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Survival strategies and growth of krill: avoiding predators in space and time

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ABSTRACT: Although Antarctic krill live in a relatively harsh and variable environment, they are extremely abundant and occur across a wide geographic range. Krill are also the dominant prey item for a variety of predators ranging from fish to whales. Thus, krill life histories and survival strategies represent an interesting and biologically relevant theoretical question: How do krill survive and what makes them so successful? The factors that influence krill size and spatial distributions and life-history patterns are not generally understood. We present a conceptual framework for studying krill life histories and patterns of distribution. This approach uses what is known about krill physiology and environmental conditions within an evolutionary framework to increase our understanding of krill distributions and abundance. Using a dynamic state-variable model, we determined the factors predicted to affect the distribution of krill among habitats and feeding behavior of krill. Habitats vary in their associated survival, predation risk, food availability, and metabolic costs. Existing data on variation in temperature, phytoplankton abundance, metabolic costs, growth rates and predator behavior are used to parameterize the model. The model predicts that krill will shrink when experiencing extreme temperatures or food deprivation (under negative energy budgets), but we also predict that krill may shrink due to predation risk (under positive energy budgets). Furthermore, predation patterns are predicted to strongly influence krill size and spatial distributions. If predation risk is size-dependent, krill are predicted to shrink between reproductive events which reduces predation. Differences between habitats in predation risk may cause krill to shift away from risky habitats even if this slows growth. In the presence of predation risk when feeding, krill are predicted to experience a tradeoff between growth and survival and shift their feeding behavior and habitat distribution accordingly. Differences between habitats in water temperature and travel costs are also predicted to cause size-dependent shifts in habitat use and migration behavior. Our results reinforce the importance of predator behavior on krill life histories, growth, and distributions. Patterns of predation risk may be the key to understanding krill distribution in space, time and size.

KEY WORDS: Habitat distribution · Predation risk · Life-history theory

INTRODUCTION

Despite the harsh and variable environment they inhabit, Antarctic krill *Euphausia superba* are extremely abundant across a wide geographic range (Marr 1962, Mackintosh 1973, Mauchline 1980, Miller & Hampton 1989). Antarctic krill experience annual fluctuations in water temperature and food supply (e.g. Quetin & Ross 1991, Capella et al. 1992). Furthermore, they are the dominant prey item for a suite of predators with varying feeding behavior (e.g. Miller & Hampton 1989, Hill et al. 1996, Reid et al. 1996, Croll & Tershy 1998, Croll et al. 1998). Survival and growth in krill pose a complex ecological and evolutionary problem. How and why are krill so successful? A variety of strategies have been hypothesized to allow krill to survive harsh Antarctic winters such as shrinkage, lowered meta-

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bolic rates, and switching to omnivory. Krill also exhibit migration patterns that probably allow them to avoid predators. Given that Antarctic krill are long-lived and generally reproduce annually (e.g. Mauchline 1980, Ikeda 1985a), the ability to survive is a critical component of their success. We would expect krill to behave in a way that maximizes their survival and reproduction in response to predation risk and environmental conditions. As a result, we can use the extensive information available on krill physiology, environmental conditions, and predator behavior to gain an understanding of the factors that are expected to influence krill size and spatial distributions.

Krill life histories and distributions are well studied because of their important role in the Antarctic ecosystem and, more recently, due to interest in krill fisheries (e.g. Marr 1962, Mackintosh 1972, Miller & Hampton 1989, Everson 1992). However, extensive variation in observed patterns has made generalization difficult, and we only have a superficial understanding of the mechanisms that drive this variation (Morris et al. 1984, Daly & Macaulay 1991, Hofmann et al. 1992, Quetin et al. 1996, Ross & Quetin 1996, Folt & Burns 1999, Reid et al. 1999). A conceptual framework for understanding patterns of growth and distributions in space and time will be helpful as we seek generalization. Given that the environment they inhabit varies seasonally and annually, we would expect krill to exhibit plasticity in their life-history patterns. For example, it has been hypothesized that Antarctic krill may shrink in size to survive the winter, and shrinkage has been observed in the lab and inferred in the field (e.g. Ikeda & Dixon 1982, Thomas & Ikeda 1987, Quetin & Ross 1991, Nicol et al. 1992, Huntley et al. 1994). In the lab, Antarctic krill shrink in response to food deprivation (Ikeda & Dixon 1982, Thomas & Ikeda 1987, Nicol et al. 1992) while a related species, *Euphausia pacifica*, shrinks in response to high temperatures (Marinovic & Mangel 1999). Plasticity in growth may allow krill to survive variable food conditions and fluctuations in water temperature.

Extensive research has focused on predator behavior and the effect of krill distributions and abundance on predator survival and reproduction. A connection exists between krill abundance and the reproductive success of land-based predators (Heywood et al. 1985, Croxall et al. 1999, D. A. Croll, R. Hewitt, D. Demer and J. Jansen unpubl.). Some diving predators are known to select larger krill preferentially (Hill et al. 1996, Reid et al. 1996, 1999, Ichii et al. 1996), and thus krill predation risk may depend on size in some habitats. Predation patterns vary over the course of the day and with depth (Croxall et al. 1985, Croll et al. 1998), and the exact pattern of predation risk will be determined by the suite of predators that occur locally. We would expect krill to display local adaptations in habitat use to minimize their risk of mortality. Research has focused on the impact of krill on their predators, yet little is known regarding the impact of predator behavior on krill life histories.

The life-history patterns adopted by krill, and the way these patterns are affected by predation, temperature, and food, will influence the size and spatial distribution of krill. For this reason, understanding krill life histories is critical to managing the Antarctic ecosystem. Krill habitat distribution and growth will influence vital demographic parameters in krill and thus their populations dynamics. Furthermore, the spatial and size distribution of krill will impact the survival and reproduction of krill predators. We first present a conceptual framework for understanding krill spatial and temporal patterns. Using a dynamic state-variable model, we then examine krill life histories and habitat distribution where habitats vary in their predation risk, food availability, and water temperature. Using the model, krill growth patterns and habitat use can be predicted from environmental conditions and predator behavior for a specific location. We first examine krill growth patterns under varying environmental conditions and patterns of predation risk. Second, we examine krill habitat distributions and determine the factors that cause krill to shift in habitat use.

A CONCEPTUAL FRAMEWORK

The general idea. Although extensive research has focused on krill biology, many aspects of krill life histories, growth patterns, and distributions remain an enigma. Increasingly, we are realizing that zooplankton do not represent passive particles whose distributions are driven solely by oceanographic processes (Folt & Burns 1999). Instead, plankton can influence their growth, survival, and distribution in space and time. Furthermore, natural selection will favor krill that are adapted to local conditions and predator behavior in ways that increase their probability of surviving and reproducing. We argue that by combining what is known about krill biology and environmental conditions within an evolutionary approach, we have a framework for thinking about krill distributions and life histories. By including krill physiology and aspects of the Antarctic environment with a knowledge of how natural selection maximizes fitness, we can use theoretical models to make both qualitative and quantitative predictions (Fig. 1).

Using what is known to predict the unknown. Although we do not fully understand the forces that generate krill distributions, size and temperature effects on metabolic costs, filtration rates, variation in food abundance and water temperature are all well studied.

From these known physiological factors, we can predict krill growth in a variety of situations. The relationship between krill size and fecundity as well as general patterns of krill reproduction are well documented. We can also infer potential patterns of predation risk from predator foraging behavior and distributions. As a result, much is known about the general processes important to natural selection. We can then use the basic concept of maximizing lifetime reproductive success to predict krill habitat use, and thus krill growth and distribution in space and time for a given set of environmental conditions. Here we focus on making qualitative predictions that examine how temperature, food abundance, and predation risk are predicted to shift krill among habitats.

Using the model. The strength of this approach lies in using real data to formulate and structure the model while the application of basic evolutionary processes predicts patterns of habitat use. However, it is clear that it is not possible to examine all plausible patterns of environmental conditions and predator behavior. The general framework has the ability to address almost any situation. However, the model we present must be analyzed numerically. This implies that any single solution of the model cannot address the wide variety of possible conditions. However, by varying parameter values across a wide range, we can examine the general effects of each variable. We then present predictions that are robust to a wide range of values. Furthermore, our intent is not to examine all possible situations. Instead we apply the conceptual framework to make qualitative predictions about the factors that may influence krill habitat use, distribution and growth. We also use the models to highlight the processes that are critical to understand and thus warrant further study before quantitative predictions can be made. In the end, this approach is an iterative process. Our intent is not only to predict what has been observed, but to make new predictions that can be tested in the field. Our purpose in this paper is to demonstrate a conceptual framework for understanding krill distributions and life histories by choosing representative values and plausible situations to make general qualitative predictions regarding the factors that influence krill growth and habitat use.

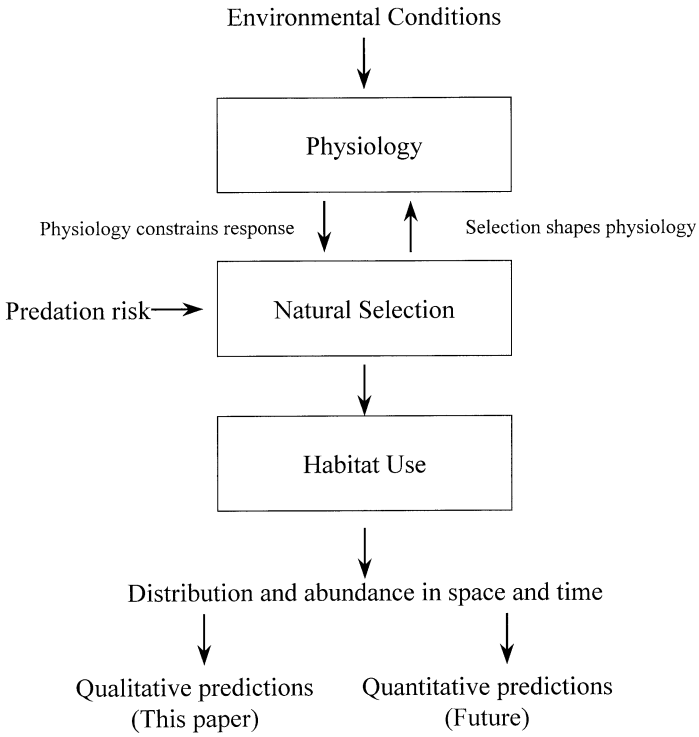

Fig. 1. A conceptual framework for understanding krill distributions in space and time

BASIC MODEL STRUCTURE

The model focuses on 2 aspects of krill biology: habitat distribution and growth. We use a dynamic state-variable model (Mangel & Clark 1988, Houston & McNamara 1999, Clark & Mangel 2000) and consider 3 habitats: surface, shallow, and deep water. Though we focus on vertical migration, this framework can also easily be applied to horizontal migration as well. The 3 habitats can differ in their food availability, water temperature, predation risk, and travel costs to the surface. We allow for the possibility that krill may migrate between habitats on a daily basis. Since krill are mainly observed feeding at the surface during the night (Mauchline 1980, Morris et al. 1983, but see Morris & Ricketts 1984), we assume for simplicity that krill feed only at night at the surface. In the model, krill may (1) feed at the surface and remain in surface waters during the day, (2) migrate to shallow or deep water during the daytime and then return to the surface to feed, or (3) remain in shallow or deep waters without feeding at the surface. Krill growth depends on environmental conditions, their habitat, and whether they feed. The model finds the habitat and feeding behavior that maximizes expected lifetime reproductive success based on annual fecundity and survival to reproduction. The model predicts habitat use and migration behavior based on krill length and time in the season. Consequently, the model predicts the daytime and nighttime habitats of individual krill as well as krill growth patterns. From this, we can determine the factors that are predicted to cause changes in the distribution of krill among habitats as well as changes in size

distributions. By varying environmental conditions and predation risk, we can determine the qualitative shifts that are expected to occur with changing water temperature, food availability, and predator behavior. As a result we can make qualitative predictions and determine the factors expected to influence krill distributions in space and time.

COMPONENTS OF GROWTH

There are 2 main components of the model: growth and fitness. First, we calculate expected krill growth in each habitat as a function of their length, feeding behavior, and environmental conditions. Krill size is represented by length. In the model, krill length L ranges from 12 mm (juveniles) to a maximum of 60 mm in 0.1 mm increments (Mauchline 1980, Ikeda 1985a). Krill growth depends on the difference between feeding rate (energy intake) and metabolic costs (energy output). We use laboratory or field estimates whenever possible to parameterize the model. Although krill can migrate daily, for computational simplicity we examine weekly time periods (t). Thus, krill are assumed to adopt one behavior for each 1 wk period. We consider krill growth and behavior over 5 yr or 260 time periods.

Length-weight allometry. We use the following relationship from Mauchline (1980) to translate length in mm (L) to wet weight (W) in g.

$$W(L) = e^{3.3874 \log L - 2.7531} \quad (1)$$

This measure of weight is then used in calculating food intake and metabolic costs.

Metabolic costs. Metabolic costs, usually measured as oxygen consumption, depend on individual size and water temperature. Although mass specific metabolic rates tend to decrease with krill size, total metabolic costs increase with length. We use the following relationship derived by Ikeda (1985b) that gives metabolic cost (C) as a function of water temperature [$T(H,t)$ in habitat H at time t] and krill weight [$W(L)$]:

$$C(H,L,t) = e^{-0.2512 + 0.8 \ln W(L) + 0.049 T(H,t)}$$

Individual metabolic cost (in µl O_2 ml^{-1}) increases exponentially with increasing temperature and krill length (Fig. 2a). The above relationship holds if krill remain in 1 habitat for the entire time period. Therefore, the metabolic costs of staying in one habitat and not traveling to the surface to feed will be $C_{stay}(H,L,t) = C(H,L,t)$. However, if krill feed at the surface at night but spend the day in another habitat, their metabolic rate for the whole day will depend on the temperature at the surface and of their daytime habitat as well as the proportion of time they spend in each habitat τ. For the analyses presented here, we assume $\tau = 0.5$. Total metabolic costs per time period t for a krill of length L that feeds at the surface S at night and spends the daytime in habitat H will be

$$C_{feed}(H,L,t) = (1 - \tau)\, C(S,L,t) + (\tau)\, C(H,L,t) \quad (2)$$

where metabolic costs implicitly depend on water temperature in the daytime habitat $T(H,t)$ and at the surface $T(S,t)$.

Food intake depends on a number of factors described below.

Food availability: We treat food availability $P(t)$ as the proportion of maximum food conditions at any time t. At $P(t) = 1$, food is so abundant that further increases would not change krill ingestion rates (Boyd et al. 1984, Ikeda & Thomas 1987). Thus, $P(t)$ ranges from 0 (no food) to 1 (maximum food conditions). Although we do not model food quality explicitly, varying $P(t)$ can represent variation both in the abundance and quality of food available at any time t. Food availability can be interpreted as the potential metabolic energy available per volume of water (µl O_2 ml^{-1}).

Assimilation rate: Assimilation rate (A) is the proportion of food ingested available as energy for growth. For the results presented we use $A = 0.9$, and but we also considered $A = 0.8$ and 1.0. Although higher assimilation rates increase growth rates and lower assimilation rates decrease growth rates, the exact value has no effect on the qualitative predictions.

Filtration rate: We use an allometric relationship measured by Holm-Hansen & Huntley (1984) where filtration rate is a function of krill size such that volume of water cleared of food particles h^{-1} is $4.64\, W^{0.8}$ (in ml h^{-1}) where W represents krill wet weight in g.

Temperature-dependence: We assume feeding rate increases asymptotically with temperature. T_{min} represents the temperature below which krill cannot feed. At T_{min} the feeding rate will be 0 and then increase with temperature toward the maximum feeding rate. We use the relationship $[T(S,t) - T_{min}]/[T(S,t) + T_0]$ to model this temperature-dependence where T_0 determines the speed with which relationship asymptotes. For the analyses presented here, we use $T_{min} = -5$ and $T_0 = 10$.

Travel time: The amount of time krill spend traveling between habitats is assumed to decrease the amount of time spent feeding. We assume krill can swim 2 body lengths (in mm) s^{-1}. If $D(H)$ is the distance (in m) from a habitat H to the surface, then the movement time in seconds to travel to the surface [$M_S(H,L)$] is

$$M_S(H,L) = D(H)/0.002\, L \quad (3)$$

Travel costs decrease with increasing krill length. It is useful to express M_S as the proportion of time available for feeding $(1 - \tau)$ left after traveling to the surface. For a krill of length L traveling from habitat H, the proportion of feeding time remaining after travel $M_P(H,L)$ is

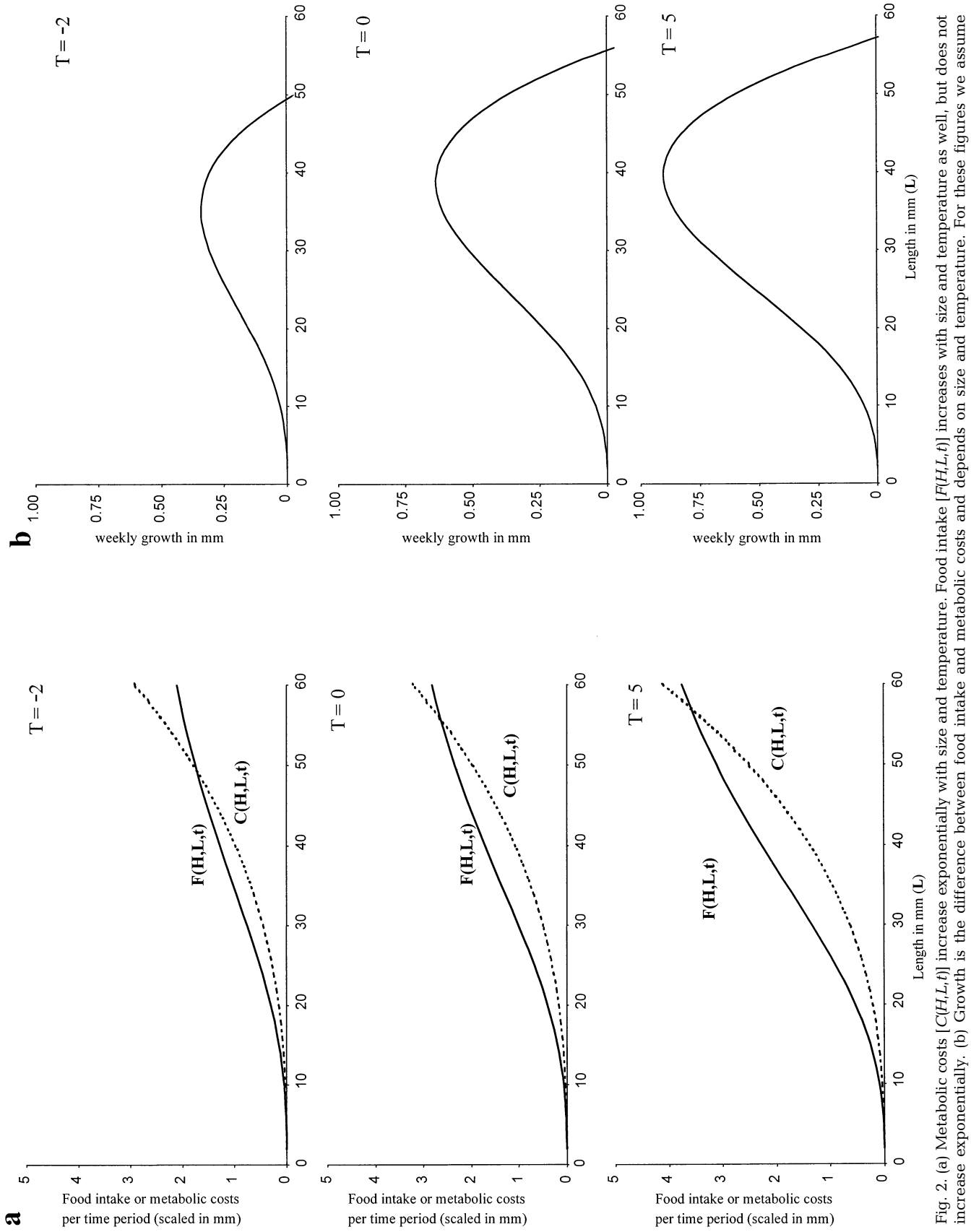

Fig. 2. (a) Metabolic costs [$C(H,L,t)$] increase exponentially with size and temperature. Food intake [$F(H,L,t)$] increases with size and temperature as well, but does not increase exponentially. (b) Growth is the difference between food intake and metabolic costs and depends on size and temperature. For these figures we assume $P(t) = 1$ and $A = 0.9$ (see text)

$$M_P(H,L) = \{(1-\tau) - [M_S(H,L)/(24 \cdot 60 \cdot 60]\}/(1-\tau) \quad (4)$$

For the results shown here, we assumed that the distance between the surface and shallow water is 100 m and the distance between shallow and deep waters is 200 m. These values represent realistic migration distances for *Euphausia superba* (e.g. Morris et al. 1984). Varying the distance between habitats will change the quantitative distribution of krill with respect to size and habitat. However, the basic qualitative patterns remain.

Size-dependence: Antarctic krill growth trajectories asymptote below 60 mm and larger krill are rarely found in the field (e.g. Mauchline 1980, Ikeda 1985a). We assume that food intake asymptotes with size where γ is a constant determining the size at which growth ceases. The size-dependent function of food intake is then $(1/(1 + \gamma W^{0.8})$. For the results presented, we use $\gamma = 0.005$ so size asymptotes at $L = 60$ mm in maximum growth conditions.

Total energy intake: Consequently, the food intake $F(H,L,t)$ per time period for a krill of length L traveling from habitat H feeding at the surface at time t is

$$F(H,L,t) = \frac{M_P(H,L) \cdot P(t) \cdot A \cdot 4.64 \cdot W(L)^{0.8} [T(S,t) - T_{\min}]}{[T(S,t) + T_0]\,[1 + \gamma \cdot W(L)^{0.8}]} \quad (5)$$

Food intake increases with water temperature at the surface and krill length (Fig. 2a). Only filtration rate (in ml h^{-1}) and food availability (in µl O_2 ml^{-1}) have units, so food intake is measured in µl O_2 h^{-1}.

Growth. Growth is given by the difference between energy intake and metabolic costs (Atkinson 1994). Food intake $F(H,L,t)$ depends on habitat, krill length and the current time period. Metabolic costs will differ if krill are feeding $C_{\text{feed}}(H,L,t)$ or if they are not feeding $C_{\text{stay}}(H,L,t)$. Because food intake and metabolic costs are both represented in terms of metabolic energy (in µl O_2 h^{-1}), we take the difference $(F - C)$ between food intake and metabolic costs to represent net energy gain. However, for growth in mm, we must translate µl O_2 h^{-1} into mm wk^{-1}. We do this by scaling $F - C$ by a constant K (with units mm µl O_2^{-1} h wk^{-1}) converting hourly metabolic rates to weekly growth in mm. We choose K such that growth rates match observed rates (e.g. Clarke & Morris 1983, Ikeda et al. 1985). For the analyses represented here we use $K = 0.01$. If a krill of length L feeds at the surface and then goes to habitat H during the daytime, its growth ΔL_{feed} wk^{-1} will be

$$\Delta L_{\text{feed}}(H,L,t) = K[F(H,L,t) - C_{\text{feed}}(H,L,t)] \quad (6)$$

If a krill of length L remains in habitat H, its growth ΔL_{stay} wk^{-1} will be

$$\Delta L_{\text{stay}}(H,L,t) = K[-C_{\text{stay}}(H,L,t)] \quad (7)$$

where $\Delta L_{\text{stay}}(H,L,t)$ will usually be less than or equal to $\Delta L_{\text{feed}}(H,L,t)$. However, high water temperatures at the surface could cause $\Delta L_{\text{feed}}(H,L,t)$ to be less than $\Delta L_{\text{stay}}(H,L,t)$, and krill might shrink more when feeding than by staying in deep colder water (Marinovic & Mangel 1999). Krill growth is also bounded so that $L \geq 12$ mm and $L \leq 60$ mm. Growth rates depend on krill size and water temperature (Fig. 2b). At some temperatures and length, positive growth will not be possible.

Reported growth rates for *Euphausia superba* range from negative growth to as high as 0.33 mm d^{-1} (Mauchline 1980, Ikeda 1985a, Siegel 1987, Siegel & Nicol 2000). This variation complicates comparing growth in our model to empirical results. However, we can compare both observed growth patterns as well as absolute growth rates to predictions made by our model. First of all, growth appears to depend on individual size. Absolute growth rates tend to be lower at small size, increases with intermediate size, and then asymptotes at some maximum size (e.g. see Ikeda 1985a, Figs. 1 & 2, Siegel 1987, Fig. 6). Krill growth rates in our model capture this basic pattern (Fig. 2b). Close comparison with published results, shows higher observed growth rates at small size than in our growth model (e.g. Ikeda 1985a, Siegel 1987). However, this difference is driven by the empirical result that filtration rates increase exponentially with size (Holm-Hansen & Huntley 1984). We could vary K and γ to consider different growth rates. However, in our model, growth rates under maximum growth conditions range from 0.01 to 0.15 mm d^{-1}. These rates agree closely with some published results (e.g. Ikeda 1985a) and are slightly higher than other rates (e.g. Siegel 1987). However, we would expect growth rates under natural conditions to be lower than under maximum growth conditions in the model. Given varying environmental conditions, growth rates in our model span the entire range of observed growth rates allowing us to examine the impact of variation in growth rates on krill life histories.

COMPONENTS OF EXPECTED REPRODUCTIVE SUCCESS

In the previous section, we used known patterns of environmental variation, growth, and krill physiology to calculate expected krill growth rates that resemble krill growth in the wild. We now use these possible growth patterns within an evolutionary framework where fitness depends on patterns of predation risk and size-dependent fecundity to predict, given natural selection, the expected patterns of krill distribution among habitats and observed growth patterns.

Survival. For each habitat, we assume there is a baseline size-independent probability of survival, which may vary with time, and we let $\sigma_b(H, t)$ represent the baseline probability of a krill surviving between time periods in habitat H at time t. If predation risk varies between habitats independent of krill size, then $\sigma_b(H,t)$ will vary as well. For example if the risk of mortality is higher at the surface than in shallow waters, then $\sigma_b(\text{surface},t) < \sigma_b(\text{shallow},t)$. In addition, we describe size-dependent survival between time periods in habitat H for a krill of length L in time t by $\sigma_s(H,L,t)$. If predators preferentially select large krill (e.g. Hill et al. 1996, Reid et al. 1996), then the probability of survival in the presence of these predators will decrease with individual size. The size-dependent portion of survival of a krill of size L in habitat H at time t is modeled by

$$\sigma_s(H,L,t) = 1 - e^{-\zeta(H,t)(70 - L)} \quad (8)$$

where $\zeta(H,t)$ represent a constant that increases as the strength of size-dependence decreases (Fig. 3). The total probability of survival per time period will be the product of the baseline and size-dependent portions of survival. We examine 2 main patterns: First, where survival is size-independent, and second where survival is both size-dependent and size-independent. Although a variety of other predation patterns might occur, we focus on this dichotomy for simplicity. If a krill remains in 1 habitat and does not feed, then its probability of survival is

$$\sigma_{stay}(H,L,t) = \sigma_b(H,t) \cdot \sigma_s(H,L,t) \quad (9)$$

If a krill migrates between a daytime habitat H and the surface S at night, its probability of survival per time period will be

$$\sigma_{feed}(H,L,t) = (\tau) \cdot \sigma_b(H,t) \cdot \sigma_s(H,L,t) + (1 - t) \cdot \sigma_b(S,t) \cdot \sigma_s(S,L,t) \quad (10)$$

If the probability of survival is lower at the surface than in shallow or deep waters, then krill may tradeoff growth and survival. Similarly, if predation risk increases with size, krill may tradeoff growth with survival. The actual pattern of predation risk will clearly depend on the suite of predators that occur locally and will vary across space and time. In the model, the age distribution of krill depends solely on their probability of survival. For example, if krill have a 0.99 probability of survival wk^{-1}, then approximately 60% of krill will survive to Year 1, 35% to Year 2, 20% to Year 3, 12 % to Year 4, and only 7% to Year 5. This represents a plausible age distribution for a single cohort given patterns inferred from field data (Siegel & Nicol 2000). Clearly increasing the probability of survival increases the frequencies in larger age classes and increased predation risk decreases the frequency of older and larger krill. Survival probabilities are inherently difficult to measure in the field, therefore we examine a variety of values and patterns of predation risk to determine the qualitative patterns.

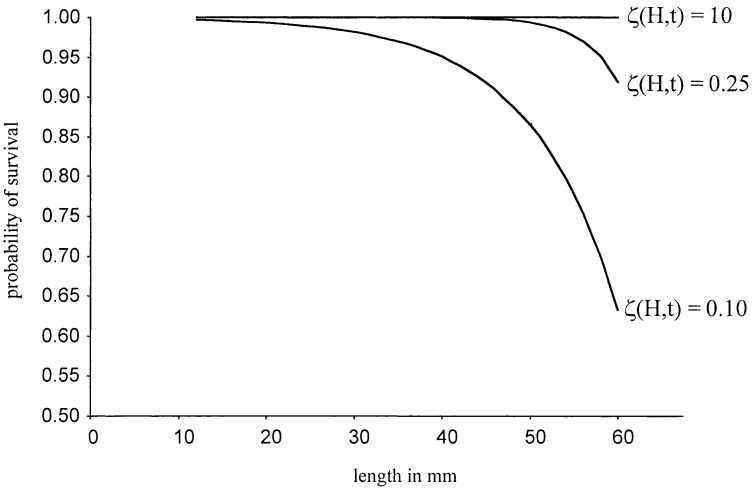

Fig. 3. The probability of survival may have a size-dependent component $\sigma_s(H,L,t)$. Increasing $\zeta(H,t)$ decreases the strength of the size-dependence

Fecundity and reproduction. We assume reproduction occurs annually. At the end of each year krill above a minimum length for reproduction $L_{rep} = 38$ mm (Mauchline 1980) can reproduce. Once reproductive, fecundity increases linearly with length. We use a length-fecundity allometric relationship (in eggs produced per female) measured by Siegel (1985) to represent fecundity $R(L)$ as a function of krill length L.

$$R(L) = -7396.8 + 245.7L \quad (11)$$

We also assume krill allocate resources to reproduction based on their current length such that $R(L) = L$ if it is not a reproductive period (which occur at the end of each year). Since each time period represents 1 wk, krill may reproduce every 52 time periods. Reproductive increment $R(L,t)$ per time period t is then

$$\begin{aligned} &\text{If } L < L_{rep} \quad R(L,t) = 0 \quad \text{for all } t \\ &\text{If } L \geq L_{rep} \quad R(L,t) = -7396.8 + 245.7L \quad \text{for } t = 52, 104, 156, 208, 260 \\ &\qquad\qquad\quad R(L,t) = L \quad \text{otherwise} \end{aligned} \quad (12)$$

EVALUATING EXPECTED REPRODUCTIVE SUCCESS

Given the equations for growth, fecundity and survival, we can calculate the expected reproductive value of adopting each behavior. To do this, let

$Z(L,t)$ represent the maximum expected future accumulated reproduction for a krill of size L in time t. At the final time period, $Z(L,260) = R(L,260)$. Otherwise fitness is the sum of current and future reproduction. Fitness depends on habitat, size, and time in the season.

The value of staying in habitat H without feeding when size L in time t is

$$V_{stay}(H,L,t) = R(L,t) + \sigma_{stay}(H,L,t) \cdot Z(L + \Delta L_{stay}(H,L,t),\ t+1) \quad (13)$$

And the expected reproductive value of feeding at the surface and then going to habitat H when size L in time t is

$$V_{feed}(H,L,t) = R(L,t) + \sigma_{feed}(H,L,t) \cdot Z(L + \Delta L_{feed}(H,L,t),\ t+1) \quad (14)$$

We then find the habitat and feeding behavior that maximizes expected lifetime reproductive success for a krill of length L at time t or

$$Z(L,t) = \max_H\{\max[V_{feed}(H,L,t),\ V_{stay}(H,L,t)]\} \quad (15)$$

The solution of this dynamic programming equation (Mangel & Clark 1988, Houston & McNamara 1999, Clark & Mangel 1999) predicts the size- and time-dependent habitat use and feeding behavior. Using the growth equations and predicted behavior, we can calculate individual growth trajectories. By making an assumption about the initial size distribution, we can calculate shifts in size and habitat distributions based on the predicted habitat and feeding behavior. This allows us to ask how variation in predation risk, food availability, and water temperature affect individual growth and size and habitat distributions in Antarctic krill. For the results presented here, we examine growth trajectories of individuals starting as juveniles (L = 12 mm at t = 1). When presenting habitat distributions, we consider uniform size distributions at the time period under consideration. Although krill size-distributions in the field are not usually uniform, this distribution allows the size-specific habitat use to be most simply presented. Using other initial distributions alters the quantitative, but not the qualitative predictions. In the next section, we present the results of the model and make qualitative predictions regarding the impact of predation risk, environmental conditions, and habitat use on the distribution and growth of krill. It is critical to keep in mind that our purpose is to illustrate the results under different scenarios rather than consider all possible situations. By examining a wide range of parameter values and situations, we can identify general qualitative patterns that are independent of any specific parameter value.

MODEL RESULTS: GROWTH AND SHRINKAGE

Evidence exists that krill may shrink both in the field and in the laboratory. There has been some discussion of whether this represents an empirical artifact or whether krill shrink naturally in the field. Using the model, we examine the conditions under which krill are predicted to shrink in size. We find that 2 basic mechanisms lead to krill shrinkage. First, environmental conditions may lead to a deficit between energy intake and metabolic costs ($F < C$). For example, high temperatures might increase metabolic costs to the point where krill shrink even in the presence of abundant food (e.g. Marinovic & Mangel 1999). Second, under positive energy budgets ($F > C$), if krill experience a tradeoff between growth and survival, krill may avoid feeding at the surface. Using the model, we explore each of these possibilities to determine conditions that lead to shrinkage and the predicted growth patterns.

Shrinkage under negative energy budgets. Shrinkage can occur whenever metabolic costs exceed energy intake ($C > F$). There are 2 main patterns of shrinkage that can occur under negative energy budgets. First, krill of all sizes shrink ($F < C$ for all L). Second, large krill may shrink while smaller krill are capable of growth ($F < C$ for large L). Both patterns can occur due to extreme temperatures and food limitation. For any set of environmental conditions, there is some size L at which metabolic costs equal energy intake [$F(H,L,t) = C(H,L,t)$]. We refer to this as the maximum achievable size. This maximum size L_{max} varies with temperature and food availability. With seasonal or annual variation in temperature or food, krill may achieve a large size under good growth conditions, and then shrink when temperature or food conditions change. The factors that lead to shrinkage are described in detail below.

Food availability: Decreases in food availability $P(t)$ cause decreases in food intake $F(H,L,t)$. To find the maximum achievable size L_{max}, we assume krill remain at the surface, $T(S,t)$ = 2°C and A = 0.9. Given these conditions, we can find the size at which $F(H,L,t) = C(H,L,t)$ as $P(t)$ varies from 0 to 1. As food availability decreases, so does the maximum achievable size (Fig. 4). The food required such that $F(H,L,t) \geq C(H,L,t)$ also depends on temperature and assimilation rate.

We also examine the effect of fluctuations in food availability. We present results for representative water temperatures [T(surface) = 2°C, T(shallow) = 0°C, T(deep) = −2°C] where A = 0.9 and survival is equal between habitats and size-independent. We consider 10 wk periods of lowered food availability in the middle of each year. We examine the cases where $P(t)$ = 1 and then drops to as low as $P(t)$ = 0. If a period

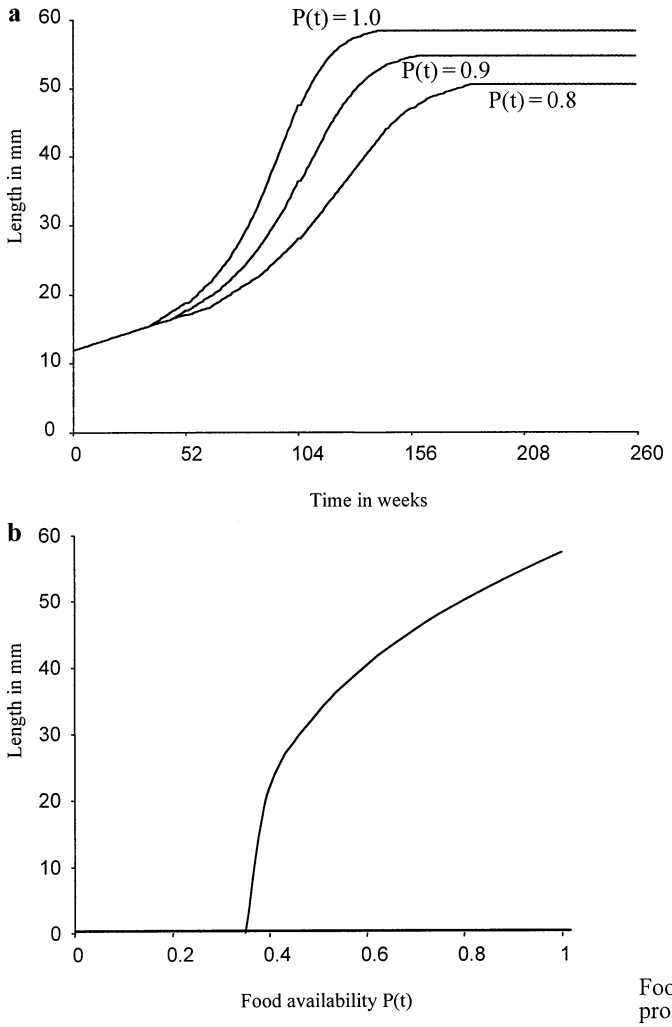

Fig. 4. (a) Lower food availability $P(t)$ decreases both growth rate and the maximum size achieved. (b) The maximum achievable size L_{max} varies with food availability $P(t)$. At low food availability ($P(t) < 0.4$) growth is not possible at any size. For this figure we assume the water temperature is 2°C, no travel costs, and $A = 0.9$

of high food availability is followed by food deprivation (e.g. $P(t)$ drops to < 0.4), krill of all sizes will shrink until food availability increases (Fig. 5). However, when food availability decreases [$P(t) > 0.4$], only large krill are predicted to shrink. Periods of extreme food deprivation are predicted to cause all krill to shrink, while in less extreme conditions only the largest krill are expected to shrink.

Temperature: Metabolic costs increase exponentially with size while feeding rates do not (Fig. 2a). Consequently, there will be some size at which metabolic costs exceed food intake even under abundant food conditions. However this maximum achievable size, L_{max}, will vary with environmental conditions. At extreme temperatures for any size growth is impossible ($F < C$ for all L). However, at less extreme temperatures, the maximum sustainable size may decrease, causing krill above that size to shrink. Therefore we may see 2 different patterns of shrinkage. At extreme temperatures, krill of all sizes shrink. However at less extreme temperatures we see size-dependent shrinkage where small individuals may grow and large individuals shrink. The temperature below which shrinkage occurs is influenced by T_{min}, while the high temperature at which shrinkage occurs is driven by T_0. If we change T_{min} or T_0 the qualitative pattern remains, but the exact temperatures at which shrinkage is predicted will change. Therefore, these results should be taken as qualitative and not quantitative predictions.

To find L_{max}, for simplicity, we assume krill remain at the surface, $P(t) = 1$, and $A = 0.9$ (Fig. 6). We also examined a variety of temperature regimes. First we examined static temperature regimes. We evaluated the temperature range −4 to 4°C in 2°C increments for all possible combinations of differences between the 3 habitats where T(surface) ≥ T(shallow) ≥ T(deep). Shrinkage is not predicted under static water temperature conditions. We also examined the situations where there were seasonal fluctuations in temperature. We considered a pattern where temperatures increased or decreased in all 3

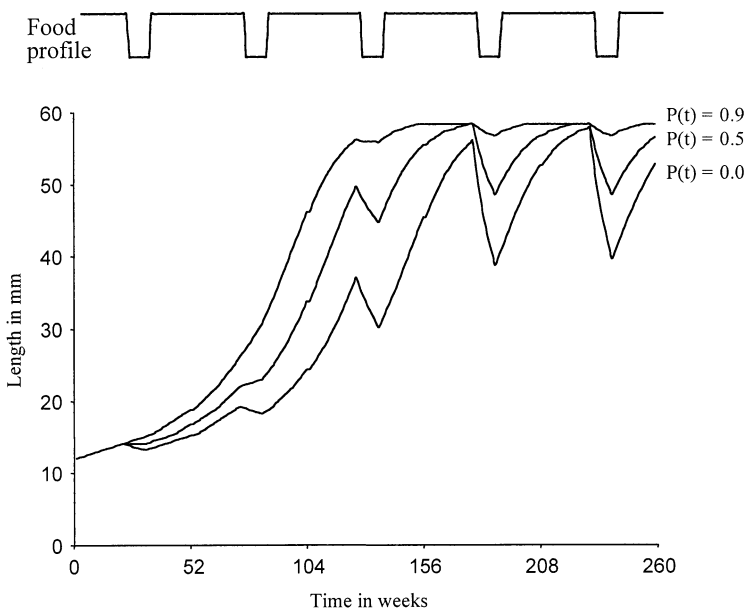

Fig. 5. Krill are predicted to shrink in size when food availability decreases seasonally from $P(t) = 1$ to a lower value $P(t) = 0$, 0.5, 0.9. Decreases occur as shown by the food profile. In abundant food conditions, krill grow quickly to their maximum size (2 years), but under variable food conditions, average growth slows considerably

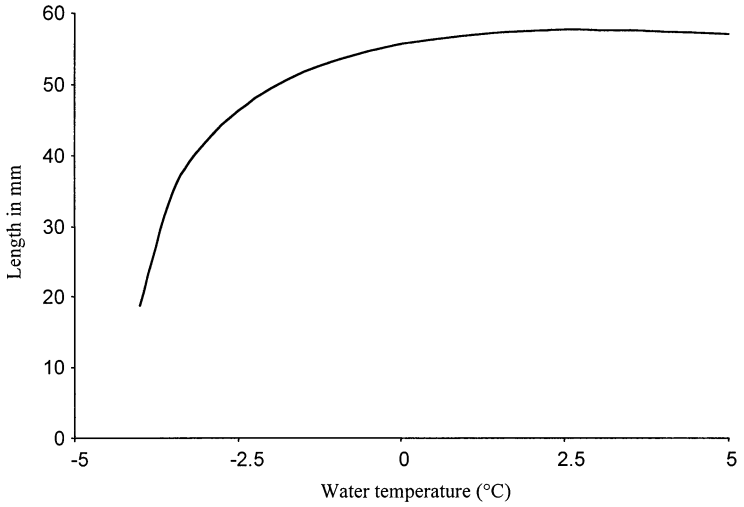

Fig. 6. The maximum achievable size L_{max} also depends on water temperature. At extreme temperatures growth is not possible. For this figure we assume krill remain at the surface, $P(t) = 1$, and $A = 0.9$

habitats for a period of 10 wk out of each year. The baseline conditions were T(surface) = 2°C, T(shallow) = 0°C, T(deep) = –2°C. During 10 wk in the middle of each year, we examined the impact of temperature increases in all 3 habitats (T = 5°C, 10°C) and temperature decreases (T = –2°C, –4°C) in all 3 habitats. Periodic extreme temperatures cause krill to shrink during these episodes (Fig. 7).

Antarctic krill experience variable water temperatures and exist throughout a wide geographic range. The ability to shrink may allow krill to survive despite this variation. If krill could not shrink, then they would experience negative energy budgets with changing environmental conditions. However, by shrinking, krill can achieve a size at which positive energy budgets are possible even in harsh conditions. Furthermore, since fecundity increases with size, being able to take advantage of good conditions and grow to large size during the summer and then shrink to survive harsh conditions during the winter will lead to higher overall fitness then simply evolving a smaller maximum size. The ability to shrink could be as much an adaptation to variable temperatures and food conditions as a side-effect of harsh environmental conditions. Furthermore the ability to grow across a wide range of temperatures may also play an important role in the success of Antarctic krill.

Shrinkage under positive energy budgets. For these analyses, we assume abundant food $P(t) = 1$, and representative water temperatures [T(surface) = 2°C, T(shallow) = 0°C, T(deep) = –2°C]. We consider a variety of situations. First, predation risk may be size-independent [$\zeta(H,t) = 10$ for all H], and the same or vary between habitats. For simplicity, the analyses presented here assume predation risk is higher at the surface and σ_b(surface,t) ≤ σ_b(shallow,t) ≤ σ_b(deep). Given that assumption, we consider all possible combinations of $\sigma_b(H,t)$ = 0.8, 0.85, 0.9, 0.95, and 0.99. Although small differences exist in growth patterns, the most important parameter is survival at the surface. If $\sigma_b(H,t) = 0.8$ at the surface, krill will shrink in size between reproductive events (Fig. 8). However this weekly survival represents a 9.14×10^{-6} chance of surviving for 1 yr. Otherwise, krill grow to the maximum achievable size (Fig. 8). It is important to remember that the growth trajectories shown are under maximum growth conditions.

Predation risk may have both size-dependent and size-independent components if predators preferentially select large krill. To examine this situation, we assume σ_s(surface,t) ≤ σ_s(shallow,t) ≤ σ_s(deep,t) and examine all possible combinations of $\zeta(H,t)$ = 10, 0.5, 0.25, 0.2, 0.15, 0.1 that meet that assumption. If risk has a size-dependent component at the surface [$\zeta(H,t) \neq 10$], krill are predicted to shrink between reproductive events (Fig. 9). The stronger the size-dependence, the

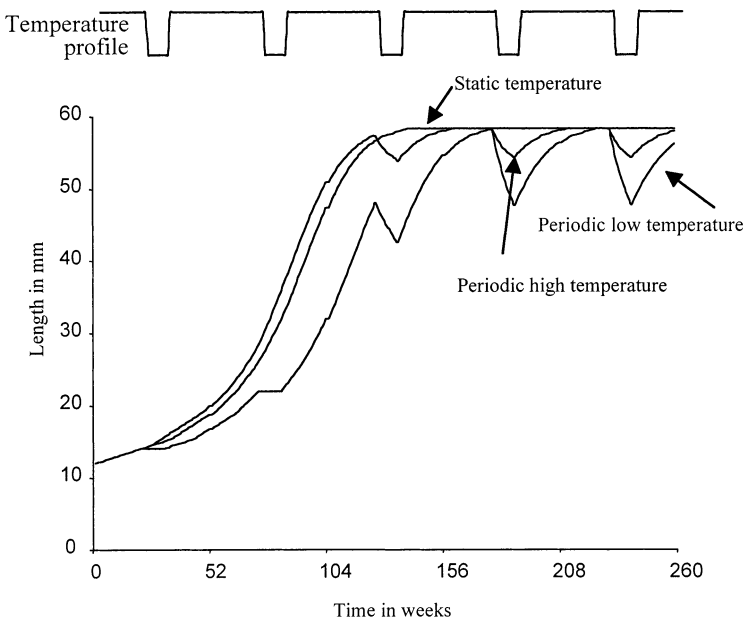

Fig. 7. Krill are predicted to shrink in size with periodic increases or decreases in water temperature at the surface. Temperature regimes are static [T(surface) = 2°C, T(shallow) = 0°C, T(deep) = –2°C] or with periodic decreases to $T(H)$ = –2°C, or increase to $T(H)$ = 10°C

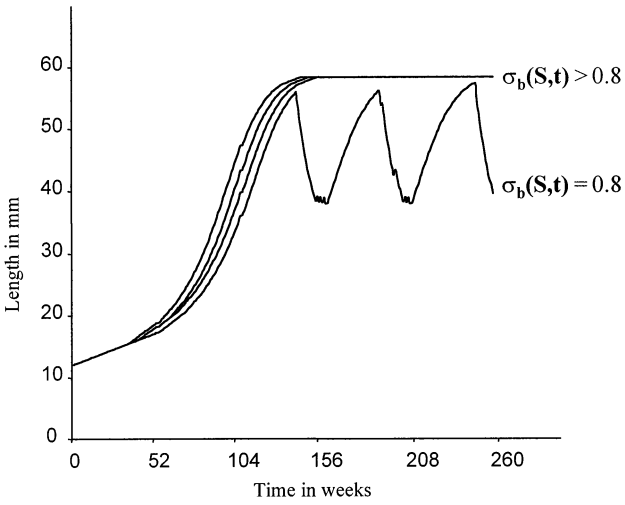

Fig. 8. Size-independent predation risk is predicted to drive shrinkage only at lower probabilities of survival at the surface

more krill shrink between reproductive bouts (Fig. 9). If all habitats are very risky [$\zeta(H,t) \leq 0.1$ for all H], krill are actually predicted to shrink before reproductive events, if they achieve a large size. This occurs because when survival is low in all habitats, the only way to survive to reproduction at all is by remaining small. In reality, all habitats will not be equally risky, and krill, by moving between habitats, can drastically reduce their overall risk of mortality.

Even in the presence of very small relative differences in size-dependent risk [$\sigma_s(\text{surface}, 50, t) = 0.98$ versus $\sigma_s(\text{shallow}, 50, t) = 0.99$], we predict seasonal shrinkage of individual krill. In contrast, in the absence if size-dependent predation, it is only when the size-independent risk of mortality is very high [$\sigma_b(\text{surface}, t) = 0.80$] that shrinkage is predicted. Clearly, size-dependent risk of mortality is another mechanism that could explain shrinkage in krill. Patterns of growth in krill are predicted to depend mainly on relative differences between habitats rather than absolute mortality. It is notable that individual krill are predicted to shrink between reproductive seasons even if risk of predation does not vary with time. In this case shrinkage is predicted even under abundant food and maximum growth conditions and occurs because feeding or growing is risky. It also important to realize that we would not predict that shrinkage occurs universally. Instead differences in predation risk between habitats will vary across space and time, and krill growth patterns are predicted to differ as well. In general, however, krill shrinkage is predicted to occur due to extreme temperatures, food limitation, and under size-dependent predation risk. The model also predicts that shrinkage is an evolutionary plausible adaptation to harsh conditions. Though shrinkage has been observed in the lab and inferred in the field, further research must study the mechanisms and patterns of shrinkage to test our predictions.

MODEL RESULTS: HABITAT DISTRIBUTION

While environmental conditions clearly have an effect on krill growth patterns and shrinkage, these same processes can influence the distribution of krill among habitats. We have seen that if krill experience size-dependent predation risk, they are predicted to feed less frequently at the surface. Although predator behavior is predicted to have a striking effect on krill growth patterns, it will also affect the relative abundance of krill in each habitat. We examine the effect of food availability, temperature, and predation risk on krill habitat use. We consider the same food availability values, temperature regimes, and survival probabilities as described above focusing now on the impact of those parameters on krill habitat use. We focus on making predictions about qualitative shifts in krill habitat use and determining the factors that most strongly affect the distribution of krill among habitats.

Food availability. We examined food availability $P(t)$ ranging from 0.5 to 1.0. We again considered the water temperatures $T(\text{surface}) = 2°C$, $T(\text{shallow}) = 0°C$, $T(\text{deep}) = -2°C$. Although food availability has drastic

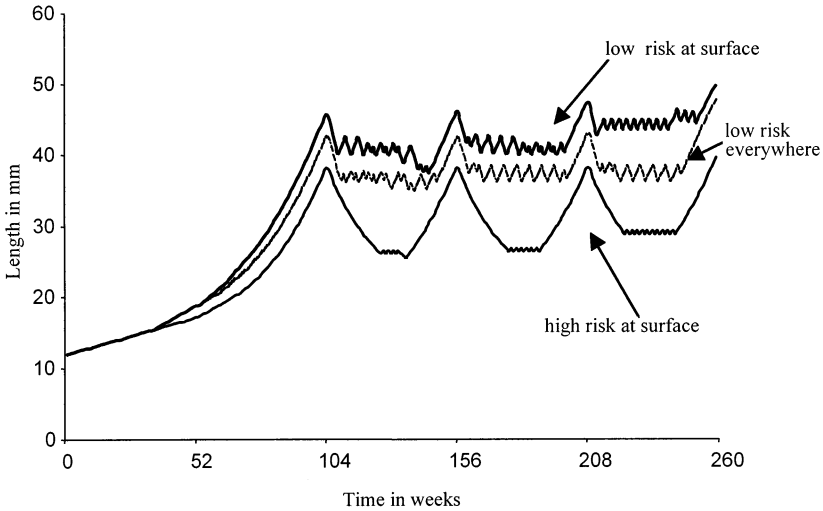

Fig. 9. Size-dependent predation risk is predicted to drive shrinkage between reproductive events for even small values of size-dependent risk. As risk at the surface increase, krill shrink more and for longer periods

effects on growth rates and maximum size, it has little effect on habitat distribution itself. As food availability decreases, the size at which krill shift from remaining at the surface to migrating to shallow waters decreases with decreasing food availability. As feeding rate decreases, time spent traveling matters less and saving metabolic costs more. $P(t)$ does have an indirect effect on the proportion of krill in each habitat because of its effect on krill growth rates and thus the size distribution. Unless food is so low that growth isn't possible (e.g. where $F < C$), krill are predicted to go to the surface to feed at night and migrate to shallow and deep water habitats as dictated by differences between habitats in water temperature, predation risk, and expected growth. However, decreasing food availability slows growth rate. There will be few large krill, and thus a smaller proportion of krill in deep waters.

Temperature effects. We consider the same static temperature regimes as described above and assume survival is size-independent and equal between all habitats $\sigma(H,t) = 0.99$. If the 3 habitats do not differ in water temperature, krill are predicted to remain at the surface. If the surface is not risky, only lower water temperatures (and thus lower metabolic costs) cause krill to migrate. Because travel costs decrease with size while metabolic costs increase with size, larger krill are predicted to migrate to colder waters while small krill remain at the surface. For small differences in temperature (2°C) between the 3 habitats, small krill remain at the surface, while intermediate krill travel to shallow waters, and large krill go to deep waters. Within the temperature range –4 to 4°C, relative but not absolute differences between habitats causes shifts in habitat use. As the shallow or deeper water become colder relative to the surface, a larger proportion of krill are predicted to migrate to shallow and deep water during the daytime. As the relative difference between shallow and deeper water increases, more krill migrate to deep waters.

Within the range considered, absolute differences in water temperature have little affect on size-dependent habitat distribution. However, decreased temperatures at the surface and increased temperatures in the shallow and deep water decrease growth rates and thus affect size-distributions. These size-distributions can have an indirect affect on quantitative patterns of habitat distribution. When temperatures are lower, krill grow more slowly, so fewer large krill exist and thus there are fewer krill in deeper waters. At extreme temperatures, shrinkage occurs, and habitat use shifts are predicted as a result of the change in size distribution.

Predation risk. The pattern of predation risk strongly influences predicted krill habitat use. Most important is the relative difference between habitats and whether predation is size-dependent. For the results presented here we assume $P(t) = 1$ and representative water temperatures [T(surface) = 2°C, T(shallow) = 0°C, T(deep) = –2°C]. When predation risk is size-independent and $\sigma(S,t) > 0.8$, krill are predicted to go the surface to feed at night (Fig. 10). If the 3 habitats are equally risky, krill are predicted to be found in all 3 habitats during the day (Fig. 10a). However risk at the surface can cause krill to avoid the surface during the daytime (Fig. 10b). If both the shallow and surface waters are risky, a large proportion of krill will be found in the deep waters during the day (Fig. 10c). Krill are expected to shift away from risky habitats during the daytime, but feed at the surface at night unless the surface is extremely risky [$\sigma(S,t) = 0.8$].

The existence of a size-dependent component of predation risk reduces the proportion of krill feeding at the surface at night (Fig. 11). Differences between the 3 habitats also influences the proportion of krill in each

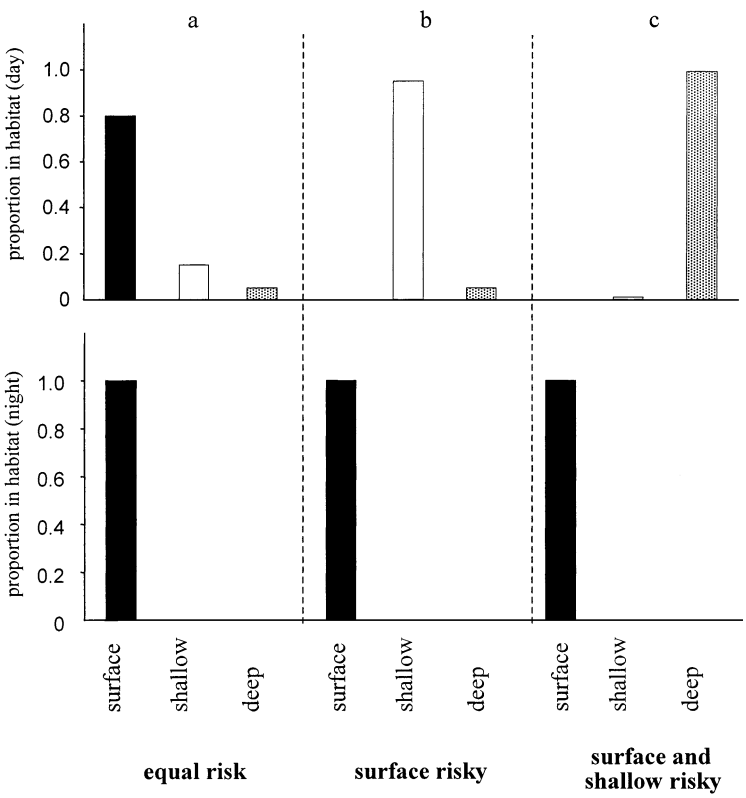

Fig. 10. Krill distribution among habitats when risk is size-independent. Krill are predicted to distribute themselves between the habitats based on risk in the daytime (top) and feed at the surface at night (bottom). Results shown are for uniform size distribution at $t = 2$

habitat. If it is risky at the surface, and less risky in shallow and deeper waters, krill are expected to be found at the surface only when feeding and will migrate to shallow and deep waters during the day (Fig. 11b). During the night, only a proportion of krill will be found feeding at the surface. This proportion increases as reproduction approaches, and decreases between reproductive events. If shallow waters are riskier than the deep water, an increasing proportion of krill will migrate to deeper waters as the risk in shallow waters increase (Fig. 11c). When predation risk is high at the surface for all sizes, krill are predicted to adopt a typical diel vertical migration pattern. However, when risk is size-dependent, small krill may be found at the surface while larger krill adopt the typical migration pattern. In contrast to temperature and food availability, small differences in risk can cause major qualitative shifts in habitat distribution. In a long-lived annually reproducing species, survival may be more important than slowed growth rates. This argues that predation may be an important factor driving size and spatial distributions of krill. Our results imply that we may need to gain a better understanding of predation risk and patterns of predator behavior in order to explain and predict krill growth and habitat distributions.

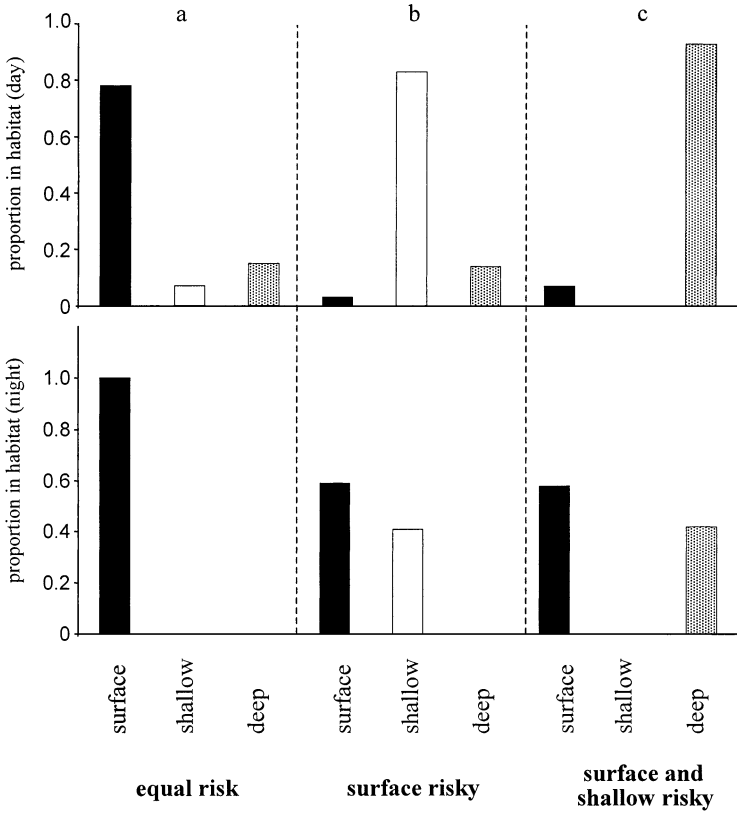

Fig. 11. Krill distribution among habitats when risk is size-dependent. Krill avoid risky habitats during the daytime and only a proportion of the krill feed at the surface at night when the surface is risky compared to other habitats. Results shown are for uniform size distribution at $t = 2$

DISCUSSION

Antarctic krill are extremely successful despite the harsh and variable environment they inhabit and the suite of predators they must avoid to survive to reproduction. Plasticity in growth and habitat selection are 2 mechanisms that may increase krill survival and success. A variety of conditions are predicted to cause shrinkage in krill to occur. Krill are predicted to shrink during food deprivation and extreme temperature conditions. Although the exact level of food abundance and temperature at which shrinkage will occur depend in part on some of the assumptions we have made, the qualitative predictions remain the same. Our results indicate that shrinkage may be a common pattern of krill growth. We predict that 2 patterns of shrinkage will be observed. In some cases, krill of all size will shrink, as was observed in laboratory experiments where krill were starved for up to 120 d (Ikeda & Dixon 1982). Krill were found to survive these conditions, but negative growth was observed in individuals of all sizes. However, in cases of food limitation, large individual krill are predicted to shrink while smaller krill may be able to grow. A similar pattern emerges for extreme temperatures. Cold temperatures are predicted to slow growth because they slow feeding rates while high temperatures increase metabolic costs exponentially. Therefore as temperature is increased we would expect to see large krill shrinking first, and smaller krill only shrinking at higher temperatures. The same basic pattern is predicted for decreasing temperatures. The ability to shrink may have evolved in krill since their habitat commonly leads to negative energy budgets. The ability to shrink to a size where positive energy budgets are possible could be a survival strategy for the Antarctic environment. Another important outcome of this model is that shrinkage under positive energy budgets is also possible. To date, all explanations of krill shrinkage have focused on metabolic costs and food intake. However, we predict that shrinkage may also occur in response to predation risk. Even if negative energy budgets are the primary cause of shrinkage, the benefit of avoiding predation could reinforce the evolution of this plasticity. The model thus

can predict the observed patterns of krill growth and shrinkage. Further observations are needed to test the model predictions directly.

Most organisms in the Antarctic are 1 or 2 trophic levels away from krill. Therefore, it is important to understand the factors driving krill growth, survival, and distribution. Variation in krill habitat distributions is well documented. However, little is known about the underlying mechanisms that drive this variation. Ideally, we would like to understand these mechanisms in order to predict how environmental conditions and commercial fisheries might impact krill distribution and abundance, and thus the survival and reproduction of the many krill predators found in the Antarctic. We presented a general theoretical and conceptual framework for understanding krill growth and habitat distributions. This general framework allowed us to make the following qualitative predictions. We predict that relative temperature differences between habitats will influence krill habitat distributions while food limitation has a mainly indirect and weak effect on habitat selection though having a direct effect on growth. However predation risk is predicted to be a key factor influencing krill habitat use and growth. Understanding predator behavior and krill responses to predation may be the key to predicting krill spatial distributions and explaining their life-history patterns. Research has focused mainly on land-based and diving predators, while much remains unknown regarding predation risk from other predators and at depth. The importance of predation also implies that we need to know more about which species are the most important predators on krill and how this varies through space and time. Furthermore, we need to know the spatial scale at which selection occurs on krill. Recent evidence points to some genetic differences between populations of krill, but that selection probably occurs at a very large scale.

Although these predictions are mainly qualitative, the model also tells us what we need to know more about before we can make strong quantitative predictions. First, knowledge of predation risk as a function of time, size, and habitat is expected to be critical in understanding krill life histories. Second, knowledge of the size-dependence of energy intake and output will help make quantitative predictions about habitat distributions. Although the quantitative predictions do depend on parameters values and exact growth functions, as long as the basic shapes of these functions are correct the qualitative patterns will hold. Krill are predicted to shrink due to extreme temperatures, food deprivation, and to avoid predation risk. These predictions are very resilient. This model gives us the capability to make predictions about krill size and spatial distributions based on information about water temperature, predator behavior, and food availability. Using the model, we can then make relative predictions regarding shifts in size distributions and habitat use with changes in water temperature, food availability or predator behavior. This makes it possible to make concrete predictions based on knowledge of these environmental conditions to be tested in the field.

Although we have focused our discussion on krill predators, commercial fisheries will clearly also influence krill survival. In the short-term predicting krill distributions can be used to manage commercial fisheries. However, in the long term fisheries may act as a selective force and influence krill habitat use and distributions. Fisheries are inherently size-selective, and the model predicts that an increased size-dependent risk will drive krill into deeper water and cause them to shrink more between reproductive events and achieve smaller maximum sizes. Although this questions warrants further consideration, it is important to realize that fisheries, as another krill predator, may have an indirect effect on krill abundance and distributions.

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