

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

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Received December 12, 2008; accepted in principle June 17, 2009; accepted for publication June 28, 2009; published online 30 July, 2009

Corresponding editor: Mark J. Gibbons

*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; Godlewska, 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, Everson (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. Godlewska (Godlewska, 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, “superswarms” contain densities in excess of  $1000 \text{ g m}^{-3}$  ( $660 \text{ ind. m}^{-3}$  assuming a population consisting of 45 mm krill) and “standard” swarms  $10\text{--}100 \text{ g m}^{-3}$  ( $6\text{--}60 \text{ ind. m}^{-3}$ ). Around the WAP, Lascara *et al.* (1999) found that high density swarms ( $>100 \text{ ind. m}^{-3}$ ) 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.

## 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

Table I: Parameters used in the model

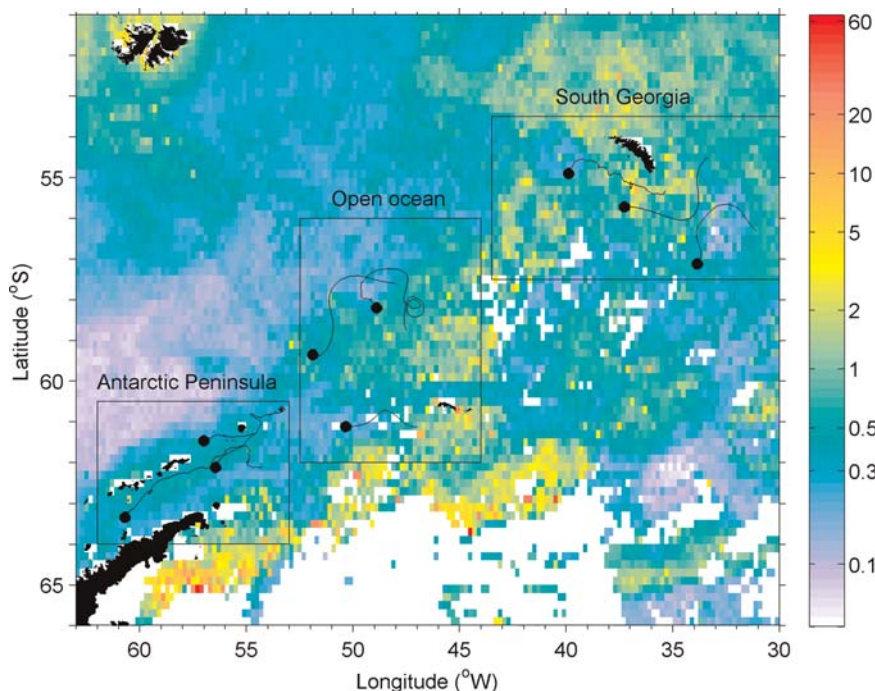
Symbol	Parameter	Value	Unit
$W(e, t z, l)$	Expected fitness from accumulated energy between $t$ and $T$ of an individual krill of size $l$ in zone $z$ between $t$ and $T$	0 to 200	–
$i$	Behavioral decisions made by individual krill at each time step	1 to 18	–
$T$	Final time step	360	6 h
$t$	Time step	6	h
$L$	Light intensity, calculated from $t$	0 night, 1 day	–
$d$	Krill depth	1 surface-layer or 2 deep	–
$s$	Nearest neighbor distance, high to low, representing local swarm density, low to high	1 to 3	–
$z$	Zone, from closest distance to shore	1 to 4	–
$e$	Accumulated energy	0 to 200	mg C
$l$	Size class based on total length (TL)	small 30, med 40, large 50	mm
$j$	Categories for chlorophyll concentration	0 to 20	–
$P_j$	Probability of chlorophyll of concentration $j$	0 to 0.4	–
$C_c$	Carbon from chlorophyll	0 to 150	mg C
$C_h$	Carbon from heterotrophic food	0 to 73.5	mg C
$C_p(d)$	Carbon from detritus	0 to 135	mg C
$\gamma(l)$	Target accumulated energy	Small 53.1, large 51.3	mg C
$w(l)$	Dry mass, based on TL	Small 45, large 226	mg
$\alpha(l)$	Carbon weight, based on TL	Small 19, large 101	–
$F(s, l)$	Filtration rate of chlorophyll	–	mg C $h^{-1}$
$g(s)$	Filtration reduced by factor with krill density	0.1 to 1	–
$l(s, l, d)$	Assimilated ingested energy	–	mg C $h^{-1}$
$R(s, l)$	Respiration rate	$0.01 < R(l, s) < 0.05$	mg C $h^{-1}$
$q(s)$	Respiration decreases by factor with density	1 to 0.8	–
$R_f$	Respiration increases by factor with ingestion	1 to 2	–
$M_I(d, s, z, L)$	Mortality risk close to an island	$1 \times 10^{-8} < M_I(d, s, z, L) < 0.67$	$P(\text{death})$ 6 $h^{-1}$
$M_O(d, s, L)$	Mortality risk in the open ocean	$1.6 \times 10^{-8} < M_O(d, s, L) < 0.2$	$P(\text{death})$ 6 $h^{-1}$

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.expotech.com/sunrise.html](http://www.expotech.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



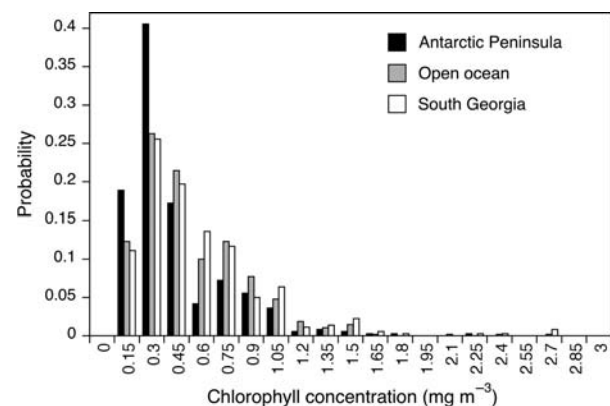
**Fig. 1.** Chlorophyll-*a* concentrations ( $\text{mg m}^{-3}$ ) derived from MODIS, representing the mean of all chlorophyll data acquired in January for the years 2003–2005. White patches represent no data, where cloud or ice cover obscured the sea. We show segments from observed drifters and model-predicted 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  $0.22 \text{ m s}^{-1}$  for the upper 60 m, and  $0.2 \text{ ms}^{-1}$  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  $C_c$  in  $\text{mg Chl } a \text{ m}^{-3}$  (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.



**Fig. 2.** Distribution of discrete values for chlorophyll concentration for each of the defined model regions in the Scotia Sea, with data taken from track latitude and longitude positions.

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

$$\begin{aligned} z = 1 & : \text{distance to shore} \leq 50 \text{ km} \\ z = 2 & : 50 \text{ km} < \text{distance to shore} \leq 100 \text{ km} \\ z = 3 & : 100 \text{ km} < \text{distance to shore} \leq 200 \text{ km} \\ z = 4 & : \text{distance to shore} > 200 \text{ km} \end{aligned} \tag{1}$$

**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

$$E(t) = \text{the accumulated energy of an individual krill at time } t \tag{2}$$

The energy accumulated by an individual krill in one time step  $E(t+1)$ , measured in  $\text{mg C}$ , 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  $200 \text{ mg C m}^{-3}$  (Atkinson and Snyder, 1997). The maximum clearance rate represents the saturation level for filtration plus ingestion rate. Thus, the dynamics of energy are

$$E(t+1) = \begin{cases} E(t) + I(s, l, d) - R(l, s) \\ 0 \\ E_{\text{max}} \end{cases} \times \begin{cases} ; 0 < [E(t) + I(s, l, d) - R(l, s,)] \leq E_{\text{max}} \\ ; [E(t) + I(s, l, d) - R(l, s,)] < 0 \\ ; [E(t) + I(s, l, d) - R(l, s,)] > E_{\text{max}} \end{cases} \tag{3}$$

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

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

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

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

### Fitness

We define fitness by

$$W(e, t|z, l) \text{ maximum Expected} \\ \text{[fitness from accumulated energy between } t \text{ and} \\ T \text{ of an individual krill of size } l \text{ in zone } z \\ \text{between } t \text{ and } T, \text{ given that } E(t) = e]. \quad (7)$$

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  $0.162 \pm 0.129 \text{ mm day}^{-1}$  and  $0.0224 \pm 0.036 \text{ mm day}^{-1}$  for small (30 mm) and large (50 mm) krill, respectively (Atkinson *et al.*, 2006). A target growth level of  $0.092 \text{ mm day}^{-1}$  for medium (40 mm) krill is inferred from the midpoint between that of small and large krill. From the growth rate in mm, we calculate growth  $\gamma(l)$  in  $\text{mg C day}^{-1}$  to be  $\gamma(1)=0.103 \text{ mg C day}^{-1}$  for small krill,  $\gamma(2)=0.108 \text{ mg C day}^{-1}$  for medium krill and  $\gamma(3)=0.045 \text{ mg C day}^{-1}$  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

$$W(e, t|z, l) = \max_i (1 - \beta_i) \\ \times \sum_{j=0}^{20} \bar{P}_j \cdot W(e'_j, t+1|z, l) \quad (10)$$

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

$$C_h = 0.09C_c + 60 \quad (11)$$

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

$$C_p(d) = 20.42 + \frac{0.77C_c}{20^{d-1}} \quad (12)$$

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  $M_I(d, s, z, L)$  (if  $z \leq 3$ , or distance from shore  $< 200$  km) from mortality in the open ocean  $M_O(d, s, L)$  (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  $\bar{M} = 0.00085$  close to land and  $\bar{M} = 0.00035$  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  $\bar{\alpha}_I$  by the logistic transformation.

$$\bar{\alpha}_I = \log_{10} \left[ \frac{\bar{M}_I}{1 - \bar{M}_I} \right] \quad (13)$$

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

$$\alpha_I(d, s, z, L) = \bar{\alpha}_I + \alpha_{d,L} + \alpha_s + \alpha_z \quad (14)$$

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

$$M_I(d, s, z, L) = \frac{10^{\alpha_I(d, s, z, L)}}{1 + 10^{\alpha_I(d, s, z, L)}} \quad (15)$$

Table II: The scaling of mortality in relation to habitat components [see equations (16)–(21)]

Component	Symbol	Value	Reference
Day surface	$\alpha_{d,t}$	2.6	Murphy and Reid (2001); Fiksen
Day deep	$\alpha_{d,t}$	−3.4	and Giske (1995)
Night surface	$\alpha_{d,t}$	0.9	
Night deep	$\alpha_{d,t}$	−4	
Swarm density 1	$\alpha_s (s = 1)$	0.3	Hamilton (1971); Ritz (2000)
Swarm density 2	$\alpha_s (s = 2)$	0	
Swarm density 3	$\alpha_s (s = 3)$	−0.3	
On-shelf	$\alpha_z (z = 1)$	0.3	Hunt <i>et al.</i> (1992); Perissinotto
Shelf-break	$\alpha_z (z = 2)$	0	and McQuaid (1992); Houston
Off-shelf	$\alpha_z (z = 3)$	−0.3	and Mcnamara (1985)

To calculate mortality in the open ocean  $M_O(d, s, L)$  given  $\bar{M}_O$  we set

$$\bar{\alpha}_O = \log_{10} \left[ \frac{\bar{M}_O}{1 - \bar{M}_O} \right] \tag{16}$$

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

$$\alpha_O(d, s, L) = \bar{\alpha}_O + \alpha_{d,L} + \alpha_s \tag{17}$$

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

$$M_O(d, s, L) = \frac{10^{\alpha_O(d,s,L)}}{1 + 10^{\alpha_O(d,s,L)}} \tag{18}$$

### 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  $z$ , 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 65–50°S and 30–55°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 (Coetzee, 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 SWDBA TS 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. All



swarms falling within these ranges were assumed to be krill swarms. Backscatter within swarms was converted into krill density (ind.  $\text{m}^{-3}$ ) 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.  $\text{m}^{-1}$ ) 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.

### Observed krill depth in each region.

The vast majority of observed swarms were estimated to have a density of  $<100$  ind.  $\text{m}^{-3}$  in all three regions, with a maximum of 10% of krill swarms containing densities  $>100$  ind.  $\text{m}^{-3}$  (Table IV). The Antarctic Peninsula region contained the highest proportion of swarms with densities  $>100$  ind.  $\text{m}^{-3}$  (10%), while only 4% of swarms around South Georgia reached this density. These swarms were much more likely to occur in the upper 60 m. Only 7 out of 4653 krill swarms had a density  $>1000$  ind.  $\text{m}^{-3}$ . The observation that the density of the majority of swarms was  $<100$  ind.  $\text{m}^{-3}$  is in line with the predictions from our model. However,

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

	Low food	Medium food	High food
Antarctic Peninsula (30 mm krill)	Medium DVM, with a proportion in surface layers during the day High density swarm deep Low density swarm in surface layer	No DVM, always deep Always low density	No DVM, always deep Always low density
Open Ocean (40 mm krill)	Medium DVM, proportion in surface layers during day increases with distance from shore ( $>50\%$ surface-layer during day at $>100$ km from shore) High density swarm deep Low density swarm in surface layer	Medium DVM, proportion in surface layers during day increases with distance from shore ( $>50\%$ surface-layer during day at $>100$ km from shore) High density swarm deep Low density swarm in surface layer	DVM further from shore Always deep close to shore ( $<100$ km) Always low density
South Georgia (50 mm krill)	Medium DVM, proportion in surface layers during day increases with distance from shore ( $>50\%$ surface-layer during day at $>100$ km from shore) High density swarm deep Low density swarm in surface	DVM further from shore Always deep close to shore ( $<100$ km) Always low density	DVM further from shore Always deep close to shore ( $<100$ km) Always low density

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.

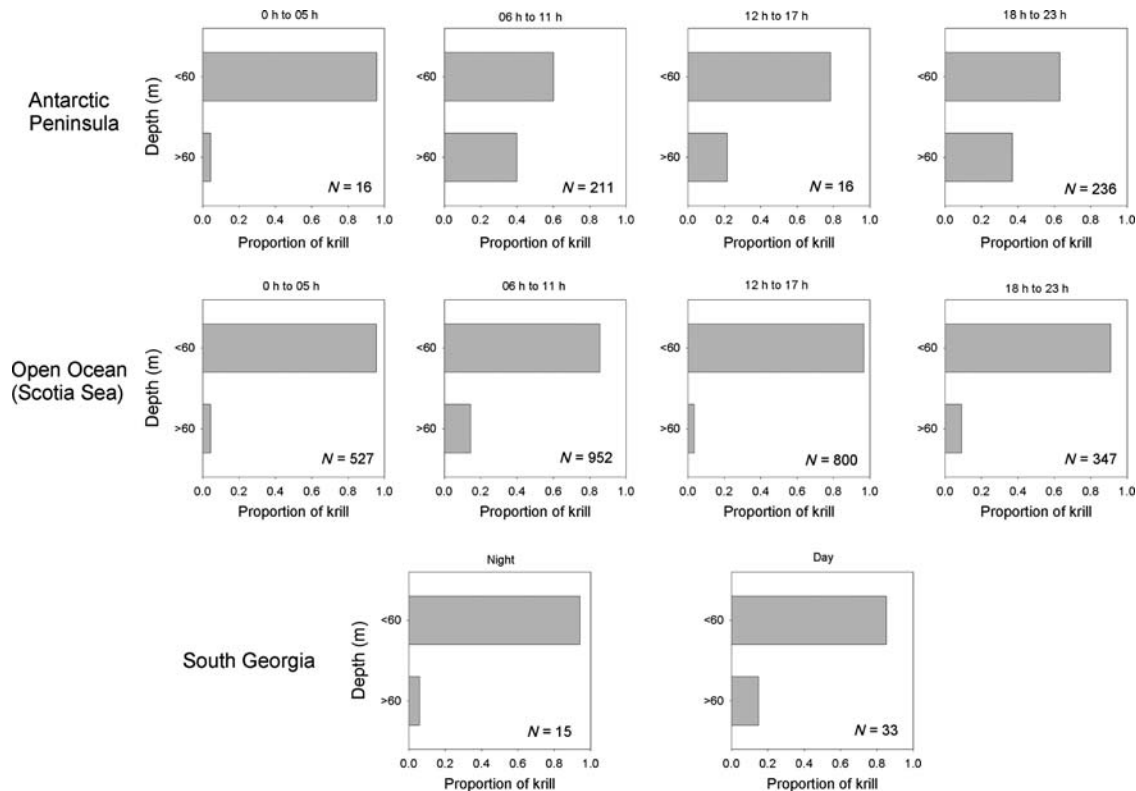
*Table IV: Results of acoustic observations on the density of krill swarms across three regions of the Southern Ocean Atlantic sector*

	Antarctic Peninsula	Open Ocean	South Georgia
Proportion of swarms between 0 and 100 krill m <sup>-3</sup>	0.90	0.95	0.96
Proportion of swarms between 100 and 1000 krill m <sup>-3</sup>	0.09	0.05	0.04
Proportion of swarms between 100 and 1000 krill m <sup>-3</sup>	0.01	0.00	0.00

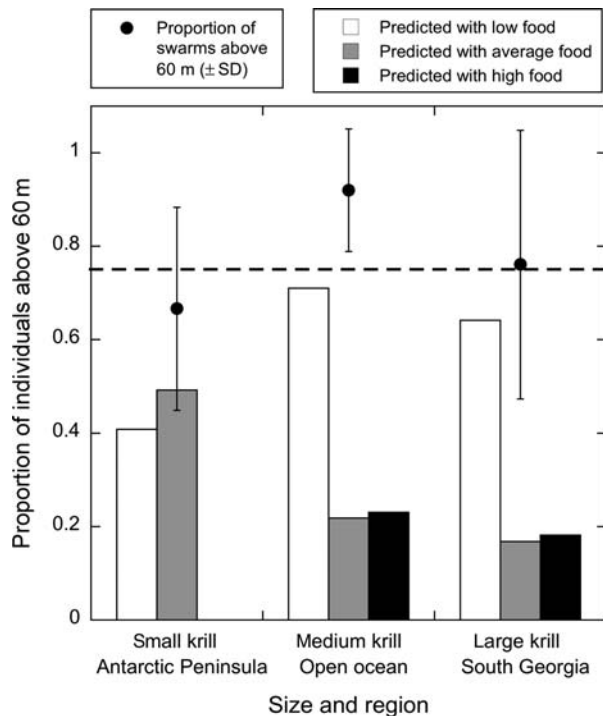
the prediction of swarm densities >1000 ind. m<sup>-3</sup> in certain food-poor situations was not supported by observations, given that such swarms were very rarely found.

The majority of krill (ind. m<sup>-1</sup>) 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



**Fig. 3.** 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.

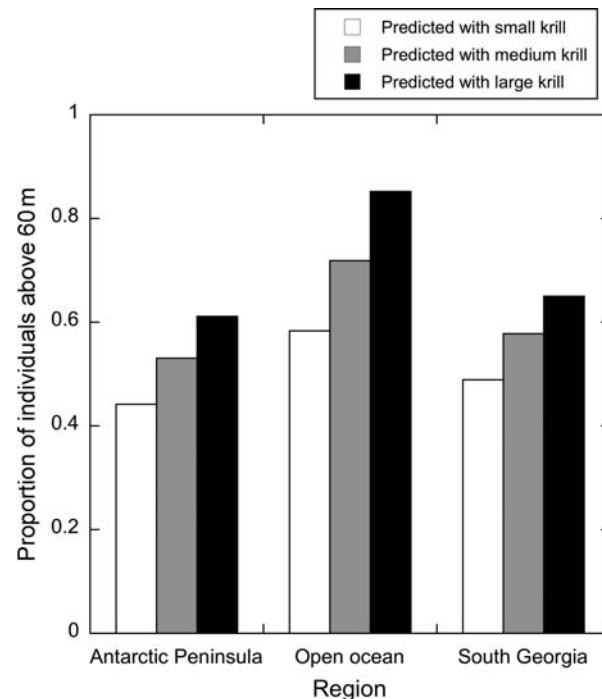


**Fig. 4.** Bars represent the average-predicted behavior of krill with the low-food conditions (white bar), average food conditions (grey bar) and high-food conditions (black bar). In comparison, three points represent the average depth of krill swarms observed in each of the regions, taken from acoustic data. Error bars denote bootstrap variance calculated through random sub-sampling of the empirical data set. The dotted line shows the proportion of krill in the surface layers that would result if krill adopted a fixed DVM.

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



**Fig. 5.** The effect of krill size on depth choice for small, medium and large krill in each of the regions, for low-food conditions.

scenario, and predict that krill size has the greatest effect on final accumulated energy at the Antarctic Peninsula region (Fig. 7).

### Sensitivity analysis

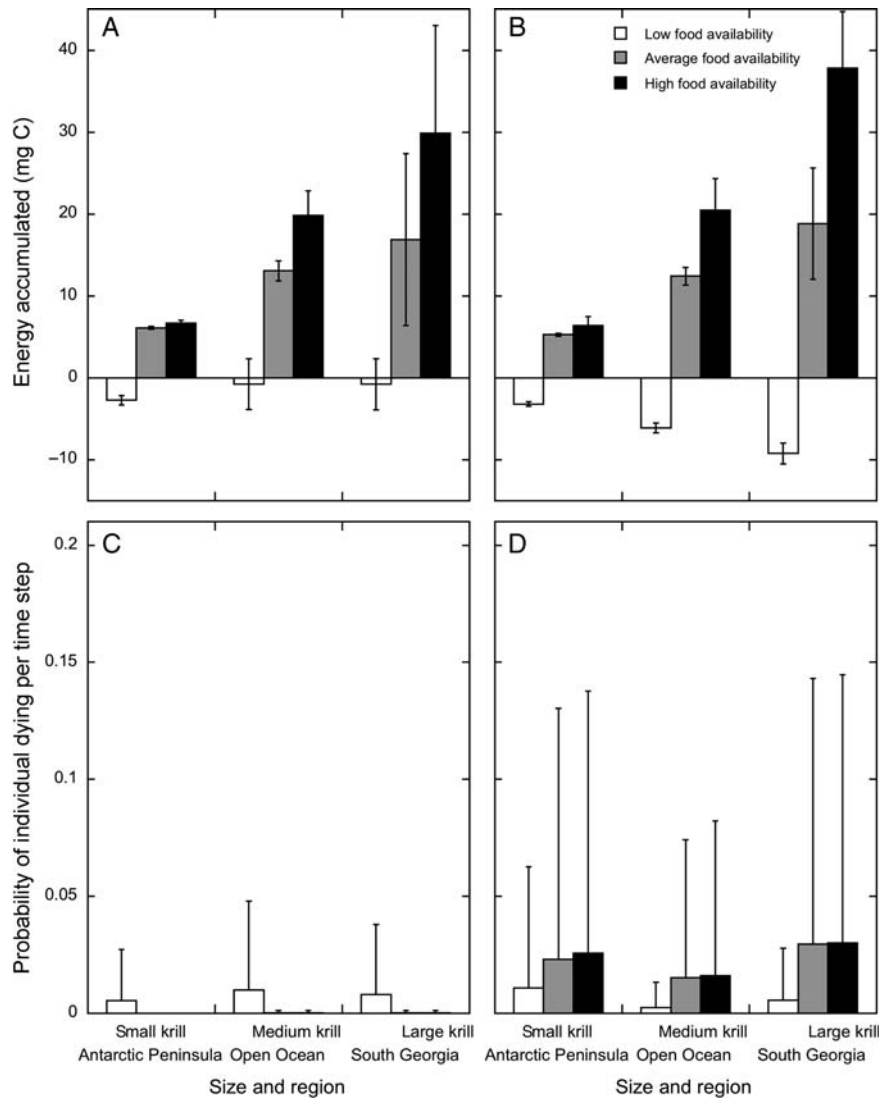
We calculate sensitivity by dividing the percentage change in the result of interest by the percentage change in the parameter value.

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



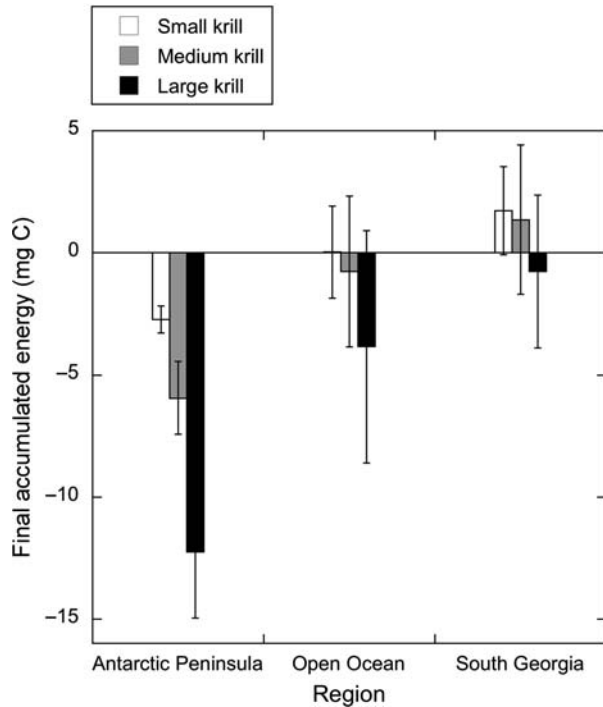
**Fig. 6.** The predicted average energy in mg C ( $\pm$ SD) accumulated when krill choose their depth in the model (A) compared with a model where DVM is fixed and depth is not a choice (B) and average mortality per individual per time step ( $\pm$ SD) in the model where depth is a choice (C) compared 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.

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.

### 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





**Fig. 7.** The effect of krill size on average final accumulated energy  $\pm$  SD in each of the model regions in low-food conditions.

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

*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)*

Result	Chlorophyll conc. ( $C_c$ )	Heterotrophic food ( $C_f$ )	Max. clearance rate ( $C_{max}$ )
Energy	1.13	<b>1.86</b>	0.95
DVM	0.86	<b>1.96</b>	0.36
Low-density swarm	0.47	<b>0.6</b>	0.01
Medium-density swarm	1.07	0.6	<b>1.65</b>
High-density swarm	0.67	<b>1.06</b>	0.03

The parameter of highest sensitivity is highlighted in bold (DVM, diel vertical migration of zooplankton).

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).

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<sup>-3</sup>). There was no depth trend in the observed small number of higher density swarms (>100 ind. m<sup>-3</sup>), 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 (Weihs, 1975; O'Brien, 1987; Ritz, 2000). Schooling behavior is inherently difficult to study in both the field and the laboratory (Strand and Hamner, 1990; Hamner and Hamner, 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; Godlewska, 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-scale in which major changes in the biomass of their main food source, phytoplankton, occurs. We predict that krill respond on short time scales to changing conditions, as proposed by Ross *et al.* (Ross *et al.*, 2000).

### 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.

### ACKNOWLEDGEMENTS

Thanks to P. Trathan for help and support throughout, P. Fretwell for invaluable help with mapping food and nearest distance to shore, A. Fleming for data on phytoplankton, and A. Atkinson and K. Schmidt for conversations about heterotrophic food.

### FUNDING

This work is part of a PhD through the British Antarctic Survey (BAS) and Open University, funded through National Environmental Research Council and contributing to the FLEXICON project of the DISCOVERY 2010 programme at BAS. The Lenfest Ocean Program supported the latter stages of this research.

### REFERENCES

- Alonzo, S. H. and Mangel, M. (2001) Survival strategies and growth of krill: avoiding predators in space and time. *Mar. Ecol. Prog. Ser.*, **209**, 203–217.
- Alonzo, S. H., Switzer, P. V. and Mangel, M. (2003) Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, **84**, 1598–1607.
- Anon (1986) Post-FIBEX acoustic workshop, Frankfurt, Germany. *BIOMASS Rept. Ser.*, **40**, 106.
- Atkinson, A. (1996) Subantarctic copepods in an oceanic, low chlorophyll environment: ciliate predation, food selectivity and impact on prey populations. *Mar. Ecol. Prog. Ser.*, **130**, 85–96.
- Atkinson, A. and Snyder, R. (1997) Krill-copepod interactions at South Georgia, Antarctica. I. Omnivory by *Euphausia superba*. *Mar. Ecol. Prog. Ser.*, **160**, 63–76.
- Atkinson, A., Shreeve, R., Hirst, A. G. *et al.* (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex and maturity stage. *Limnol. Oceanogr.*, **51**, 973–987.
- Atkinson, A., Siegel, V., Pakhomov, E. *et al.* (2008) Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Prog. Ser.*, **362**, 1–23.
- Barlow, K. E. and Croxall, J. P. (2002) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Mar. Ecol. Prog. Ser.*, **232**, 291–304.

- Barlow, K. E., Boyd, I. L., Croxall, J. P. *et al.* (2002) Are penguins and seals in competition for Antarctic krill at South Georgia? *Mar. Biol.*, **140**, 205–213.
- Boyd, I. L. and Croxall, J. P. (1992) Diving behavior of lactating Antarctic fur seals. *Can. J. Zool.*, **70**, 919–928.
- Boyd, C. M., Heyraud, M. and Boyd, C. N. (1984) Feeding of the Antarctic krill, *Euphausia superba*. *J. Crustac. Biol.*, **4**, 123–141.
- Brinton, E., Loeb, V. J., Macaulay, M. C. *et al.* (1987) Variability of *Euphausia superba* populations near Elephant Island and the South Shetland—1981 vs 1984. *Polar Biol.*, **7**, 345–362.
- Burrows, M. T. and Tarling, G. (2004) Effects of density dependence on diel vertical migration of populations of northern krill: a Genetic Algorithm model. *Mar. Ecol. Prog. Ser.*, **277**, 209–220.
- Clark, C. W. and Mangel, M. (2000) *Dynamic State Variable Models in Ecology*. Oxford University Press, Oxford.
- Clarke, A. (1984) Lipid-content and composition of Antarctic krill, *Euphausia superba* Dana. *J. Crustac. Biol.*, **4**, 285–294.
- Clarke, A. and Morris, D. J. (1983) Towards an energy budget for krill—the physiology and biochemistry of *Euphausia superba* Dana. *Polar Biol.*, **2**, 69–86.
- Clarke, A. and Tyler, P. A. (2008) Adult Antarctic krill feeding at abyssal depths. *Curr. Biol.*, **18**, 282–285.
- Coetzee, J. (2000) Use of a shoal analysis and patch estimation system (SHAPES) to characterize sardine schools. *Aquat. Living Resour.*, **13**, 1–10.
- Conti, S. G. and Demer, D. A. (2006) Improved parameterization of the SDWBA for estimating krill target strength. *ICES J. Mar. Sci.*, **63**, 928–935.
- Cresswell, K. A., Tarling, G. A. and Burrows, M. T. (2007) Behaviour affects local distribution of Antarctic krill at South Georgia. *Mar. Ecol. Prog. Ser.*, **343**, 193–206.
- Croxall, J. P., Everson, I., Kooyman, G. L. *et al.* (1985) Fur seal diving behaviour in relation to krill vertical distribution. *J. Anim. Ecol.*, **54**, 1–8.
- Croxall, J. P., Briggs, D. R., Kato, A. *et al.* (1993) Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J. Zool.*, **230**, 31–47.
- Daly, K. L. and Macaulay, M. C. (1991) Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the antarctic marginal ice zone. *Mar. Ecol. Prog. Ser.*, **79**, 37–66.
- Demer, D. A. and Hewitt, R. P. (1995) Bias in acoustic biomass estimates of *Euphausia superba* due to diel vertical migration. *Deep Sea Res. I Oceanogr. Res. Pap.*, **42**, 455–475.
- De Robertis, A. (2002) Size-dependent visual predation risk and the timing of vertical migration: an optimization model. *Limnol. Oceanogr.*, **47**, 925–933.
- Everson, I. (1982) Diurnal variation in mean volume backscattering strength of an Antarctic krill (*Euphausia superba*) patch. *J. Plankton Res.*, **4**, 155–161.
- Everson, I. (1983) Variations in vertical distribution and density of krill swarms in the vicinity of South Georgia. *Mem. Natl. Inst. Polar Res.*, 84–92. (Special Issue 27).
- Everson, I. and Bone, D. G. (1986) Detection of krill (*Euphausia superba*) near the sea-surface—preliminary results using a towed upward-looking echo-sounder. *Br. Antarct. Surv. Bull.*, **72**, 61–70.
- Fach, B. A., Hofmann, E. E. and Murphy, E. J. (2002) Modeling studies of Antarctic krill *Euphausia superba* survival during transport across the Scotia Sea. *Mar. Ecol. Prog. Ser.*, **231**, 187–203.
- Fach, B. A., Hofmann, E. and Murphy, E. J. (2006) Transport of Antarctic krill (*Euphausia superba*) across the Scotia Sea, Part II: Krill growth and survival. *Deep-Sea Res. I*, **53**, 1011–1043.
- Fiksen, O. and Giske, J. (1995) Vertical-distribution and population-dynamics of copepods by dynamic optimization. *ICES J. Mar. Sci.*, **52**, 483–503.
- Froneman, P. W., Pakhomov, E. A., Perissinotto, R. *et al.* (1996) Role of microplankton in the diet and daily ration of Antarctic zooplankton species during austral summer. *Mar. Ecol. Prog. Ser.*, **143**, 15–23.
- Godlewska, M. (1996) Vertical migrations of krill (*Euphausia superba* Dana). *Pol. Arch. Hydrobiol.*, **14**, 9–63.
- Green, J. A., Butler, P. J., Woakes, A. J. *et al.* (2002) Energy requirements of female macaroni penguins breeding at South Georgia. *Funct. Ecol.*, **16**, 671–681.
- Green, J. A., Butler, R. J., Woakes, A. J. *et al.* (2003) Energetics of diving in macaroni penguins. *J. Exp. Biol.*, **206**, 43–57.
- Hamilton, W. D. (1971) Geometry for the selfish herd. *J. Theor. Biol.*, **31**.
- Hamner, W. M. and Hamner, P. P. (2000) Behavior of Antarctic krill (*Euphausia superba*): schooling, foraging, and antipredatory behavior. *Can. J. Fish. Aquat. Sci.*, **57**, 192–202.
- Hays, G. C. (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, **503**, 163–170.
- Hewitt, R. P., Watkins, J., Naganobu, M. *et al.* (2004a) Biomass of Antarctic krill in the Scotia Sea in January/February 2000 and its use in revising an estimate of precautionary yield. *Deep-Sea Res. II*, **51**, 1215–1236.
- Hewitt, R. P., Watters, G., Trathan, P. N. *et al.* (2004b) Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. *CCAMLR Sci.*, **11**, 81–97.
- Hill, H. J., Trathan, P. N., Croxall, J. P. *et al.* (1996) A comparison of Antarctic krill *Euphausia superba* caught by nets and taken by macaroni penguins *Eudyptes chrysolophus*: Evidence for selection? *Mar. Ecol. Prog. Ser.*, **140**, 1–11.
- Hofmann, E. E. and Lascara, C. M. (2000) Modeling the growth dynamics of Antarctic krill *Euphausia superba*. *Mar. Ecol. Prog. Ser.*, **194**, 219–231.
- Hofmann, E. E., Klinck, J. M., Locarnini, R. A. *et al.* (1998) Krill transport in the Scotia Sea and environs. *Antarct. Sci.*, **10**, 406–415.
- Hofmann, E. E., Haskell, A. G. E., Klinck, J. M. *et al.* (2004) Lagrangian modelling studies of Antarctic krill (*Euphausia superba*) swarm formation. *ICES J. Mar. Sci.*, **61**, 617–631.
- Houston, A. I. and McNamara, J. M. (1985) A general-theory of central place foraging for single-prey loaders. *Theor. Pop. Biol.*, **28**, 233–262.
- Houston, A. and McNamara, J. (1999) *Models of Adaptive Behavior: An Approach based on State*. Cambridge University Press, Cambridge.
- Hunt, G. L., Heinemann, D. and Everson, I. (1992) Distributions and predator-prey interactions of macaroni penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. *Mar. Ecol. Prog. Ser.*, **86**, 15–30.
- Kalinowski, J. and Witek, Z. (1983) Some aspects of biology, forms of aggregation and stocks of Antarctic krill *Euphausia superba* Dana (In Polish). Joint PhD Thesis.



- Korb, K. E., Whitehouse, M. J. and Ward, P. (2004) Sea WiFS in the southern ocean: spatial and temporal variability in phytoplankton biomass around South Georgia. *Deep-Sea Res. II*, **51**, 99–116.
- Korb, B., Whitehouse, M. J., Thorpe, S. E. *et al.* (2005) Primary production across the Scotia Sea in relation to the physico-chemical environment. *J. Mar. Syst.*, **57**, 231–249.
- Lascara, C. M., Hofmann, E. E., Ross, R. M. and Quetin, L. B. (1999) Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. *Deep-Sea Res. Part I*, **46**, 951–984.
- Lawson, G. L., Wiebe, P. H., Ashjian, C. J. *et al.* (2008a) Euphausiid distribution along the Western Antarctic Peninsula—part B: distribution of euphausiid aggregations and biomass, and associations with environmental features. *Deep-Sea Res. Part II*, **55**, 432–454.
- Lawson, G. L., Wiebe, P. H., Stanton, T. K. *et al.* (2008b) Euphausiid distribution along the Western Antarctic Peninsula—part A: development of robust multi-frequency acoustic techniques to identify euphausiid aggregations and quantify euphausiid size, abundance and biomass. *Deep-Sea Res. II*, **55**, 412–431.
- Ligowski, R. (2000) Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off west Antarctica and in Admiralty Bay, South Shetland Islands. *Polar Biol.*, **23**, 619–625.
- Loeb, V. J., Amos, A. F., Macaulay, M. C. *et al.* (1993) Antarctic krill stock distribution and composition in the Elephant-Island and King-George-Island areas, January–February, 1988. *Polar Biol.*, **13**, 171–181.
- Mackintosh, N. (1973) Distribution of post-larval krill in the Antarctic. *Disc. Rep.*, **36**, 95–156.
- Mangel, M. and Clark, C. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton.
- Marinovic, B. and Mangel, M. (1999) Krill can shrink as an ecological adaptation to temporarily unfavourable environments. *Ecol. Lett.*, **2**, 338–343.
- Marr, J. W. S. (1962) The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Disc. Rep.*, **32**, 33–464.
- Miller, D. G. M. and Hampton, I. (1989) Biology and ecology of the Antarctic krill. *BIOMASS Sci. Ser.*, **9**, 1–166.
- Miller, D. G. M., Barange, M., Klindt, H. *et al.* (1993) Antarctic krill aggregation characteristics from acoustic observations in the Southwest Atlantic-Ocean. *Mar. Biol.*, **117**, 171–183.
- Morris, D. J., Ward, P. and Clarke, A. (1983) Some aspects of feeding in the Antarctic krill, *Euphausia superba*. *Polar Biol.*, **2**, 21–26.
- Murphy, E. J., Watkins, J. L., Reid, K. *et al.* (1998) Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fish. Oceanogr.*, **7**, 381–390.
- Murphy, E. J. and Reid, K. (2001) Modelling Southern Ocean krill population dynamics: biological processes generating fluctuations in the South Georgia ecosystem. *Mar. Ecol. Prog. Ser.*, **217**, 175–189.
- Murphy, E. J., Thorpe, S. E., Watkins, J. L. *et al.* (2004) Modeling the krill transport pathways in the Scotia Sea: spatial and environmental connections generating the seasonal distribution of krill. *Deep-Sea Res. II*, **51**, 1435–1456.
- O'Brien, D. P. (1987) Description of escape responses of krill (Crustacea, Euphausiacea), with particular reference to swarming behavior and the size and proximity of the predator. *J. Crustac. Biol.*, **7**, 449–457.
- Perissinotto, R. and McQuaid, C. D. (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern-Ocean archipelago. *Mar. Ecol. Prog. Ser.*, **80**, 15–27.
- Price, H. J., Boyd, K. R. and Boyd, C. M. (1988) Omnivorous feeding-behavior of the Antarctic krill *Euphausia superba*. *Mar. Biol.*, **97**, 67–77.
- Quetin, L. B., Ross, R. M. and Clarke, A. (1994) Krill energetics: seasonal and environmental aspects of the physiology of *Euphausia superba*. In Sayed, E. (ed.), *Southern Ocean Ecology: the BIOMASS Perspective*. Cambridge University Press, Cambridge, pp. 165–184.
- Reid, K., Trathan, P. N., Croxall, J. P. *et al.* (1996) Krill caught by predators and nets: differences between species and techniques. *Mar. Ecol. Prog. Ser.*, **140**, 13–20.
- Reiss, C. S., Cossio, A. M., Loeb, V. *et al.* (2008) Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. *ICES J. Mar. Sci.*, **65**, 497–508.
- Ritz, D. (1994) Social aggregations in pelagic invertebrates. *Adv. Mar. Biol.*, **30**, 155–216.
- Ritz, D. A. (2000) Is social aggregation in aquatic crustaceans a strategy to conserve energy? *Can. J. Fish. Aquat. Sci.*, **57**, 59–67.
- Ross, R. M., Quetin, L. B., Baker, K. S. *et al.* (2000) Growth limitation in young *Euphausia superba* under field conditions. *Limnol. Oceanogr.*, **45**, 31–43.
- Russell, F. S. (1927) The vertical distribution of plankton in the sea. *Biol. Rev.*, **2**, 213–262.
- Strand, S. W. and Hamner, W. M. (1990) Schooling behavior of Antarctic krill (*Euphausia superba*) in laboratory aquariums—reactions to chemical and visual-stimuli. *Mar. Biol.*, **106**, 355–359.
- Swadling, K. M., Ritz, D. A., Nicol, S. *et al.* (2005) Respiration rate and cost of swimming for Antarctic krill, *Euphausia superba*, in large groups in the laboratory. *Mar. Biol.*, **146**, 1169–1175.
- Taki, K., Hayashi, T. and Naganobu, M. (2005) Characteristics of seasonal variation in diurnal vertical migration and aggregation of Antarctic krill (*Euphausia superba*) in the Scotia Sea, using Japanese fishery data. *CCAMLR Sci.*, **12**, 163–172.
- Tarling, G., Shreeve, R. S., Hirst, A. G. *et al.* (2006) Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermoult period. *Limnol. Oceanogr.*, **51**, 959–972.
- Thorpe, S. E., Heywood, K. J., Stevens, D. P. *et al.* (2004) Tracking passive drifters in a high resolution ocean model: implications for interannual variability of larval krill transport to South Georgia. *Deep-Sea Res. I*, **51**, 909–920.
- Verity, P. G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.*, **130**, 277–293.
- Weih, D. (1975) Some hydrodynamical aspects of fish schooling. In Wu, T. Y., Brokaw, C. J. and Brennen, C. (eds), *Swimming and Flying in Nature*. Plenum Press, New York, pp. 203–218.
- Williams, T. D. and Croxall, J. P. (1991) Annual variation in breeding biology of macaroni penguins, *Eudyptes chrysolophus*, at Bird Island, South Georgia. *J. Zool.*, **223**, 189–202.
- Witek, Z., Kalinowski, J., Grelowski, A. *et al.* (1981) Studies of aggregations of krill (*Euphausia superba*). *Meeresforschung/Rep. Mar. Res.*, **28**, 228–243.