

# More than passive drifters: a stochastic dynamic model for the movement of Antarctic krill

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**ABSTRACT:** Antarctic krill *Euphausia superba* are a key part of the marine food web and are the target of the largest fishery in the Southern Ocean. Although ecosystem and management models typically assume that krill are passive drifters, their relatively large size and strong swimming ability suggest that the active movement of krill may play an important role in their spatial distribution. Thus, active swimming behavior by krill may influence spatial structure of food web interactions (e.g. feeding behavior of seabirds and marine mammals) and regional commercial fishery activity. The objective of this work was to model the potential for active movement to affect krill distribution, and consequently growth, reproductive success, and survival. We used state-dependent life history theory, implemented by stochastic dynamic programming, in combination with spatial information on food availability, current velocity, temperature, and predation risk, to predict krill swimming behavior near the northern Antarctic Peninsula. We found that including active krill behavior resulted in distribution patterns that are associated with increased survival, growth, and reproductive success compared to a model that treats krill as passive drifters. The expected reproductive success of actively behaving krill was about 70% greater than that of passively diffusing krill, suggesting that there are strong selective pressures for active behavior along oceanic drift trajectories. This modeling framework will benefit assessments of new catch limits as krill fishing grounds are partitioned into smaller spatial management units.

**KEY WORDS:** *Euphausia superba* · Behavior · Stochastic dynamic programming · Management · Advection · Southern Ocean

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## INTRODUCTION

Antarctic krill *Euphausia superba* (hereafter krill) play a fundamental role in the trophodynamics of the Southern Ocean ecosystem (Nicol & de la Mare 1993). They are a crucial link in the transfer of nutrients and energy to higher trophic levels and are a major prey source for many species of fish, squid,

seabirds, and marine mammals (Smetacek & Nicol 2005). Fluctuations in krill biomass availability can have important consequences for predator reproductive success (Croxall et al. 1999, Reid & Croxall 2001, Lynnes et al. 2004, Trivelpiece et al. 2011), although the relationships between krill biomass and predator reproductive performance are complex (Croxall et al. 1999).

Effective management of human impacts on krill stocks is a matter of great concern for the Southern Ocean ecosystem. A commercial krill fishery has been operating in the Southern Ocean since the 1970s, and catches have been increasing over the past 2 decades (Nicol et al. 2012). The increased demand for krill products, such as nutritional supplements and aquaculture feed, along with new harvesting technologies may lead to increased fishing activity and the potential for localized depletion in the vicinity of land-based predator colonies, particularly during the breeding season (Nicol et al. 2000, 2012, Nicol & Foster 2003, Hewitt et al. 2004). In addition, krill recruitment is correlated with the extent and duration of winter pack ice, leading to concerns that climate change and declining sea ice could negatively impact krill populations (Atkinson et al. 2004, Wiedenmann et al. 2009).

Although most management models treat krill as passively drifting along ocean currents, krill are a schooling species with strong swimming abilities, perhaps more akin to small fish than plankton. They can swim at a steady cruising speed of up to 15 cm s<sup>-1</sup>, move at 40–50 cm s<sup>-1</sup> for short periods (Kils 1982), perform diel vertical migrations (Godlewska 1996, Hernández-León et al. 2001), exhibit schooling behavior (Hamner & Hamner 2000), undertake sustained directed movement (Marr 1962, Kanda et al. 1982), and actively migrate, especially in regions with lower current velocities (Siegel 1988, Trathan et al. 1993). While it is unlikely that krill make large-scale directed migrations in the open ocean where current velocities are high, localized responses to small-scale cues may affect the broad-scale distribution of krill (Lascara et al. 1999, Murphy et al. 2004). In addition, modeling studies indicate that behavior can influence local-scale krill distributions (Cresswell et al. 2007). Thus, accounting for krill behavior may have important implications for our understanding of krill population dynamics at local to regional scales, their interactions with predators, and ultimately the effective management of krill fisheries.

The Southern Ocean krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Due to concerns over localized fishing impacts on krill-dependent predators, CCAMLR established 15 small-scale management units (SSMUs) in the Scotia Sea region in order to facilitate spatial management on a scale more relevant to land-based predators and to avoid localized depletion (Constable & Nicol 2002, Hewitt et al. 2004). Options for allocation of catch limits within SSMUs include limits based on (1) historical

catches in the SSMU; (2) estimated predator demand (the estimated annual demand by Adelie, chinstrap, gentoo and macaroni penguins, lactating female Antarctic fur seals, baleen whales, and fish) in the SSMU; (3) the standing stock of krill in the SSMU; (4) standing stock minus predator demand in the SSMU; and (5) allocation based on predator surveys conducted each year before the fishing season (Hewitt et al. 2004). Several modeling tools are currently being used to assess these potential strategies (Watters et al. 2005, 2006, 2009, 2013, Hill et al. 2007, Plagányi & Butterworth 2012). In these models, krill are assumed to either stay in the SSMU of their birth for their entire lives, or to move passively with ocean currents. Thus, these models do not account for the possibility of active behavior by krill, and may therefore miss an important component of krill movement and consequent spatial distribution. In addition, spatial location is likely to influence the growth, mortality, and reproductive success of krill (Siegel & Nicol 2000, Hofmann & Hüsrevoğlu 2003, Atkinson et al. 2006). By accounting for the influence of krill behavior on spatial distributions, we can make further inferences about the importance of behavior in krill dynamics.

Dynamic state variable models (Mangel & Clark 1988, Houston & McNamara 1999, Clark & Mangel 2000, Mangel 2014) provide a useful tool for exploring krill behavior across space and time because krill must balance the energetic costs of movement with feeding, growth, reproduction, and the risk of predation. These models use state-dependent life history theory, implemented through stochastic dynamic programming, to predict optimal behavioral decisions within a set of constraints. Dynamic state variable models allow organisms to make decisions about growth, maturation, and behavior based on both their own internal state as well as external cues such as environmental factors or time to some reproductive event.

Here, we used a dynamic state variable model to predict krill swimming speed and movement direction near the North Antarctic Peninsula (NAP). We then used forward simulations to explore how the spatial distribution, growth, survival, and reproductive success of krill vary relative to active and passive transport behaviors. In particular, we investigated the following: (1) krill swimming speed and movement direction (our overarching research question); (2) conditional on (1), how does the spatial distribution of krill vary relative to active and passive transport behaviors; and (3) how does active swimming influence growth, egg production, and survival?

## METHODS

Our modeling study focused on the vicinity of the South Shetland Islands, near the NAP (Fig. 1). We chose this area because: (1) it is home to a large number of krill and krill-dependent predators (Reiss et al. 2008, Santora & Veit 2013); (2) it is a major krill fishing ground (Jones & Ramm 2004) and there is potential for competition between krill predators and the

fishery (Croll & Tershy 1998); and (3) observed patterns of krill distributions have been theorized to arise in part because of active krill migration (Siegel 1988, Watkins et al. 1992, Trathan et al. 1993). Circulation in this area is complex, with contributions from the Antarctic Circumpolar Current, the Weddell Gyre, and the Antarctic Coastal Current (Thompson et al. 2009). The bathymetry of the region is varied, including the continental shelf around the islands as

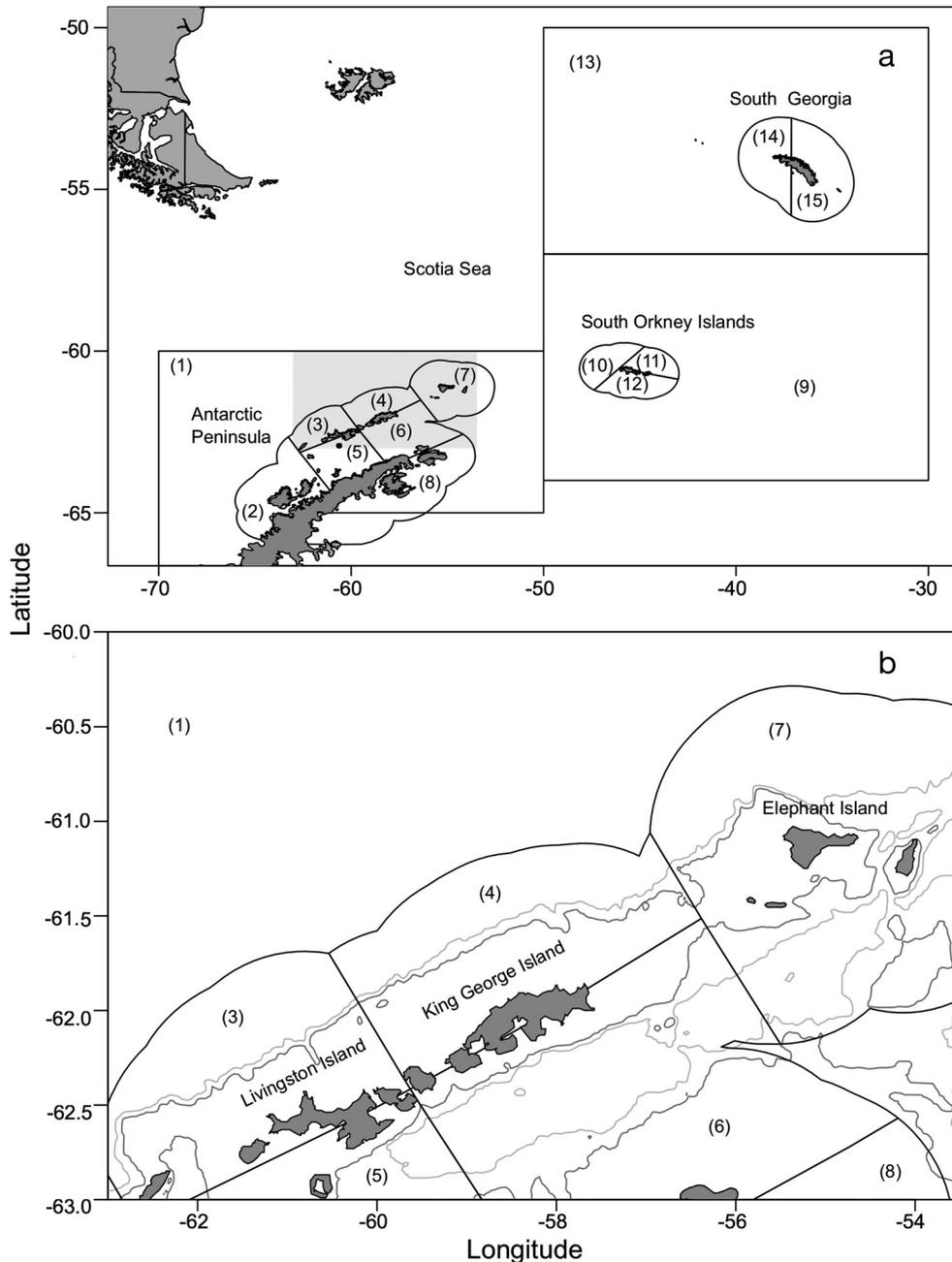


Fig. 1. (a) Southwest Atlantic Ocean showing locations of the 15 small-scale management units (SSMUs), with the area of focus shaded. (b) Focal area, including SSMUs, 500 m isobath (dark gray), and 1000 m isobath (light gray)

well as deeper waters in the Bransfield Strait and Drake Passage (Figs. 1 & 2c). We focused our model on January of the austral summer, when most spawning in the vicinity of the Antarctic Peninsula begins (Quetin & Ross 2001). During this late summer period, observed spatial segregation of adults and juveniles, with aggregations of spawning adults in oceanic regions and the continental shelf, are hypothesized to be the result of active movement by adult krill (Siegel 2000).

### Environment

Although krill are omnivorous, their summer diet consists mainly of phytoplankton (Falk-Petersen et al. 2000). Across the Southern Ocean, krill densities are positively correlated with chlorophyll *a* (chl *a*) (Atkinson et al. 2008), although the relationship is complex and may be complicated by depletion at smaller scales due to grazing (Wright et al. 2010). However, chl *a* is a significant predictor of growth

rate (Atkinson et al. 2006). Thus, we used satellite estimates of chl *a* from the GlobColour Project ([www.globcolour.info/](http://www.globcolour.info/)), which combines information from the MERIS, MODIS, and SeaWiFS sensors, as a proxy for food abundance. For all available years (1998–2013), we obtained the 8 d mean chlorophyll concentrations across the study area at the 4 km scale and averaged across years to produce a mean chl *a* field for each 8 d period in January.

Surface currents were calculated from geostrophic velocities derived from mean sea level measured by satellite altimetry. The mean sea level data used to calculate the geostrophic velocities are the merged sea level product created by Archiving, Validation, and Interpretation of Satellite Oceanographic data (AVISO; [www.aviso.altimetry.fr](http://www.aviso.altimetry.fr)). From AVISO's Maps of Absolute Dynamic Topography (MADT, 7 d intervals) we calculated geostrophic velocities by assuming geostrophy and using centered finite differencing on the MACT product to obtain  $u_g$  and  $v_g$  (zonal and meridional geostrophic current components, respectively) (Sudre et al. 2013, their Eqs. 1a & 1b).

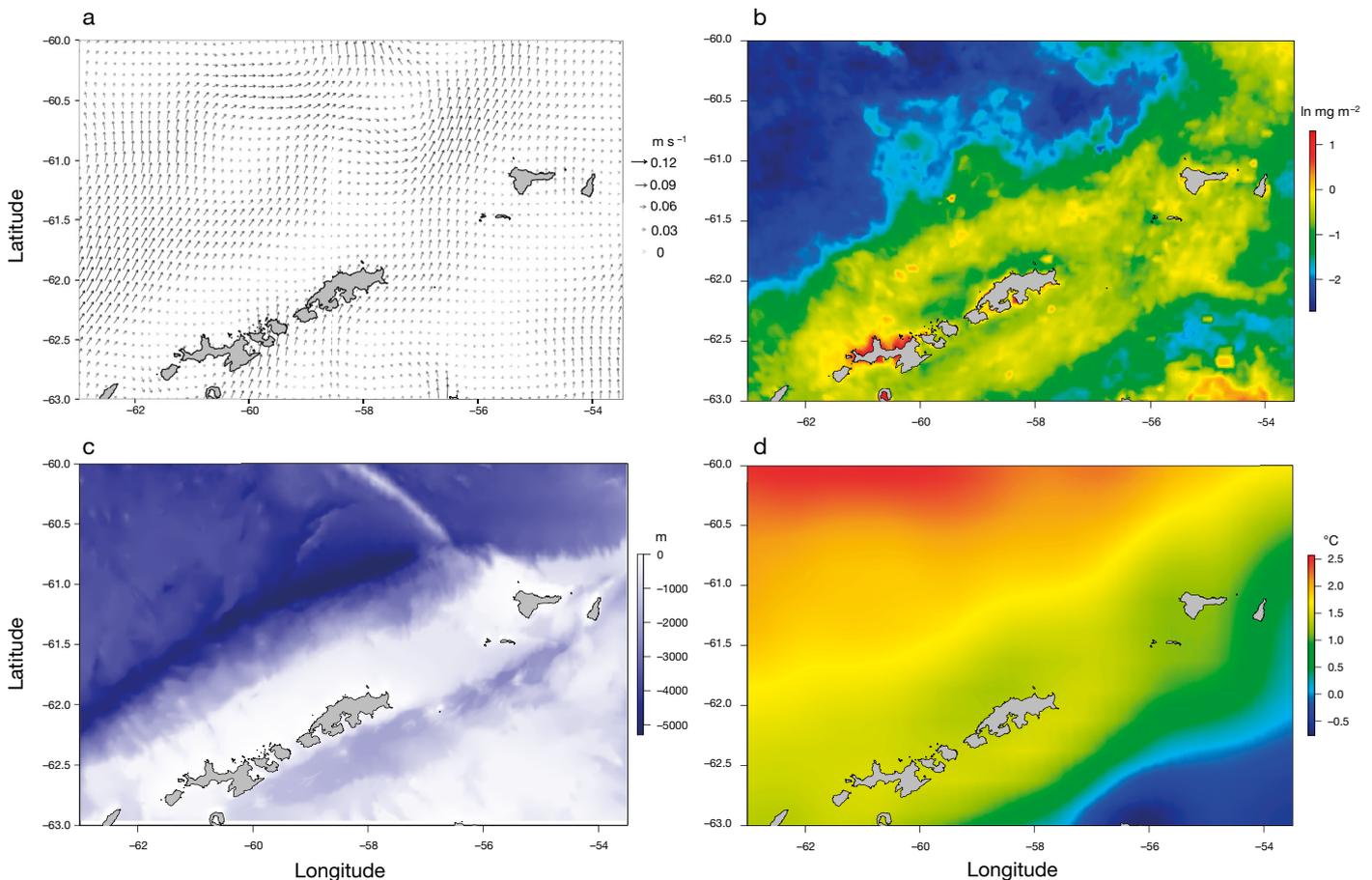


Fig. 2. (a) Mean January current vectors ( $\text{m s}^{-1}$ ), 2003–2011. (b) Log mean January chlorophyll *a* concentrations ( $\text{mg m}^{-3}$ ), 1997–2013. (c) Bathymetry (m). (d) Mean January temperature ( $^{\circ}\text{C}$ ), 2003–2011

Monthly means of  $u_g$  and  $v_g$  for January were calculated and a final climatology was constructed from the monthly means for the years 2003 to 2011. The MACT product we used was based on the older AVISO product and not the product introduced in April 2014 ([www.aviso.altimetry.fr/fileadmin/documents/data/duacs/Duacs2014.pdf](http://www.aviso.altimetry.fr/fileadmin/documents/data/duacs/Duacs2014.pdf)). The resulting surface velocity vectors derived from the older AVISO product have better coherence with observed drifter buoys (Thompson et al. 2009) and circulation models (Jiang et al. 2013), particularly around the islands and the Shackleton Fracture Zone. We suspect that the new optimal interpolation method used in creating the more recent product may be smoothing out some of the circulation features that are present in the older data and that appear in drifter studies and circulation models; thus we chose to use the older product.

Krill are ectotherms, with a dome-shaped growth rate/temperature profile and maximum growth rates occurring around  $0.5^\circ\text{C}$  (Atkinson et al. 2006, Wiedenmann et al. 2008). In addition, krill densities are negatively correlated with sea surface temperature (SST), although this may simply reflect krill responses to temperature correlates such as food availability (Trathan et al. 2003). To characterize the temperature environment experienced by krill in our model, we used  $\frac{1}{4}$  degree resolution mean January SST data averaged over 2003 to 2011 from the Group for High Resolution Sea Surface Temperature at the NOAA National Climatic Data Center (Reynolds et al. 2007, obtained from <http://coastwatch.pfeg.noaa.gov/erddap/griddap/>).

We obtained bathymetry data at the 30 arc second scale from the General Bathymetric Chart of the Oceans (GEBCO, [www.gebco.net/](http://www.gebco.net/)). We obtained coastline polygons from the SCAR Antarctic Digital Database ([www.add.scar.org/](http://www.add.scar.org/)). We gridded all data at the 1 km scale and linearly interpolated when necessary using the Akima package version 0.5-11 (Akima et al. 2013) in R 3.0.2 (R Development Core Team 2013). Fig. 2 shows sample current, chl *a*, temperature, and bathymetry landscapes.

### Growth and the cost of movement

In order to estimate baseline growth (i.e. growth that does not include the cost of active movement), we used the model of Atkinson et al. (2006; also see Wiedenmann et al. 2009), in which instantaneous growth is used to predict krill growth as a function of size, temperature, and chl *a* concentration. We used a parameterization for all age and sex classes com-

bined, where daily growth rate (DGR) for a krill of size  $L$  (mm) experiencing chl *a* concentration  $F$  ( $\text{mg m}^{-3}$ ) at temperature  $T$  ( $^\circ\text{C}$ ) is:

$$\text{DGR}(L, F, T) = -0.066 + 0.002L - 0.000061L^2 + 0.385 \frac{F}{0.328 + F} + 0.0078T - 0.0101T^2 \quad (1)$$

Thus, for a non-swimming krill of length  $L_0$  at time  $t$ , the new length at time  $t + \Delta t$  is:

$$L_0(t + \Delta t) = L_0 + \text{DGR} \cdot \Delta t \quad (2)$$

We then converted length to dry weight  $DW_0(t)$  (where  $DW = 6.46 \times 10^{-5} L^{3.89}$ ; Atkinson et al. 2006) and then to carbon weight  $CW_0(t)$  (where  $CW = 0.366 DW^{1.037}$ ; Hofmann & Lascara 2000), both measured in mg.

Swadling et al. (2005) found a linear relationship between current speed  $S$  (in  $\text{cm s}^{-1}$ ) and krill respiration rate  $R$  (in  $\text{mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$  dry weight):

$$R = 2.16 + 0.35S \quad (3)$$

This relationship holds true for speeds from 5 to  $18 \text{ cm s}^{-1}$ , and Swadling et al. (2005) hypothesized that krill are not strongly influenced by currents below  $3 \text{ cm s}^{-1}$ . Although the authors suggested a nonlinear relationship between respiration rate and speed at low velocities, for simplicity we assumed here that krill expend the same energy swimming  $0\text{--}3 \text{ cm s}^{-1}$ , and that at speeds above  $3 \text{ cm s}^{-1}$ , respiration rises linearly with a slope of 0.35 (Fig. 3). This is a reasonable assumption because at  $3 \text{ cm s}^{-1}$ , krill appear to be operating at their routine metabolic

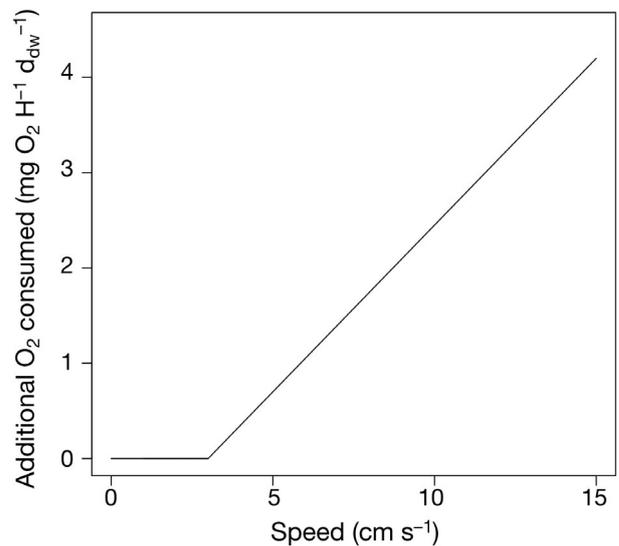


Fig. 3. Additional metabolic cost ( $\text{mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$  dry weight) as a function of swimming speed ( $\text{cm s}^{-1}$ ) in Antarctic krill *Euphausia superba*, based on Swadling et al. (2005)

rate and are likely maintaining the minimum pleopod rate required to keep them from sinking (Swadling et al. 2005). Thus, using a respiratory quotient of 0.72 (following Lowe et al. 2012) and the molar masses of carbon and oxygen, we estimated the additional carbon  $C$  lost due to swimming at speed  $S$  as:

$$C(S) = 0.35 \cdot \frac{12.011}{32.0} \cdot 0.72 = 0.0946 \cdot S \quad (4)$$

if  $S > 3 \text{ cm s}^{-1}$ , or

$$C(S) = 0 \quad (5)$$

if  $S \geq 3 \text{ cm s}^{-1}$ .

In order to estimate the change in size of a krill swimming at speed  $S$  over  $\Delta t$ , we calculated the baseline growth using Eq. (2), converted the new length to carbon weight, and decremented the cost of swimming, such that the new carbon weight is:

$$CW(t+\Delta t) = CW_0 - C(S) \cdot 24\Delta t \cdot DW_0 \cdot 10^{-3} \quad (6)$$

We then reconverted carbon weight to length using the allometric relationships given above. Thus, we were able to predict the change in length at each time step given length, environmental conditions, and swimming behavior.

### Mortality

Estimates of krill mortality rates vary widely, perhaps due in part to spatial and interannual variability in mortality (Siegel & Nicol 2000). There is considerable predation pressure from land-based krill predators, which are more abundant on the continental shelf (Croll & Tershy 1998). Thus, following Cresswell et al. (2007), we separated mortality into on-shelf, shelf slope, and off-shelf zones. We let average mortality  $\bar{\beta} = 0.0025 \text{ d}^{-1}$ , an intermediate value from the range reported for the Antarctic Peninsula that translates to an approximate 40% annual survival rate (Siegel & Nicol 2000). Mortality in cell  $x$  is:

$$\beta(x) = \frac{10^\alpha}{1+10^\alpha} \quad (7)$$

We scaled  $\alpha$  by zone (on-shelf, shelf break, and off-shelf), such that:

$$\alpha = \bar{\alpha} + \alpha_z \quad (8)$$

where  $\alpha_z$  represents the mortality of a habitat relative to the mean mortality. Here, we let  $\alpha_z = 0.5$  on-shelf,  $\alpha_z = 0$  on the shelf break, and  $\alpha_z = -0.5$  off-shelf (Cresswell et al. 2007). We let:

$$\bar{\alpha} = \log_{10} \left( \frac{\bar{\beta}}{1-\bar{\beta}} \right) \quad (9)$$

such that in the absence of a scaling parameter  $\alpha_z$  (i.e.  $\alpha_z = 0$ ), mortality is equal to mean mortality  $\bar{\beta}$ .

### Krill movement model

We gridded the entire study area (63 to 60° S, 63 to 53.5° W) into  $\sim 1 \text{ km}^2$  cells and let  $\bar{x}$  denote the position of the center of a cell. We let  $F(l, \bar{x}, t)$  denote the maximum expected reproductive success (measured in terms of viable eggs, i.e. those laid in water sufficiently deep for their survival) at time  $T$  for a krill with current length  $L(t) = l$  and in cell  $\bar{x}$ . Here, the maximum is taken over the behavioral choices concerning swimming. We determined the fitness function as follows.

#### End condition

Stochastic dynamic programming models begin at the final time step and iterate backwards in time to solve for the behavior that maximizes expected future fitness given current conditions and time to the terminal timestep. Thus, it is necessary to define a measure of Darwinian fitness at the last time step, called the end condition. Here, we assumed that female krill spawn their eggs in the final timestep and that this represents the terminal fitness reward. Following Nicol et al. (1995), we assumed that a krill of length  $l$  releases  $E(l)$  eggs, given by:

$$E(l) = \max(0, -5293.1 + 144.84l) \quad (10)$$

Krill eggs are released in the upper water column, where they sink to 700–1000 m before hatching into free-swimming larvae and beginning their ascent back towards the surface (Quetin & Ross 1984). Therefore, eggs released on the continental shelf are unlikely to develop, because they will reach the ocean floor before hatching (Hofmann & Murphy 2004). However, in many areas near the Antarctic Peninsula, krill eggs are predicted to successfully hatch well within the 1000 m isobath (Hofmann & Hüsrevoğlu 2003). Thus, we set the egg-survival threshold to 500 m, such that eggs deposited in water shallower than 500 m are lost and eggs released in deeper water are expected to survive. Clearly, a less-sharp egg-survival/bathymetry relationship can be used when such data are available.

Therefore, the fitness  $F$  of a krill of length  $l$  in cell  $\bar{x}$  at the final timestep  $T$  is:

$$F(l, \bar{x}, T) = -5293.1 + 144.84l \quad (11)$$

if bottom depth is greater than 500 m, or:

$$F(l, \bar{x}, T) = 0 \quad (12)$$

if bottom depth is less than 500 m. Thus, the fitness accrued by a krill in the final timestep of the model depends on both its size and location; although being bigger leads to more eggs, getting bigger (for example, by feeding in high-chlorophyll areas close to land) has associated risks (e.g. predation by land-based predators) that lead to a growth-survival trade-off.

#### Dynamic programming equation

After setting the end condition, we iterated backwards with timesteps of  $\Delta t = 12$  h (0.5 d) to solve for the optimal behavioral choice using the dynamic programming equation (DPE). The DPE is an algorithm that solves for the behavior that maximizes expected future fitness given the organism's current state and the time to the final time step, when it will gain an increment in fitness as defined by the end condition described above. We solved the DPE for krill size varying from 40 to 50 mm over 28 d (1 to 28 January) in the entire study area. At each timestep  $t$ , we allowed krill to choose from 6 swimming speeds (0 to  $15 \text{ cm s}^{-1}$ ) and 8 directions of movement (0 to  $7\pi/4$

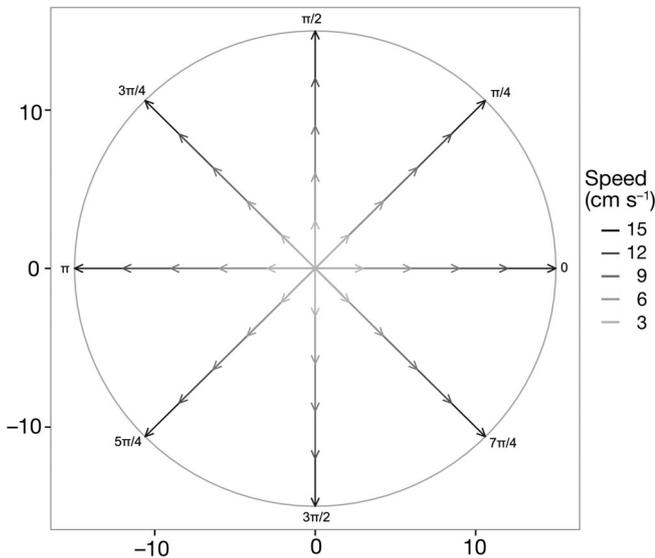


Fig. 4. Potential swimming velocity choices for Antarctic krill *Euphausia superba* in the model

radians), giving 41 swimming velocity  $\bar{m}$  choices (Fig. 4). A krill swimming at velocity  $\bar{m}$  beginning in cell  $\bar{x}$  with current velocity  $\bar{v}(\bar{x})$  ( $\text{km h}^{-1}$ ) will have a new location  $\bar{x}'$ :

$$\bar{x}' = \bar{x} + \bar{m}\Delta t + \bar{v}(\bar{x})\Delta t \quad (13)$$

and a new length  $l'$ , calculated from Eq. (6) and the allometric relationships given previously. We leave assigning a probability distribution on  $\bar{x}'$  to future work.

Thus, for a krill in cell  $\bar{x}$  with current velocity  $\bar{v}(\bar{x})$ , the DPE is:

$$F(l, \bar{x}, t) = \max_{\bar{m}} [e^{-\beta(x)} \cdot F(l', \bar{x}', t+1)] \quad (14)$$

The movement velocity choice  $\bar{m}^*(l, \bar{x}, t)$  that results in maximum expected fitness can then be used in forward simulations of krill behavior.

#### Forward simulations

The DPE produces a set of predicted behaviors  $\bar{m}^*(l, \bar{x}, t)$  for a female krill given its size, location, and the time to the terminal timestep, when it will release eggs. Using these behavioral rules, we can run forward Monte Carlo simulations for large numbers of krill to explore how krill spatial distribution will change through time as krill behave according to the rules set up by the DPE. We can also compare these distributions to simulations where krill act as passive drifters (i.e. in the model, a swimming speed of 0).

In order to illustrate the potential for active movement to influence krill distributions, we conducted 61 simulations of 45 mm krill ( $n = 10\,000$ ) beginning near King George Island and Livingston Island (see Fig. 7 for starting locations). We chose these starting locations because krill are relatively abundant in much of this area during summer (Reiss et al. 2008) and because it allowed us to follow krill trajectories for most or all of the simulation time window without leaving the study area. We began with krill of 45 mm because this is a common size class in the area (Reiss et al. 2008). We then iterated forward through time for 28 d, with change in size each time step calculated according to Eq. (6) and predicted behavior at each timestep drawn from the solution to the DPE. Following Thorpe et al. (2004), we added a stochastic component to the advective current flow, such that for the  $i^{\text{th}}$  simulated krill:

$$\bar{x}_i(t + \Delta t) = \bar{x}_i + \bar{m}(l_i, \bar{x}_i, t) \cdot \Delta t + \bar{v}(\bar{x}) \cdot \Delta t + \bar{w} \quad (15)$$

where  $\bar{w} = (d\cos(\tau), d\sin(\tau))$  is a random walk mimicking eddy diffusivity, with  $d = \sqrt{12\Delta t D_h R_1}$  and

$\tau = 2\pi R_2$ .  $D_h$  is the horizontal diffusion coefficient (set to  $100 \text{ m}^2 \text{ s}^{-1}$ ), and  $R_1$  and  $R_2$  are random numbers between 0 and 1 drawn from the uniform distribution (Hilborn & Mangel 1997). We ran each simulation twice, once for 'active' krill, where  $\vec{m}(l(t), \vec{x}(t), t)$  is taken from the solution to the DPE, and once for 'passive' krill, where  $\vec{m}(l(t), \vec{x}(t), t) = 0$ . Varying  $D_h$  by  $\pm 50\%$  does not change the general pattern of the results.

## RESULTS

We considered (1) krill swimming speed and movement direction; (2) conditional on (1), how the spatial distribution of krill varies relative to active and passive transport behaviors; and (3) how active swimming influences growth, egg production, and survival.

### Predicted behavior

Based on the backwards algorithm, we predicted that krill swim an average of  $3.65 (\pm 2.62 \text{ SD}) \text{ cm s}^{-1}$ , or about  $3.15 \text{ km d}^{-1}$ . Mean swimming speeds were similar across size classes (Fig. 5). Mean swimming speeds showed an increase, then a sharp decrease close to the terminal time, likely indicating a critical window when krill inside the 500 m isobath must move quickly in order to be in a favorable area for releasing eggs by the final timestep. After this critical window, many krill are close enough to the final time that swimming in the

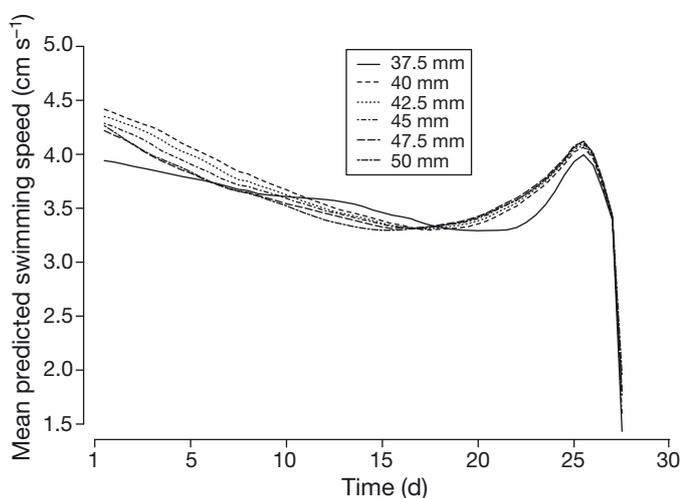


Fig. 5. Mean predicted swimming speed ( $\text{cm s}^{-1}$ ) for Antarctic krill *Euphausia superba* of different sizes

last few timesteps is unlikely to greatly alter their reproductive outcome, so mean speeds decrease near the terminal time.

Predicted swimming behavior also varied across space and time, reflecting the differing environmental conditions and the effect of time on the terminal fitness reward in the model. Fig. 6 shows the predicted swimming velocities for 45 mm krill at several sample timesteps.

After running the forward simulations of 10 000 female krill (45 mm) with and without active behavior over 28 d, we found that by the final timestep (or when krill reached the edge of the study area), the mean distance between an active krill and a passive krill with the same point of origin ranged from 7.73 to 168.51 km (mean 67.50 km). In 27 of 61 simulations, the average locations of passive and active krill were in different SSMUS by the end of the simulation (Fig. 7).

Although overall actively behaving and passively drifting krill reached similar mean sizes (mean  $47.88 \pm 1.34 \text{ mm}$  for active krill,  $47.07 \pm 1.77 \text{ mm}$  for passive krill; Fig. 8a), actively behaving krill produced on average more viable eggs per individual in all simulations (mean  $1602.31 \pm 215.78$  for active and  $944.39 \pm 655.97$  for passive krill; Fig. 8b). Predicted mean eggs across passive simulations ranged from 0 to  $1737.10 \pm 10.72$  and across active simulations from  $1124.16 \pm 10.96$  to  $1868.44 \pm 24.99$ . Survival rates for active krill were higher than for passive krill in 36 of 61 simulations (mean 93.8% for active krill, 91.4% for passive krill; Fig. 8c). A measure of the strength of natural selection on active swimming behavior is the ratio of these expected reproductive successes, i.e.  $0.938 \times 1602 / (0.914 \times 944) = 1.74$ . With multiple reproductive bouts per year, the strength of natural selection is magnified. See Table S1 in the Supplement, available at [www.int-res.com/articles/suppl/m529p035\\_supp.pdf](http://www.int-res.com/articles/suppl/m529p035_supp.pdf) for individual results from all simulations.

Although tests of statistical significance are not appropriate for model simulation data (White et al. 2014), we report a measure of effect size (Cohen's  $d$ ) for both length and egg production. Cohen's  $d$  is a measure of the difference between 2 sample means as multiples of their weighted standard deviation; values of 0.2, 0.5, and 0.8 are considered small, medium, or large effect sizes (Cohen 1988). In our studies, effect sizes varied between simulations, from 0.8 to 35.5 for length and from 0.67 to 176.1 for egg production (see Table S1 for all values).

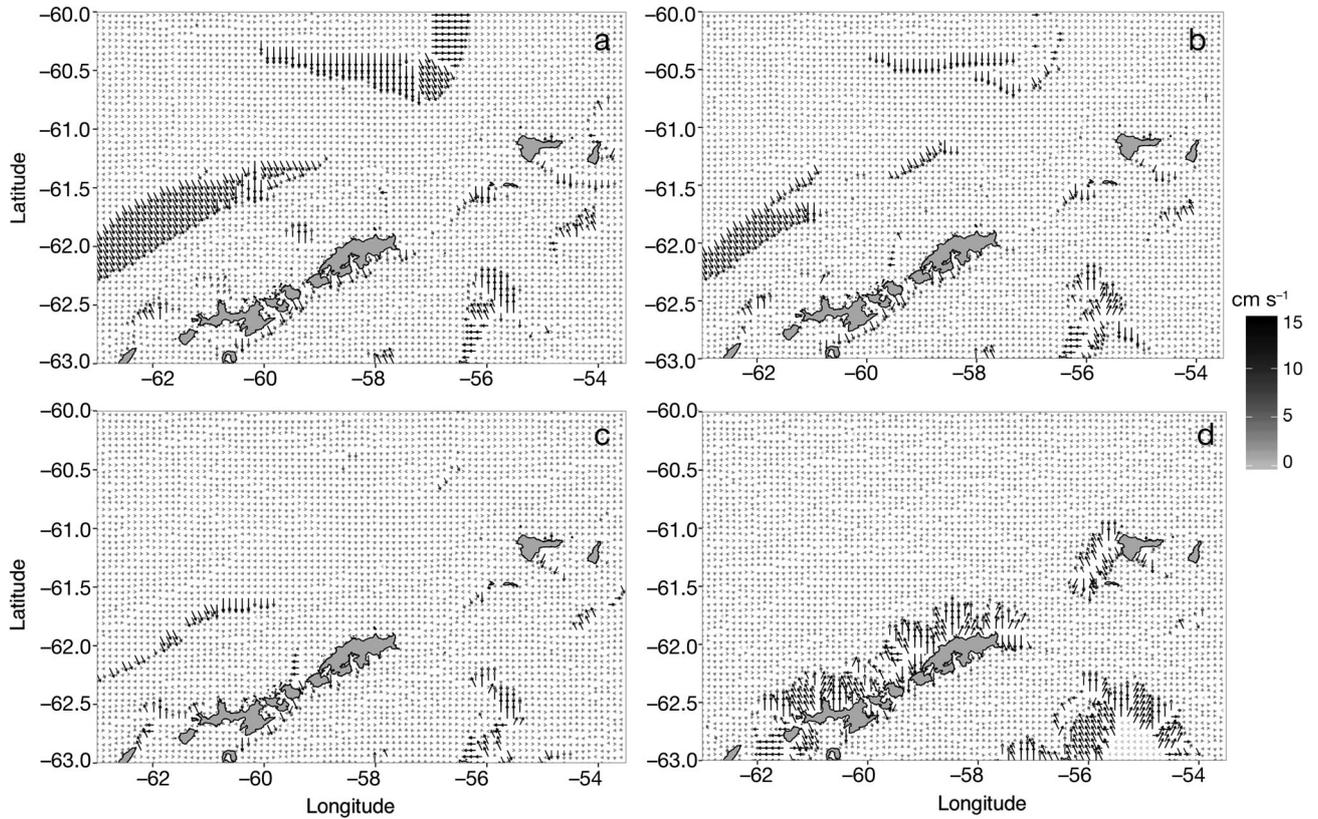


Fig. 6. Predicted swimming velocities ( $\text{cm s}^{-1}$ ) for 45 mm Antarctic krill *Euphausia superba* at different timesteps  $t$ : (a)  $t = 1$ , (b)  $t = 15$ , (c)  $t = 30$ , and (d)  $t = 50$

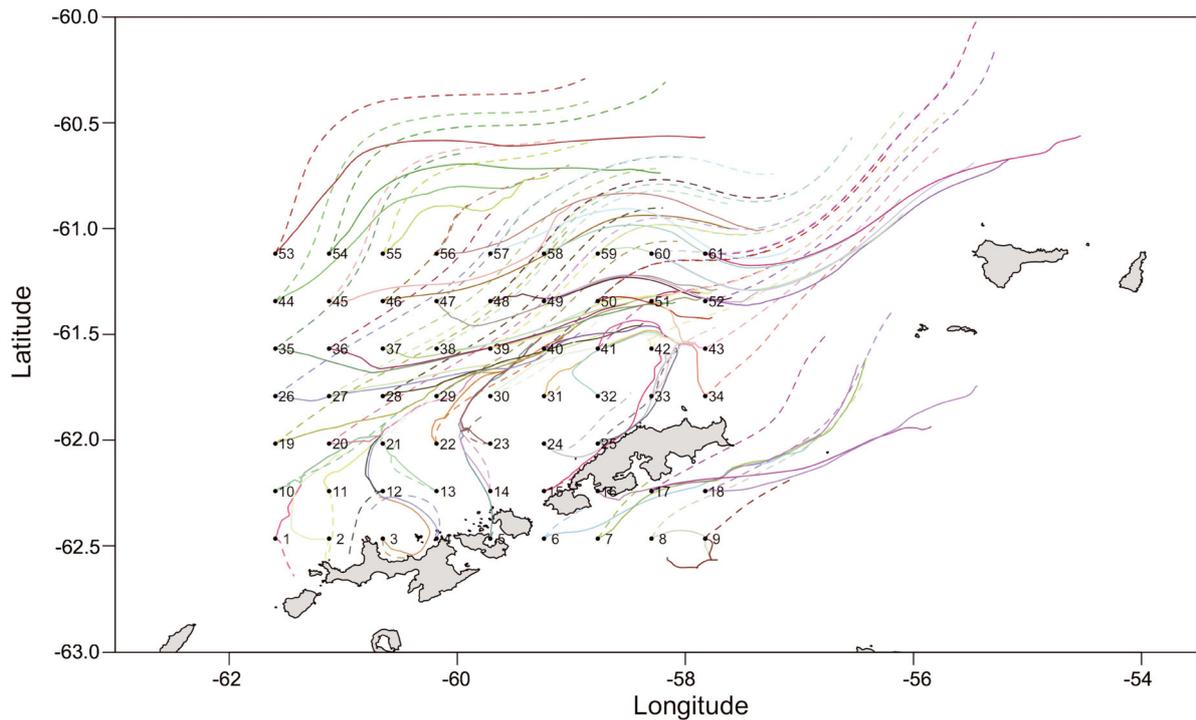


Fig. 7. Mean trajectories of simulated active (solid lines) and passive (dashed lines) Antarctic krill *Euphausia superba* released at numbered starting points

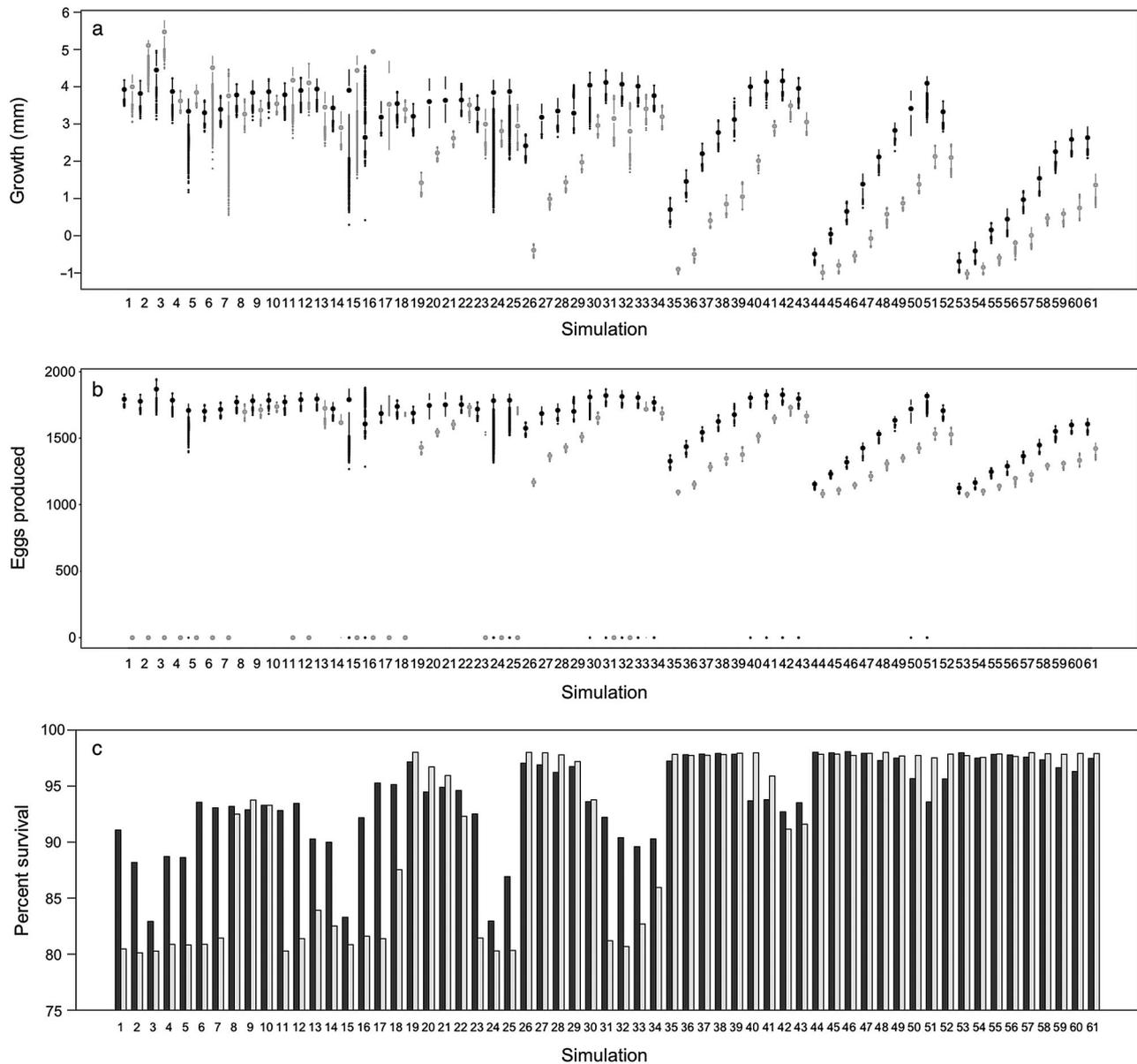


Fig. 8. Results from forward simulations of active (black) and passive (gray) Antarctic krill *Euphausia superba*. (a) Growth (mm) over the simulation window. Large dots represent the median, vertical bars represent upper and lower quartiles, small dots represent outliers. (b) Eggs released outside the 500 m isobath. (c) Percent survival over the simulation

## DISCUSSION

Our results indicate that active krill movement plays an important role in determining the spatial distribution of krill in the vicinity of the northern Antarctic Peninsula. This accords with field observations that spatial distributions of krill in this area unlikely to result from advective processes alone (Siegel 1988, Watkins et al. 1992, Trathan et al. 1993, Lascara et al. 1999). Those studies found a clear segregation of size and maturity stages, suggesting that

ontogenetic migrations may in part explain observed spatial patterns. In our study, reproductive females appeared to actively move in order to release eggs in more favorable areas, suggesting a possible mechanism for the segregation of sex and age classes. Although our forward simulations only tracked krill for a single month, if the pattern we observed here continued over the course of a season, for some locations active krill could be on the order of hundreds of kilometers away where they would be predicted to be using a passive drift model of krill transport.

Clearly, model predictions are unlikely to be a perfect reflection of behavior in the field, and krill may not always act according to the optimal swimming trajectories in our model. However, this result underscores the potential for behavior to alter our conceptions of krill distributions across space and time.

Since SSMUs are relatively small (10 800–927 400 km<sup>2</sup>; Hewitt et al. 2004), and current management models resolve on a bi-annual timescale (Plagányi & Butterworth 2012, Watters et al. 2013), the predicted movement of krill between SSMUs could be very different if behavior were included in the management models. These models either assume no movement or use transport rates based on passive particle tracking models. Including some assumptions about active movement into estimates of transport rates could provide an opportunity to include more biological realism in these models. Furthermore, our work shows that movement behavior may play an important role in reproductive success and predator avoidance.

Our simulations suggest that for some other areas near the South Shetland Islands, krill distributions (whether assumed to be passive or active) may be locations that accumulate krill and therefore, catch limits based on the assumption that krill are quickly advected past these islands may be overly optimistic. In some areas near the Antarctic Peninsula, there is evidence of quasi-resident krill populations (Wiebe et al. 2011, Piñones et al. 2013). Krill tend to be concentrated in areas with moderate levels of eddy kinetic energy (Santora et al. 2012) and may be associated with gyres that link the Antarctic Circumpolar Current and the Antarctic Coastal Current (Nicol 2006), suggesting that krill may use current features to stay in favorable habitats.

Although previous modeling studies have investigated krill behavior (Alonzo & Mangel 2001, Alonzo et al. 2003, Cresswell et al. 2007), ours is the first to explicitly account for the metabolic cost of active movement and its potential to affect growth and reproduction. Because swimming costs may represent a significant fraction of daily energy expenditure (13 to 73%; Swadling et al. 2005), a detailed understanding of krill energy budgets, swimming cost, and growth would best inform our model. However, to our knowledge, only one laboratory study (Swadling et al. 2005) has attempted to quantify the cost of movement for Antarctic krill. This experiment may not be directly applicable to krill under the natural conditions of our study area, in particular because it did not account for swarming behavior, which is thought to decrease oxygen consumption

(Ritz 2000). In addition, it did not distinguish between size classes and was conducted at 1°C, while temperatures in our model ranged from –0.84 to 2°C. Because krill metabolism is strongly influenced by both temperature and size (Buchholz & Saborowski 2000), the cost of active swimming in our study should only be considered an approximation.

The growth model of Atkinson et al. (2006) is based on field measurements in the southwest Atlantic, meaning that it may already reflect the metabolic cost of some average level of active movement, especially because krill make daily vertical migrations and have been observed undertaking directed movement (Marr 1962, Godlewska 1996, Hernández-León et al. 2001). However, while other energetics models, such as that of Hofmann & Lascara (2000), do not include the cost of active movement, they predict considerably lower growth rates at the levels of chl *a* found in our study area compared to those found by Atkinson et al. (2006). Atkinson et al. (2006) suggested that ingestion of protozoans in areas of low chl *a* may in part explain the higher growth rates compared to those predicted by Hofmann & Lascara (2000). Therefore, because this model is based on growth rates of krill experiencing field conditions similar to those in our study area, we consider it the best available estimate of baseline growth in the absence of movement, although it may already account for some energy expended on swimming. Thus, our estimates of growth, and consequently, predicted swimming speeds for actively swimming krill may be conservative, and our estimates of growth for slowly or non-swimming krill may be overestimated.

We used surface currents in our model, but krill perform diel vertical migrations (Godlewska 1996, Hernández-León et al. 2001), where temperature, current velocity, predation risk, and food availability at depth differ from those at the surface. Krill may use these differing conditions to avoid predation and alter transport trajectories (De Robertis 2002, Hofmann & Murphy 2004). However, vertical migration behavior in krill has already been explored in modeling studies (Alonzo & Mangel 2001, Alonzo et al. 2003, Cresswell et al. 2007, 2009), one of which suggests that vertical movement does not strongly influence location (Cresswell et al. 2007). Therefore, we assume that including diel migration would not alter the qualitative patterns in spatial distribution that we predicted here. However, because diel migration likely affects growth and predation risk (Alonzo & Mangel 2001, Alonzo et al. 2003), vertical movement may modulate our predicted impacts of active krill movement on growth and mortality.

Modeling can serve as an important tool for guiding future empirical studies (Hilborn & Mangel 1997, Clark & Mangel 2000), and much remains unknown about active krill movement under field conditions. Krill are not well-suited to mark–recapture studies (Nicol 2000); however, acoustic studies have the potential to provide a variety of information about krill. Several studies have used acoustics to examine krill swarm behavior in the field (e.g. Cox et al. 2009, Brierley & Cox 2010, Tarling & Thorpe 2014), and acoustics have been used to explore the details of swimming behavior in other euphausiids (e.g. De Robertis et al. 2003, Klevjer & Kaartvedt 2006). Tarling & Thorpe (2014) found that flow regime, salinity, distance to ice edge, and fluorescence alter krill swarm characteristics, and further acoustic studies of krill in the field may allow us to relate krill swimming behavior to further physical and biological features across the seascape. In addition to acoustic studies, videographic techniques (summarized by Hamner & Hamner 2000) could allow the collection of data on the fine details of krill swimming behavior, such as pleopod beating rate and turning frequency. Although krill appear to respond to a number of environmental features (e.g. Marr 1962, Kanda et al. 1982, Tarling & Thorpe 2014), much remains to be understood about the proximate cues that elicit krill behavior. Krill respond to chemical and visual cues (Strand & Hamner 1990), alter their behavior in response to phytoplankton (Kawaguchi et al. 2010), and show spatial segregation based on maturity (Siegel 2000), indicating that krill likely respond to physical, chemical, and biological elements of the environment. Further, these responses are likely to depend on the size, stage, condition, and location of the organism. Our model underlines the fact that there is likely strong selective pressure to evolve behavioral responses to the environment, and that these are likely to be complex and nuanced, representing tradeoffs between survival, growth, and reproduction.

In conclusion, our model suggests that krill are more than simply passive drifters, and that their predicted behavior will vary across space and time, resulting in more complex movement and distribution patterns than might be predicted by simple advection. In addition, these altered distributions can affect reproductive success and mortality. Although more work remains to be done in elucidating the degree to which active movement may affect krill populations, this model can serve as proof of concept for the importance of behavioral modeling in the management of krill fisheries.

*Acknowledgements.* This work was partially supported by an NSF Graduate Research Fellowship to K.R. and by the Center for Stock Assessment Research, a training program between the Southwest Fisheries Science Center and UC Santa Cruz.

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Editorial responsibility: Alejandro Gallego, Aberdeen, UK

Submitted: December 3, 2014; Accepted: April 22, 2015  
 Proofs received from author(s): May 23, 2015