing the east Antarctic Peninsula, the Scotia Sea and South Georgia. Acoustic data were collected using a SIMRAD EK60 Echosounder from which 38 and 120 kHz sounder data were processed using Sonardata Echoview version 4.0, following the protocol of Hewitt et al. (Hewitt et al., 2004a). A swarm detection algorithm was applied to the processed 120 kHz echogram data using Sonardata Echoview version 4.0 “School detection module”, which employs a SHAPES algorithm (Goetzee, 2000). Swarms were detected from the 120 kHz echograms, and physical and acoustic descriptors for the detected swarm-regions were exported from both 38 and 120 kHz data. The threshold used in the final swarm detection was $-70$ dB, as advised by Lawson et al. (Lawson et al., 2008b) based on estimates of the maximum distance that individual krill can remain in visual contact with each other. We followed the approach of Reiss et al. (Reiss et al., 2008) to delineate krill swarms from all other types of swarms through the use of SWDBATS model predictions for Antarctic krill (Conti and Demer, 2006) and supplementary net catch information on the size-frequency distribution of krill across the survey (Atkinson et al., 2006). Net catch information found mean body length to be 33.4 mm (SD 5.2) at the Antarctic Peninsula, 44.8 mm (SD 7.7) in the open ocean and 46.9 mm (SD 4.5) around South Georgia. From this, we calculated a mean difference in backscatter strength between the two frequencies ($\Delta S_{v120-38}$) for krill of between 4.6 and 14.7 dB at the Antarctic Peninsula, 2.5 and 14.7 dB in the open Scotia Sea and 2.5 and 11.1 dB around South Georgia.
swarms falling within these ranges were assumed to be krill swarms. Backscatter within swarms was converted into krill density (ind. m\(^{-3}\)) through application of TS values derived from the SWDBA model. At 120 kHz, this value was −74.66 dB at the Antarctic Peninsula, −74.50 dB in the open ocean and −74.45 dB around South Georgia. Mean swarm density was converted to the sum abundance of a swarm (ind. m\(^{-3}\)) through multiplying swarm density by swarm area. We classified swarms as either being above or below 60 m, based on their mean depth, assuming that the majority of the thickness resided within the same zone as the mean depth. Vertical distribution across the 24 h cycle was determined through dividing data from each region into 6 h intervals, with 0 h to 05 h covering the main hours of darkness and 06 h to 11 h, 12 h to 17 h and 18 h to 23 h, encompassing dawn, noon and dusk, respectively.

**RESULTS**

**Predicted krill depth in each region**

We predict the behavior of krill in the three different regions for a size class that corresponds with empirical observations: 30 mm at the Antarctic Peninsula; 40 mm in the open ocean region and 50 mm around South Georgia (Table III). In particular, we examine the effect of distance to shore and level of food availability, low, average and high. Krill had a choice of maintaining a low, medium or high local swarm-density, but in the vast majority of situations, krill chose to reside in low-density (large NND) swarms. The exception was low food situations, where high-density swarms were optimal. With little food around, krill can conserve energy by being closer and more streamlined with their neighbors. With more food, krill can maximize food intake by spreading away from their con-specific neighbors. Furthermore, we predict that krill of all sizes/regions stay in deeper water day and night if they are in a zone of high predator concentrations, i.e. <100 km from nearest land, and food availability is average to high. However, they cannot sustain this risk-averse behavior when food is low, at which point they perform a DVM even at the closest distance to shore.

**Table III: The predicted behavior of krill for low-, medium- and high-food conditions in the three regions of the Scotia Sea**

<table>
<thead>
<tr>
<th>Region</th>
<th>Low food</th>
<th>Medium food</th>
<th>High food</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antarctic Peninsula</td>
<td>Medium DVM, with a proportion in surface</td>
<td>No DVM, always deep</td>
<td>No DVM, always deep</td>
</tr>
<tr>
<td>(30 mm krill)</td>
<td>layers during the day</td>
<td>Always low density</td>
<td>Always low density</td>
</tr>
<tr>
<td></td>
<td>High density swarm deep</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low density swarm in surface layer</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open Ocean (40 mm krill)</td>
<td>Medium DVM, proportion in surface layers</td>
<td>Medium DVM, proportion in surface layers</td>
<td>DVM further from shore</td>
</tr>
<tr>
<td></td>
<td>during day increases with distance from</td>
<td>during day increases with distance from</td>
<td></td>
</tr>
<tr>
<td></td>
<td>shore (&gt;50% surface-layer during day at</td>
<td>shore (&gt;50% surface-layer during day at</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;100 km from shore)</td>
<td>&gt;100 km from shore)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High density swarm deep</td>
<td>High density swarm deep</td>
<td>DVM further from shore</td>
</tr>
<tr>
<td></td>
<td>Low density swarm in surface layer</td>
<td>Low density swarm in surface layer</td>
<td></td>
</tr>
<tr>
<td>South Georgia (50 mm krill)</td>
<td>Medium DVM, proportion in surface layers</td>
<td>DVM further from shore</td>
<td>DVM further from shore</td>
</tr>
<tr>
<td></td>
<td>during day increases with distance from</td>
<td>Always deep close to shore (&lt;100 km)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>shore (&gt;50% surface-layer during day at</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;100 km from shore)</td>
<td>Always low density</td>
<td></td>
</tr>
<tr>
<td></td>
<td>High density swarm deep</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Low density swarm in surface</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

No DVM means krill are not both in the surface layers at night and deep during the day, medium DVM means krill are always in the surface layers at night, but depth during the day is variable. DVM further from shore means that krill remained in the deep water closer to an island, but further than 100 km they exhibited a DVM where 100% individuals were in the surface layers at night and deep during the day. We also describe the density of the swarm, representing by the nearest neighbor distance (NND) chosen by individuals. All individuals in the deep water always chose the same NND, as did those in the surface waters.
the prediction of swarm densities >1000 ind. m$^{-3}$ in certain food-poor situations was not supported by observations, given that such swarms were very rarely found.

The majority of krill (ind. m$^{-3}$) were located in the upper 60 m across all environments and at all times of day and night (Fig. 3). However, the relative proportion above and below 60 m changed with both time of day and with region. The greatest proportion above 60 m was found during nighttime (0 h to 05 h), with only 4 and 6% being found below 60 m across all environments. However, the proportion found below 60 m during daylight hours showed much greater variation according to region. At the Antarctic Peninsula, the proportions in the deeper layers ranged between 22 and 40%, whereas, in the open ocean, it was considerably lower (3–15%). South Georgia was around mid-way between these two other environments with 15% of the population being found below 60 m during daytime. Overall, these data indicate that some degree of DVM of krill biomass occurs in all environments. However, the migration involves a much greater proportion of the population at the Antarctic Peninsula (18–36%) than in the open Scotia Sea (0–11%). Furthermore, the proportion of the population residing below 60 m during daylight hours (18 h per day) was between 7 and 37% greater at the Antarctic Peninsula than in the open ocean. The situation at South Georgia was somewhere between these two extremes, although some caution is warranted because of the small sample numbers obtained there ($n = 48$). Our predicted depths matched the overall pattern of observed depth choice, particularly for simulated low-food conditions (Fig. 4), with food

<table>
<thead>
<tr>
<th></th>
<th>Antarctic Peninsula</th>
<th>Open Ocean</th>
<th>South Georgia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of swarms between 0 and 100 krill m$^{-3}$</td>
<td>0.90</td>
<td>0.95</td>
<td>0.96</td>
</tr>
<tr>
<td>Proportion of swarms between 100 and 1000 krill m$^{-3}$</td>
<td>0.09</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td>Proportion of swarms between 1000 and 10000 krill m$^{-3}$</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Table IV: Results of acoustic observations on the density of krill swarms across three regions of the Southern Ocean Atlantic sector.

![Fig. 3](https://academic.oup.com/plankt/article-abstract/31/10/1265/1527473) Depth distribution of krill swarms observed by a Simrad EK60 Echosounder in January/February 2003 across at the Antarctic Peninsula, in the open ocean sector of the Scotia Sea and at South Georgia. Data were divided into 6 h intervals with the period 0 h to 05 h restricted to nighttime only. Bars represent the proportion of swarms above or below 60 m, dots represent the total number of swarms in the respective 10 m interval.
availability (Fig. 4) and size of krill (Fig. 5) affecting specific proportions but not the overall predicted pattern.

**Predicted average energy accumulation**

The total energy accumulated by krill on average is higher at South Georgia and in the open ocean region than around the Antarctic Peninsula (Fig. 6). When krill have a choice of depth in the model (Fig. 6A), they lose less energy in low food conditions, but gain less energy in high-food conditions compared to when DVM is fixed (Fig 6B) or krill do not have a choice of depth. When krill have a choice of depth, the average mortality per individual each time step is much lower (Fig. 6C) compared to when DVM is hardwired (Fig. 6D). Overall, a flexible DVM means that krill can stay deeper when overall food is sufficient, thus reducing predation in the surface waters, but they can maximize food intake by choosing a surface-layer depth when food availability is low at the risk of higher mortality. To separate the effects of size and region, we show results for all three sizes in each of the regions for the low food scenario, and predict that krill size has the greatest effect on final accumulated energy at the Antarctic Peninsula region (Fig. 7).

**Sensitivity analysis**

We calculate sensitivity by dividing the percentage change in the result of interest by the percentage change in the parameter value.

Nearly all of the model results, energetic and behavioral, were most sensitive to changes in the background level of heterotrophic food (Table V). After heterotrophic food, the results were most sensitive to changes in the availability of chlorophyll.

Changes in the terminal reward affected the accumulated energy of krill only when the background heterotrophic food and chlorophyll availability were low. For krill behavior, the terminal reward had the greatest effect on DVM, not noticeably affecting the swarm density chosen by krill in the model. That the terminal reward did not noticeably affect the results gives us more confidence in the model predictions.

**DISCUSSION**

We show that maintaining a flexible DVM strategy has selective advantages: krill would benefit from not
performing DVM in some environments, for instance, when close to land and food is plentiful. With low-food availability, DVM is optimal in zones of higher predator concentrations, but further from shore, we predict that a proportion of krill will remain in the upper water column to maximize food intake day and night. We predict that krill nearly always choose a large NND, resulting in low-density local swarm-structure, with the exception being low-food conditions, when krill choose a small NND, resulting in high-density swarms, when they migrate to depth.

Fig. 6. The predicted average energy in mg C (± SD) accumulated when krill choose their depth in the model (A) compared with a model where DVM is fixed and depth is not a choice (B); and average mortality per individual per time step (± SD) in the model where depth is a choice (C) compared to a model where DVM is fixed (D). We show small (30 mm), medium (40 mm) and large (50 mm) krill in each of the regions, with low-, average- and high-food simulations.

Krill depth
The predicted depth patterns for krill in the model vary most with food availability and distance from land. With low food availability, we predict the formation of high-density swarms, through changes in individual krill behavior, but only in the deep water during the day. This is most likely a strategy to conserve energy in a food-poor environment. In the same conditions but further from land, we predict that krill will more likely occupy the surface layers during the day in low-density swarms. Although the predation risk in the surface...
layers is higher, the distance from land means that the absolute level of predation is low compared to inshore regions. Krill endure this risk to maximize food intake in this generally food-poor environment.

Our empirical analyses showed that a greater proportion of swarms closer to land (Antarctic Peninsula and South Georgia) were located deeper in the water column than those in the open ocean. Between 85 and 97% of all swarms were located in the upper 60 m in the open ocean during day-time, while only 60 and 78% were found in this layer at the Antarctic Peninsula. South Georgia was between these two extremes (85%). Although a number of studies have considered krill vertical distribution, few have considered how patterns change across the gradient from on-shore to off-shore. One of the few was carried out by Everson (Everson, 1983), who found that off-shelf krill around South Georgia migrated from 150 m to closer the surface at night, whereas on-shelf krill spread through most of the 200 m water column at night. This generally agrees with our observations, although the daytime depth of off-shelf krill appears deeper in the Everson (Everson, 1983) study. Godlewska (Godlewska, 1996) found that the majority of swarms in the Atlantic Sector of the Southern Ocean had mean depths of between 30 and 60 m. Similarly, Lascara et al. (1999) found 75% of the krill biomass was above 50 m in the Antarctic Peninsula region in summer. Lawson et al. (Lawson et al., 2008a) found the number of swarms peaked between 60 and 80 m at the Antarctic Peninsula during the autumn. Taki et al. (Taki et al., 2005) analyzed Japanese fishing data to find the average trawling depth in January at the South Orkney Islands and the South Shetland Islands for krill around 50 m with a range of 15 and 23 m, respectively. No fishing data were analyzed for South Georgia during January.

Predicted regional patterns in optimal swarm depth are broadly consistent with our empirical observations, particularly in low-food conditions. Nevertheless, predicted depth is always deeper than observed depth. This may be because (i) we allowed there to be too much food intake at depth or (ii) mortality in the surface layers was assumed to be too high. Gaining accurate estimates of feeding and mortality is inherently difficult, but is fundamental to the further development of krill behavioral models. Our predictions were most sensitive to the level of heterotrophic food set within the model. Further empirical work on the relative importance of different food sources to krill is highly recommended. For instance, some preliminary work has shown that krill may feed at the sea-floor for alternative food sources, particularly in shelf environments (Ligowski, 2000).

Further error in matching predictions to observations may be incurred through the limitations of krill data obtained through acoustic analysis. Acoustic TS models that can fully account for variance in krill orientation, shape, size and body composition are still under development and there remains quite a substantial difference between packing densities estimated acoustically and those estimated visually (Hamner and Hamner, 2000).

Table V: Relative sensitivity of results in terms of accumulated energy, proportion of krill adopting DVM and total proportion of krill in low-, medium- and high-density swarms, for each of the parameters tested in the sensitivity analysis (chlorophyll concentration, heterotrophic food and maximum clearance rate).

<table>
<thead>
<tr>
<th>Result</th>
<th>Chlorophyll conc. (C)</th>
<th>Heterotrophic food (C)</th>
<th>Max. clearance (c_max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Energy</td>
<td>1.13</td>
<td>1.86</td>
<td>0.95</td>
</tr>
<tr>
<td>DVM</td>
<td>0.86</td>
<td>1.96</td>
<td>0.36</td>
</tr>
<tr>
<td>Low-density swarm</td>
<td>0.47</td>
<td>0.6</td>
<td>0.01</td>
</tr>
<tr>
<td>Medium-density swarm</td>
<td>1.07</td>
<td>0.6</td>
<td>1.65</td>
</tr>
<tr>
<td>High-density swarm</td>
<td>0.67</td>
<td>1.06</td>
<td>0.03</td>
</tr>
</tbody>
</table>

The parameter of highest sensitivity is highlighted in bold (DVM, diel vertical migration of zooplankton).
Furthermore, the echosounder is located 4 m below the sea-surface in the RRS James Clark Ross and ringing makes the sounder blind for a further 10 m approximately. It is possible that there are a number of swarms at the very surface that are missed, particularly during the nighttime. Wider use of upward looking sonars is required to quantify this source of error (Everson and Bone, 1986). At the other extreme, the maximum depth range of the sounders is between 200 m and 300 m and some swarms may migrate below these depths, especially during the daytime. Observations made by an ROV submersible have found krill at depths of more than 3500 m (Clarke and Tyler, 2008), although whether krill swarm at such depths and whether the number of such swarms is substantial remains unclear.

A further model prediction is that the optimal depth of krill becomes closer to the surface with increasing krill size when food is scarce. This may be because, in the model, small krill can afford the cost of reduced food intake in the deeper water when closer to shore, whereas large krill cannot. This seems contrary to field evidence of small krill choosing riskier habitats than large krill (Loeb et al., 1993). In the field, small krill may choose a riskier habitat through reduced mortality from size-specific predation, but there is evidence both for and against this hypothesis (Hill et al., 1996; Reid et al., 1996; Alonzo and Mangel, 2001; De Robertis, 2002; Alonzo et al., 2003).

**Swarm density**

On a logarithmic scale, the model predicts that swarm density alters little in response to changing conditions across the Scotia Sea. This parameter was most sensitive to changing food availability and depth choice. We predict low-density swarms, high average NND for krill in each of the regions day and night when food availability is low. This agrees with our observations that the majority of swarms (>97%) were within low-density category (<100 ind. m⁻³). There was no depth trend in the observed small number of higher density swarms (>100 ind. m⁻³), with the proportions found above and below 60 m being approximately the same.

The swarm density behavior of krill is classically less studied than their depth, although the proposed benefits, reduced predation through group avoidance and increased vigilance, and costs, reduced respiration from hydrodynamic advantages of swimming alongside neighbors, are similar (Wehls, 1975; Obrien, 1987; Ritz, 2000). Schooling behavior is inherently difficult to study in both the field and the laboratory (Strand and Hammer, 1990; Hammer and Hammer, 2000; Hofmann et al., 2004; Swadling et al., 2005). We predict that krill adopt a fairly stable strategy in their swarming behavior across the Scotia Sea, with swarm density changing more in response to light intensity than proximity to predator colonies or concentration of food in the water. The prediction for large krill adopting a diel rhythm in swarm density is supported by acoustic field-studies, where krill apparently “disperse” in surface-layer swarms at night for feeding then reform into deep high-density swarm during the day (Witek et al., 1981; Everson, 1982; Croxall et al., 1985; Godlewksa, 1996). It is to be noted that our model does not necessarily predict dispersal but rather a greater inter-individual distance within a coherent swarm. From the predator’s perspective, the density of a krill swarm can affect or alter its overall dimensions and hence its detectability i.e. for the same number of krill, a lower density swarm will have a larger volume and be potentially more detectable. In years of average to high phytoplankton, we predict that all krill will adopt low-density swarms day and night regardless of proximity to predators, despite the fact that high-density swarms could reduce mortality from predation in these areas.

**Energy accumulation**

We predict that adopting different depths depending on proximity to predator colonies is an optimal strategy, where a flexible DVM means increased risk from predation but less shrinkage in poor conditions, and reduced mortality but lower accumulated energy in favorable food conditions. The contrary position, that DVM is predetermined and inflexible, is a sub-optimal strategy (Verity and Smetacek, 1996; Hays, 2003). This result is most sensitive to changes in the parameterization of the heterotrophic component of the diet. The energy budget of krill (i.e. assimilated energy minus respiration) is predicted to be negative under low-food conditions at the Antarctic Peninsula region, but positive or around zero everywhere else, suggesting that krill at the Antarctic Peninsula may rely on other forms of food, such as ice algae (Daly and Macaulay, 1991; Verity and Smetacek, 1996), during lean years. We also predict that large krill would lose more than three times the accumulated energy compared with small krill at the Antarctic Peninsula during low food years. Large krill are less common at the Antarctic Peninsula (Atkinson et al., 2006) which may reflect the fact that trophic conditions there are sub-optimal.

Models of krill growth across the Scotia Sea predict both shrinkage (Hofmann and Lascara, 2000; Alonzo and Mangel, 2001; Fach et al., 2002), and growth (Fach et al., 2006) with field studies finding a mean, positive growth even in the low-chlorophyll zones of the central
Scotia Sea (Atkinson et al., 2006). We provide further support for the findings of Fach et al. (Fach et al., 2006) that krill can survive and grow in low-food conditions when including intake from detritus and heterotrophic food. Our results differ at the Antarctic Peninsula, where we predict shrinkage for small krill. In high-chlorophyll concentrations, we predict that medium to large krill can respond quickly to accumulate a lot more energy than small krill. This would make larger krill more capable of exploiting intermittent food patches in low-productivity regions. We suggest that the heterotrophic component of the diet is potentially very important to krill, especially in low-chlorophyll areas, where the background level of heterotrophic carbon available makes up a larger relative proportion of the diet. Evidence for krill eating a range of food other than phytoplankton is clear (Price et al., 1988; Atkinson and Snyder, 1997; Ross et al., 2000). However, there is little understanding of the exact contribution of heterotrophic food and detritus to the carbon budget of krill and how this contribution changes with factors such as temperature, depth and chlorophyll concentration. We suggest further research in this area, attempting to characterize the heterotrophic component of the diet.

The journey

We predict that krill respond rapidly to changing conditions as they travel across the Scotia Sea, particularly as they pass within 100 km of predator colonies, and that a flexible pattern in DVM is one way they optimize both growth and survival. In terms of their life history, krill may be able to cope with variability because of (i) a long lifespan (Brinton et al., 1987), (ii) shrinking under a negative energy budget (Quetin et al., 1994; Marinovic and Mangel, 1999) and (iii) behavioral plasticity in terms of the formation of swarms and DVM. An ability to respond to its environment in weeks or less would be a distinct advantage to krill given that this is the time-to respond to its environment in weeks or less would be important to krill, especially in low-chlorophyll areas, where the background level of heterotrophic carbon available makes up a larger relative proportion of the diet. Evidence for krill eating a range of food other than phytoplankton is clear (Price et al., 1988; Atkinson and Snyder, 1997; Ross et al., 2000). However, there is little understanding of the exact contribution of heterotrophic food and detritus to the carbon budget of krill and how this contribution changes with factors such as temperature, depth and chlorophyll concentration. We suggest further research in this area, attempting to characterize the heterotrophic component of the diet.

CONCLUSIONS

We predict differences in krill behavior between the different regions of the Scotia Sea, and that krill do respond to changes in mortality and food on short time-scales. The optimal depth is likely to be an important way that krill respond to their environment. This is seen in both model predictions and empirical observations. However, the density of swarms on a logarithmic scale is less flexible to changing conditions, and therefore less important to include in models on a management level. We suggest further observations of krill swarm depth across the Scotia Sea, related to predation intensity and chlorophyll concentrations to examine the role of depth choice as a response to variability and change in environmental conditions.

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REFERENCES


