ECOLOGICAL GAMES IN SPACE AND TIME: THE DISTRIBUTION AND ABUNDANCE OF ANTARCTIC KRILL AND PENGUINS

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Abstract. The distribution and abundance of organisms are affected by behaviors, such as habitat selection, foraging, and reproduction. These behaviors are driven by interactions within and between species, environmental conditions, and the biology of the species involved. Although extensive theoretical work has explored predator–prey dynamics, these models have not considered the impact of behavioral plasticity and life-history trade-offs on predicted patterns. We apply a modeling method that allows the consideration of a spatial, dynamic ecological game between predators and prey using a life-history perspective. As an illustrative example, we model the habitat selection of Antarctic krill and penguins during the time when penguins are land-based for reproduction. Although environmental conditions and the life-history constraints of each species have both direct and indirect effects on both species, the penguin's foraging rule (whether food-maximizing or time-minimizing) has the greatest effect on the qualitative distribution pattern of both species. Size-dependent diel vertical migration of krill also strongly affects penguin foraging patterns. This model generates suggestions for future research and qualitative predictions that can be tested in the field. The application of this method to a specific problem also demonstrates its ability to increase our understanding of important ecological interactions in general.

Key words: Antarctic krill; dynamic game model; Euphausia superba; *life-history theory; penguin foraging; predator–prey interactions.*

INTRODUCTION

Many ecological interactions are generated by individual foraging, reproductive, or migratory behaviors. Animals tradeoff growth, reproduction and survival, and these tradeoffs have important effects on the distribution and abundance of organisms in space and time. However, even as individuals respond to these trade-offs they are simultaneously influenced by the behavior of individuals of other species. Consequently, interactions between species can be viewed as the result of multiple linked life-history games, where the outcome of interactions between individuals determines patterns at the species and community level (Alonzo 2002). For example, individual habitat selection can drive the distribution patterns of communities of organisms (e.g., Abramsky et al. 1991, Rosenzweig 1991). The fitness associated with any habitat will depend on interactions with other individuals, such as avoiding predation or finding individuals that are food resources. Simultaneously, however, habitat selection will be affected by the life history of the organism and any among-habitat differences in expected survival, reproduction, and interactions with conspecifics.

Although much is known about the basic biology of many species, much less is known about interactions between species. We can use models to explore how the basic biology of each species and the nature of the interactions between them can shape their distribution and abundance as well as behavior and life-history patterns within each species. In essence, we can use what is known about each individual species and ecological interactions in general to understand what is relatively unknown—interactions between particular species. We can think of this as an inverse problem in biology where we infer an unknown relationship by examining patterns that are predicted to be the outcome of a given interaction. Species- and system-specific models can be used to help us understand ecological interactions that we cannot measure directly, and thus guide further research. Here we explore a model of predator–prey interactions where habitat selection and foraging behavior are affected by both interactions between the species and individual life-history trade-offs. We use the model to demonstrate how a game theoretical life-history perspective can inform basic understanding of ecological interactions using Antarctic krill, *Euphausia superba*, and one of their main predators, penguins, as an illustrative example.

Models, at the level of the population, concerned with interactions between predators and prey have a long history in ecology (e.g., May 1973, Kingsland

1985, Brown and Vincent 1992, Fryxell and Lundberg 1998). However, a complete understanding of the ecological predator–prey interactions in a specific system requires a realistic treatment of behavior patterns within a life-history perspective. Game-theoretic models have predicted how individuals of one or multiple species are expected to distribute themselves among habitats that vary in resources and risk of mortality (e.g., Fretwell 1972, McNamara and Houston 1990, Hugie and Dill 1994, Sih 1998). However, none of the multiple-species models examined state-dependent behavior or considered life-history effects. Dynamic state-variable models have demonstrated the importance of temporal dynamics and individual variation in condition and experience to our understanding of habitat selection, foraging, and reproductive behaviors (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000) while ignoring some of the interactions between species (Lima 2002). Other models have focused on competition between species where birth or death rates depend on both the density and frequency of other species and thus have a game-theoretic component through frequency dependence (e.g., Brown 1990, Brown and Vincent 1992). However, they assume that these characteristics are fixed rather than plastic.

Predation risk is the result of predator behavior, and predators respond to the distribution and abundance of their prey. Exactly how prey respond to predators, however, depends on their own life-history constraints. For example, if a prey species is near the end of its only reproductive season, habitat selection may be relatively unaffected by increased predation risk. In contrast, an iteroparous prey species in which additional growth has little effect on fecundity may be very sensitive to patterns of predation risk. It is clear that interactions between individuals within and between species will affect the habitat selection, growth, reproduction, and survival of individuals and thus their distribution and abundance. A modeling approach that considers the lifetime fitness consequences of dynamic state-dependent behaviors is necessary, while concurrently focusing on interactions within and between species in space and time. We use an approach that is based on multiple linked dynamic programming equations, thus allowing the inclusion of realistic environmental conditions, temporal effects on behavior, behavioral plasticity, and interactions within and between species (Alonzo 2002).

General Structure of the Model: Ecological Games in Space and Time

The model uses a method developed to examine games between species (Alonzo 2002) and consists of two sub-models that predict predator (penguin) and prey (krill) behavior and distributions. These two sub-models are linked because penguin behavior determines krill survival in the krill model and krill behavior determines the distribution and availability of food in the penguin model. Therefore, the two sub-models for krill and penguin behavior must be solved simultaneously. We use a best-response approach (McNamara et al. 1997, Clark and Mangel 2000) extended for multiple species (Alonzo 2002).

The algorithm uses the parameters values (such as environmental conditions) and initial starting conditions (krill and penguin abundance as well as size and spatial distributions) to find the predicted behavior that maximizes expected lifetime fitness of krill (see Fig. 1). The predicted behavior for penguins is then found. These behavioral predictions are used in forward simulations to find the distribution that would result if the entire population of both species adopted the predicted behavior. These two steps (finding the predicted behavior and generating new distributions) are repeated until a stable solution is found. For the model described here, we used the error method described in Clark and Mangel (2000) to stabilize the model. It is possible that the algorithm does not converge to stable strategies, but this was not a problem for the results reported here.

We focus on the time when penguins are land based for reproduction. We predict diel behavior patterns of both krill and penguins and population distributions during a 15-week period when krill and penguin distributions overlap near the shore. During the breeding season (approximately October–February), penguins are central-place foragers leaving their nesting sites to obtain food (Croxall and Prince 1980, Trivelpiece et al. 1987). We divide the foraging area near the penguin breeding grounds into two cross-shelf regions: inshore and offshore (Fig. 2). It has been observed that the number of penguins found in these larger areas is related to the abundance of krill in each region (T. Ichii, *personal communication*). Within each cross-shelf region, krill are distributed vertically between two or three depth strata: surface, shallow, and (if offshore) deep (Fig. 2). Increasing evidence suggests that, although zooplankton are influenced by ocean currents with respect to their horizontal distribution, many species are able to select their vertical position in space (Folt and Burns 1999). Antarctic krill exhibit a classic diel vertical-migration pattern (Hernandez-Leon et al. 2001). Here we assume that krill can influence their vertical distribution but maintain their distance from shore (Hernandez-Leon et al. 2001, T. Ichii, *personal communication*). Although krill may be carried large horizontal distances by ocean currents, no evidence exists that krill can influence their large-scale horizontal location. Although krill and penguins can migrate daily, for computational simplicity, we examine weekly time periods (*t*). Thus, krill and penguins are assumed to adopt one behavior for each one-week period.

Penguin Behavior and Distribution

We do not fully understand the effect of predator–prey interactions between krill and Antarctic penguin species on their distribution and abundance. Clearly,

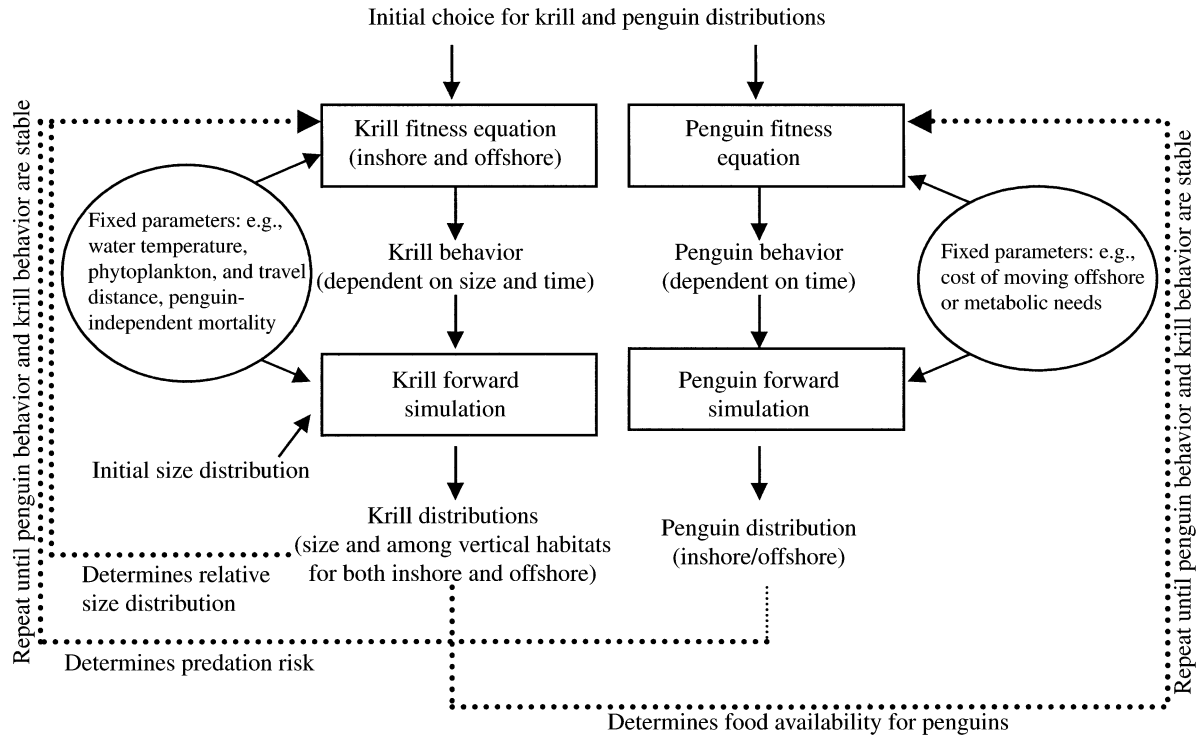Initial choice for krill and penguin distributions

FIG. 1. The algorithm used to examine the ecological game between krill and penguins in space and time. See *General structure of the model . . .* for details.

the foraging patterns of Adelie (*Pygoscelis adeliae*), Gentoo (*P. papua*), and Chinstrap (*P. antarctica*) penguins appear to respond the distribution and abundance of krill (Croxall and Prince 1980, Trivelpiece et al. 1986, 1987, T. Ichii, *personal communication*). Years of higher krill abundance are also positively correlated with penguin reproduction. However, the relationships between krill abundance and predator performance are nonlinear (Boyd and Murray 2001).

Abundant food may increase penguin fitness either by increasing the energy available to them or by decreasing the effort required to obtain the food they need for themselves and their offspring. We assume that penguin fitness and thus behavior is determined by their need to obtain food. We examine two classical foraging rules. First, penguins may forage to maximize the amount of food they consume in a day. Second, penguins may forage to meet a fixed metabolic demand and minimize their time away from the nest. The focus on penguin foraging clearly captures the link between krill and penguins through the food and time available for reproduction. It is important to be clear that we are not determining the penguin foraging rule. Rather, we are asking what the impact of different penguin foraging rules will be on the distribution of both penguins and krill when they are interacting in a dynamic spatial predator–prey game.

Penguin behavior and food intake are affected by both the abundance of krill and their relative vertical distribution. Because penguins are visual, air-breathing predators, krill are more difficult to catch at depth and during the night. Thus, the relative ability of penguins to catch krill $\alpha_{h,i,j}$ (where vertical habitat h = surface, shallow, or deep (if offshore), diel period i = day or night, and cross-shelf region j = inshore or offshore) decreases with depth and at night. We are aware of no research that has reported any seasonal or lunar variation in penguin foraging ability. We examined all possible combinations of $\alpha_{h,i,j}$ ranging from 0 to 1. Baseline conditions for $\alpha_{h,i,j}$ were surface: 1.0, shallow: 0.95, deep: 0.90, both inshore and offshore.

We denote the vertical distribution of krill biomass during week t by $\rho_{h,i,j}(t)$. The expected amount of krill a penguin can obtain foraging $Q_{i,j}(t)$ during week t with foraging costs C_j is

$$Q_{i,j}(t) = \sum_h (\alpha_{h,i,j}\rho_{h,i,j}(t)) - C_j. \tag{1}$$

We examined the cost of foraging offshore from 0 to 1 while holding the cost of foraging inshore constant at zero. Baseline conditions were $C_{\text{offshore}} = 0.1$. Although differences exist between species, in general penguins forage during the day and night (Croxall and Prince 1980, Trivelpiece et al. 1986, 1987). The solution of the krill model (see *Krill behavior and distribution*, below) is used to calculate the distribution of krill $\rho_{h,i,j}(t)$.
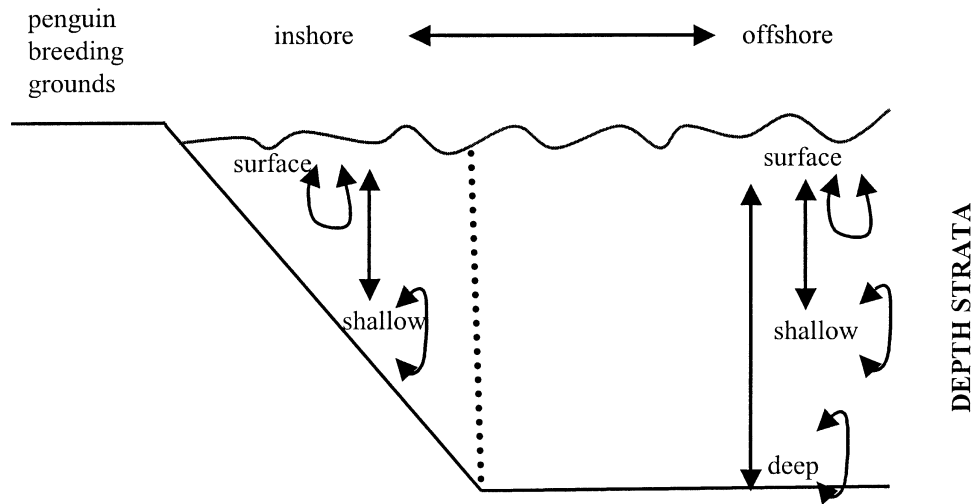
CROSS-SHELF REGIONS

FIG. 2. Spatial structure of the model. See *General structure of the model . . .* for details.

Maximizing food intake

In this case, penguins are assumed to distribute themselves relative to expected gains inshore and offshore (Fretwell 1972). If N represents the density of penguins at the breeding site, the density of penguins $N_{i,j}(t)$ predicted to be in cross-shelf region j (inshore or offshore) for diel period i (night or day) during week t is given by

$$N_{i,j}(t) = Q_{i,j}(t)N \Big/ \sum_j Q_{i,j}(t) \qquad (2)$$

as long as $Q_{i,j}(t) > 0$.

Minimizing foraging effort

We assume there is an amount of krill, m, each penguin must consume in order to meet its own energy demands and feed its chicks. Since traveling offshore will increase foraging duration, we assume that penguins only move offshore if there are not sufficient krill inshore to meet penguin energy needs (Mangel and Switzer 1998). Then $N_{i,j}(t)$ is given by:

$$\text{if} \quad Q_{i,\text{inshore}}(t) > mN \quad \begin{cases} N_{i,\text{inshore}}(t) = N \\ N_{i,\text{offshore}}(t) = 0 \end{cases}$$

$$\text{if} \quad Q_{i,\text{inshore}}(t) < mN \quad \begin{cases} N_{i,\text{inshore}}(t) = Q_{i,\text{inshore}}(t)/m \\ N_{i,\text{offshore}}(t) = N - N_{i,\text{inshore}}(t). \end{cases}$$
$$(3)$$

In other words, if sufficient krill can be found inshore, all the penguins will forage inshore. If the abundance of accessible krill is too low inshore, then penguins must forage offshore some of the time to meet their metabolic demands. Relative penguin foraging success is determined by the $\Sigma_j Q_{i,j}(t)$ (e.g., energy gain) across the entire reproductive period.

KRILL BEHAVIOR AND DISTRIBUTION

Although food (light-dependent phytoplankton) is found mainly at the surface, air-breathing visual predators are more effective and abundant at the surface as well. Since predation risk at the surface will be less at night due to lower light levels, zooplankton in general are predicted to feed at the surface at night and move to deeper and safer waters during the day (Kerfoot 1980).

Previously (Alonzo and Mangel 2001) we examined the diel vertical-migration behavior of krill when krill were trading off fixed survival and fecundity. We use this previous dynamic programming equation model (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000) to predict the vertical distribution of krill inshore and offshore and to generate $\rho_{h,i,j}(t)$ in the penguin model. The three possible depth strata (surface, shallow, and deep water) differ in food availability (phytoplankton), water temperature, predation risk, and travel costs to the surface. Predation risk may also differ between inshore and offshore, thus driving differences in the vertical distribution of krill. Since krill are mainly observed feeding at the surface during the night (Mauchline 1980, Morris et al. 1983, 1984) we assume for simplicity that krill feed only at night at the surface. Each of the equations described below will be solved once for krill that are found inshore and a second time for krill that are found offshore.

The krill model is composed of three important elements: growth, survival, and fitness.

Growth

Fecundity and survival of krill depend on length L (Siegel 1987, Reid et al. 1996). Consequently, growth

is inherently connected to krill fitness and habitat-selection behavior. For more details on the krill growth equations and parameter values described below see Alonzo and Mangel (2001).

Metabolic costs.—Based on Ikeda (1985), metabolic cost (C) is a function of water temperature ($T(h, t)$ in vertical habitat h at time t) and krill mass $M(L) = 10^{0.39\log L - 2.75}$ (Mackintosh 1972):

$$C(h, L, t) = e^{-0.25 + 0.80\ln M(L) + 0.05T(h,t)}. \quad (4)$$

Individual metabolic costs increase with increasing temperature and krill length. We examined every possible temperature combination from $4°$ to $-2°C$ where temperature decreased with depth. Baseline conditions were surface temperature $= 2°C$, shallow-water temperature $= 0°C$, and deep-water temperature $= -2°C$. The metabolic costs of staying in one vertical habitat and not traveling to the surface to feed will be $C_{\text{stay}}(h, L, t) = C(h, L, t)$. However, if krill feed at the surface at night but spend the day in another habitat, their metabolic rate will depend on the proportion of time spent in the daytime vertical habitat (τ) vs. in the nighttime vertical habitat ($1 - \tau$). For the analyses presented here, we assume for simplicity $\tau = 0.5$. 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 vertical habitat h will be $C_{\text{feed}}(h, L, t) = (1 - \tau) C(S, L, t) + (\tau) C(h, L, t)$ where metabolic costs implicitly depend on water temperature in the daytime vertical habitat $T(h, t)$ and at the surface $T(S, t)$.

Energy intake.—Total energy intake depends on food availability (P), assimilation rate (A), filtration rate ($4.64 M(L)^{0.8}$ in milliliters per hour, Holm-Hansen and Huntley 1984), water temperature $T(h, t)$, travel time between vertical habitats, and krill size L. We assume feeding rate increases asymptotically with temperature (Atkinson 1994) using the relationship $(T(S, t) - T_0)/(T(S, t) + T_A)$ where T_A determines the speed with which the relationship asymptotes. The feeding rate will be zero at T_0 and then increases with temperature toward the maximum feeding rate. For the analyses presented here, we use $T_0 = -5$ and $T_A = 10$. The amount of time krill spend traveling between vertical habitats decreases the amount of time available for feeding. We assume krill can swim two body lengths (in millimeters) per second and calculate the amount of time required to travel to the surface. We then calculate the proportion of time available for feeding after travel $P_f(h, L)$ for a krill of length L traveling from vertical habitat h. Travel time decreases with increasing krill length.

We examined all possible combinations of distances where the distance to shallow water was either 50 or 100 m and the distance to deep water was 100, 200, or 400 m. Baseline conditions were distance to shallow water $= 50$ m and distance to deep water $= 100$ m. We assume that food intake asymptotes with size and the size-dependent function of food intake is ($1/(1 +$ $0.005 M(L)^{0.8})$ so size asymptotes at $L = 60$ mm in maximum growth conditions.

Consequently, the food intake $F(h, L, t)$ per time period for a krill of length L traveling from vertical habitat h and feeding at the surface at time t is

$$F(h, L, t) = P_f(h, L)\phi A 4.64 M(L)^{0.8}$$
$$\times [T(S, t) - T_0]/[T(S, t) + T_A]$$
$$\times [1/(1 + 0.005 M(L)^{0.8})]. \quad (5)$$

Food intake increases with water temperature at the surface and krill length. We examined phytoplankton abundance (proportion of maximum food conditions) ranging 0 to 1 with baseline conditions $\phi = 1$.

Calculating growth.—Growth is determined by the difference between energy intake and metabolic costs (Atkinson 1994). Because food intake and metabolic costs are both represented in terms of metabolic energy (in microliters of O_2 per hour), the difference ($F - C$) between food intake and metabolic costs represents net energy gain, which we convert into growth (in millimeters) with a parameter κ chosen so that growth rates match observed rates (Alonzo and Mangel 2001). If a krill of length L feeds at the surface and then goes to vertical habitat h during the daytime, its growth ΔL_{feed} per week will be

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

If a krill of length L remains in vertical habitat h, its growth ΔL_{stay} per week will be

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

where for biologically realistic water temperatures $\Delta L_{\text{stay}}(h, L, t)$ will be less than or equal to $\Delta L_{\text{feed}}(h, L, t)$. Krill growth is also bounded so that $L \geq 12$ mm and $L \leq 60$ mm.

Survival

We assume there is a baseline probability of a krill surviving per foraging predator in the vertical habitat per time period. Since evidence exists that some predators may preferentially select large krill (Hill et al. 1996, Reid et al. 1996), the probability of survival in the presence of these predators will also decrease with increased individual size. We assume that larger krill have a greater chance of being caught by penguins. If penguins prefer to feed on larger krill, then the largest krill relative to their neighbors will be at the greatest risk. However, penguins may also have greater motivation and ability to catch krill that are larger. Therefore, predation risk may depend on both the absolute length of krill and on an individual krill's size relative to other krill in the same vertical habitat. We let $s_{h,i}(L, t)$ represent the proportion of krill in the same vertical habitat h for diel period i and week t that are smaller than a krill of size L, μ_0 the risk of mortality independent of krill size, and μ_1 and ε the strength of size-

dependent mortality. Thus, survival of a krill of size L in vertical habitat h during week t is modeled by

$$\sigma(h, L, t) = \exp(-\mu_0 - \mu_1 s_{h,i}(L, t)^\varepsilon L). \quad (8)$$

We assume that baseline survival decreases with depth and ranges between 0.001 and 0.005. Baseline conditions were μ_0 = surface 0.005, shallow 0.002, and deep water 0.001. We examined μ_1 ranging from 0.001 for 0.005 and ε ranging from 0 to 0.5. Baseline conditions were μ_1 = 0.001 and ε = 0.25. The overall probability of surviving the entire time period also depends on the density of predators $N_{ij}(t)$ in diel period i in region j during week t. Thus the probability a krill of length L will survive from t to $t + 1$ in vertical habitat h is

$$\sigma(h, i, L, t) = \sigma(h, L, t)^{\alpha_{h,i,j} N_{ij}(t)}. \quad (9)$$

If a krill migrates between a daytime vertical habitat h and the surface S at night, its probability of survival per time period will be the average of survival in the two vertical habitats weighted by the proportion of time spent in the daytime (τ) or nighttime vertical habitat $(1 - \tau)$. Krill survival is determined by krill size and behavior as well as penguin behavior and abundance.

Fitness

There are two components of reproductive success: incremental fitness and terminal fitness. We assume that terminal fitness depends on krill length at the end of the time during which they overlap with penguins and their probability of surviving to the next year to reproduce. We modified a length–fecundity allometric relationship (in eggs produced per female, Siegel 1985) to represent expected future fecundity $R(L, T)$ as a function of present krill length L by setting the intercept of the empirical relationship to zero so that krill of all lengths have expected future reproductive success

$$R(L, T) = 245.7L. \quad (10)$$

For incremental fitness, we assume that krill allocate resources to reproduction based on their current length such that $R(L, t) = kL$ for all $t < T$ (here $k = 1$). We 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, $Z(L,T) = e^{-\mu_a} R(L,T)$ where μ_a represents annual mortality of krill. We examine μ_a in the range 0.5 to 2.5 based on empirical estimates of annual mortality (Pakhomov 1995). For $t < T$, fitness is the sum of current and future reproduction. Fitness depends on vertical habitat, size, and time in the season. The expected reproductive value of staying in vertical habitat h without feeding when size L in time t is given by

$$V_{\text{stay}}(h, L, t)$$

$$= R(L, t) + \sigma_{\text{stay}}(h, L, t)Z[L + \Delta L_{\text{stay}}(h, L, t), \ t + 1]. \quad (11)$$

The expected reproductive value of feeding at the sur-

face and then going to vertical habitat h when size L in time t is

$$V_{\text{feed}}(h, L, t)$$

$$= R(L, t) + \sigma_{\text{feed}}(h, L, t)Z[L + \Delta L_{\text{feed}}(h, L, t), t + 1]. \quad (12)$$

Krill migration patterns are predicted by finding the vertical habitat and feeding behavior that maximizes expected lifetime reproductive success for a krill of length L at time t or

$$Z(L, t) = \max_h \ \{\max\{V_{\text{feed}}(h, L, t), V_{\text{stay}}(h, L, t)\}\}. \quad (13)$$

The solution of this dynamic programming equation (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000) predicts the size- and time-dependent vertical habitat use and feeding behavior of krill.

Forward iterations

From an initial size distribution and overall abundance of krill, the predicted behavior (from the solution of Eq. 13) and state dynamics can be used to calculate changes in the distribution of krill based on the expected growth and survival of krill in each size class and by using the above-mentioned relationship between krill mass and length. These calculations give the vertical distribution of krill biomass $\rho_{h,i,j}(t)$ used in the penguin foraging model and the relative size distribution of krill $s_{h,i,j}(L, t)$ (where h = vertical habitat, i = day or night, and j = inshore or offshore).

The algorithm requires an initial distribution of krill inshore and offshore; we assume a uniform initial distribution. We let $D_{h,i,j}(L, t)$ represent the proportion of krill of length L that are in vertical habitat h at diel period i in region j at time t. The probability that a krill of length L in diel period i in region j at time t will select vertical habitat h is $p_{h,i,j}(L, t)$, and $g_{b,h,i,j,t}(L', L)$ represents the probability (0 or 1) that a krill of length L adopting behavior b and selecting vertical habitat h will change from length L to length L'. Then, the distribution of krill in the next time period is given by

$$D_{h',i,j}(L', t + 1)$$

$$= \sum_h \sum_L p_{h',i,j}(L, t)\sigma_{jh,i,j}(L, t)D_{h,i,j}(L, t)$$

$$\times g_{b,h,i,j,t}(L', L). \quad (14)$$

The size distribution can be used to calculate the remaining biomass distribution by converting size into mass. If K_j represents the starting abundance of krill in the region (where j = inshore or offshore), then krill biomass (used in the penguin foraging equations) is

$$\rho_{h,i,j}(t) = K_j \sum_L M(L)D_{h,i,j}(L, t). \quad (15)$$

We explored cases in which krill were equally abundant

TABLE 1. Summary of results for both penguin foraging rules: food-maximizing (Rule 1) and time-minimizing (Rule 2).

Parameter	Pattern
Water temperature	Increased surface temperature increases krill biomass and growth. Lower temperatures in shallow and deep water cause krill to spend more time in these depth strata. Relative differences in water temperature drive krill vertical distributions and indirectly penguin intake rates through krill availability. *Rule 1*: Relative distribution of krill inshore and offshore drives penguin distribution. *Rule 2*: If penguins have sufficient food all penguins predicted to be inshore independent of water temperature.
Phytoplankton abundance	Increased phytoplankton abundance increases krill biomass and growth. Affects the relative distribution of krill or penguins only through the frequency of different krill size classes. *Rule 1*: Larger krill in deeper waters can actually decrease the proportion of penguins offshore even if biomass is greater. *Rule 2*: Greater biomass means weaker depletion and penguins remain inshore.
Distance between habitats	Relative distance between habitats affects the relative distribution of krill and indirectly penguins' intake rates through krill availability. *Rule 1*: Increased distance between habitats drives more krill to the surface and thus more krill are available to foraging penguins. *Rule 2*: Penguins inshore independent of distance between habitats unless food is depleted.
Relative krill abundance	Affects penguins' intake rates and krill depletion rates. *Rule 1*: Only the relative krill abundance between inshore and offshore has a strong effect on the relative abundance of penguins. *Rule 2*: Greater krill abundance leads to lower depletion and penguins stay inshore. Otherwise, there is no effect on penguin behavior.
Krill annual mortality	Very weak effect on krill and penguin behavior. However, decreased annual mortality leads to slightly more krill in safe habitats. No real effect on penguin behavior for either penguin foraging rule.
Baseline krill survival	Differences among habitats in baseline survival affect the relative distribution of krill among habitats and the krill available to penguins. *Rule 1*: Baseline survival affects the relative distribution of penguins inshore and offshore. *Rule 2*: Relative distribution of krill only affects the rate of depletion of krill and thus affects if and when penguins move offshore.
Size-dependent predation	The strength of size-dependent predation determines depletion rates of krill. No direct effect on penguin or krill behavior except as mentioned above for baseline survival.
Relative abundance of penguins	The relative abundance of penguins mainly affects the depletion rate of krill. *Rule 1*: No effect on penguin behavior. *Rule 2*: Depletion affects if and when penguins go offshore.
Penguin foraging ability	As long as ability decreases with depth, the relative difference has little effect on krill or penguin behavior. Penguin foraging ability mainly affects depletion rate. *Rule 1*: No effect as long as foraging ability is same inshore and offshore. *Rule 2*: Affects depletion and thus if and when penguins go offshore.
Cost of foraging offshore	*Rule 1*: Increased cost of going offshore decreases the proportion of penguins offshore. This affects the relative vertical distribution of krill inshore and offshore. *Rule 2*: No effect on penguins and thus no effect on krill.

inshore and offshore as well as when krill were 2 and 3 times more abundant inshore or offshore. Baseline conditions were $K_{inshore} = K_{offshore} = 1$. We also calculate the relative size distribution $s_{h,i,j}(L,t)$ from the size distribution $D_{h,i,j}(L,t + 1)$ as follows:

$$s_{h,i,j}(L, t) = \sum_{\ell < L} D_{h,i,j}(l, t). \qquad (16)$$

For this model we assumed that krill were initially distributed evenly between the three depth strata and that penguins were distributed evenly between inshore and offshore. Varying the initial conditions did not affect the final behavior or distributions predicted.

RESULTS

We first examined the baseline conditions described above and then varied each parameter of interest sequentially and compared the predictions to the baseline observations for both penguins and krill. The results

of these extensive analyses are summarized in Table 1; we make qualitative predictions that can be tested in the field regarding the impact of 10 key variables on krill and penguin distributions. Krill are predicted to be mainly in the safest vertical habitat (shallow inshore and deep offshore) during the day but then feed at the surface at night. However, krill migration behavior is size dependent: smaller individuals are predicted to stay at the surface during the day in both inshore and offshore regions, and offshore intermediate-sized krill are predicted to be in shallow water during the day.

One example of a prediction from Table 1 is shown in Fig. 3. The penguin foraging rule has drastic impacts on the distribution of penguins inshore and offshore. When adopting the food-maximizing foraging rule, more penguins are predicted to forage inshore than offshore although this difference decreases at night when all krill are found at the surface (e.g., Fig. 3a). If penguins are time minimizing, all of the penguins are pre-

a) Penguin foraging rule: food-maximizing

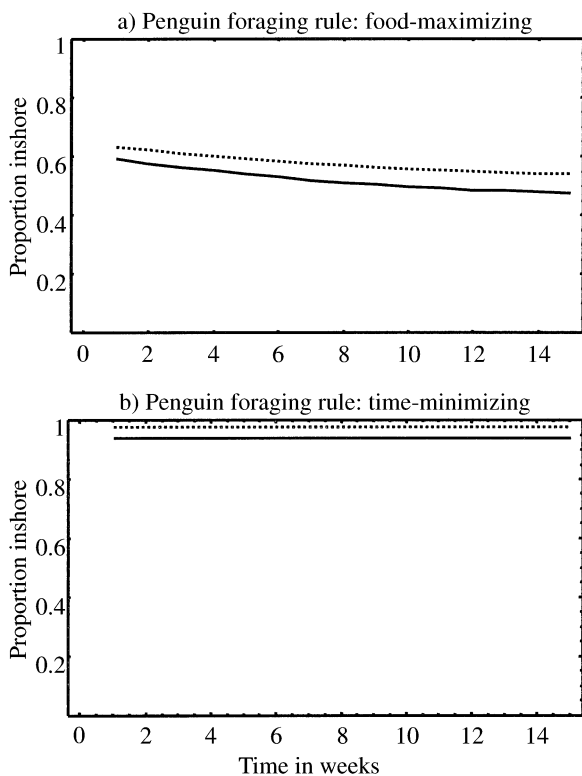## b) Penguin foraging rule: time-minimizing

FIG. 3. An example of the predictions from Table 1: the spatial and temporal cross-shelf distribution of penguins for the baseline conditions when penguins are (a) food maximizing and (b) time minimizing. The dotted lines represent the patterns during the day, and the solid lines show patterns at night.

dicted to forage inshore under the baseline conditions (e.g., Fig. 3b). When penguins are time minimizing there is no risk due to predation by penguins offshore. This alters the relative vertical distribution of krill offshore; they are found mainly at the surface both day and night if penguins are only found inshore. When food-maximizing penguins forage both inshore and offshore, most krill are found in the safest vertical habitat by day and come to the surface only to feed at night. Depletion by penguins will also alter the relative size distribution as well as the overall abundance of krill. As depletion occurs inshore, more penguins move offshore. We explore the impact of krill fisheries near land-based penguins in another paper (S. H. Alonzo, P. Switzer, and M. Mangel, *unpublished manuscript*).

Abundant food, warm surface waters, and cool shallow or deeper water all increase krill growth rates and thus krill biomass. However, when the shallow and deeper waters are cold relative to the surface water, more krill spend the daytime in these energetically cheaper (and safer) vertical habitats. Furthermore, as growth conditions increase the frequency of large krill, a greater proportion of the krill are migrating into deep waters offshore and are thus less accessible to foraging penguins. As described in detail in Table 1, good con-

ditions for krill biomass may actually be bad feeding conditions for penguins. When penguins are food maximizing, fewer penguins are predicted to be foraging offshore under good growth conditions for krill.

DISCUSSION

In our previous model (Alonzo and Mangel 2001), we ignored the effect of relative krill size on predation and found that the strength of size-dependent risk had a large effect on the relative distribution and behavior of krill. In fact, a large proportion of the krill were predicted to remain in deeper water at night to avoid the immediate risk of feeding at the surface and increased future predation risk with increased size. However, in the present model, when relative krill size affects predation risk, krill could not escape predation merely by being small and thus most krill were predicted to be found feeding at the surface at night. Similarly, when we previously ignored the fact that predators respond to krill distributions, krill could escape into deeper habitats and thus the relative difference in risk affected the relative distribution of krill among vertical habitats. In the current model, most krill remained in the safest habitat during the day (where penguins could not forage effectively) rather than spending time in habitats where penguins could forage effectively. However, there is a greater tendency of krill to congregate in the safest vertical habitats rather than be distributed among vertical habitats based on size, as in the past model. Thus, we conclude that allowing predators to respond to the distribution of prey leads to qualitative and quantitative differences in predicted patterns.

Our model predicts that environmental conditions such as water temperature and phytoplankton abundance will directly influence the growth and vertical distribution of Antarctic krill. However, these factors also influence the food available to penguins and thus indirectly affect their cross-shelf distribution. The exact patterns predicted however are only intuitive if we consider the behavior of both the predator and prey species. For example, the prediction that more penguins forage inshore when the frequency of large krill is greater offshore can only be understood by considering krill behavior. It is necessary to think about the multiple interactions within and between species as well as the environmental and evolutionary factors impacting their behavior (e.g., Fig. 1) in order to generate predictions and understand observed patterns (Table 1).

The most important factor in determining penguin behavior was not the absolute abundance of krill. Rather, constraints on penguin foraging ability and the foraging rule they adopt have the greatest influence on their cross-shelf distribution. Similarly, the ability of krill to escape predation by going into deep water offshore has a strong influence both on penguin foraging rates and krill vertical distribution patterns. If deeper strata are much safer than the surface, then krill will

remain in deep water during the day. However, if penguins forage well at depth and risk is relatively equal between depth strata then krill will be more evenly distributed with depth. Similarly, if risk is equal across depth strata, then environmental conditions such as water temperature will have a large effect on krill behavior. However, if predation risk decreases with depth then water temperature is predicted to have little effect.

In general, the links between krill and penguins are intuitive but not necessarily linear. This fits with empirical observations (Boyd and Murray 2001) and other models (Mangel and Switzer 1998) linking krill abundance and predator performance. Krill avoid risk, but they will also be influenced by the cost of vertical migration and the environmental conditions in each vertical habitat. Krill will also be influenced by any differences among vertical habitats in predation risk that is independent of penguins. Similarly, variation among depth strata in conditions may not cause krill to shift their vertical distribution patterns until they are sufficiently different to cause one vertical habitat to exceed another in expected fitness. And even if one depth stratum is better due to environmental conditions, the response of penguins to krill vertical distribution patterns can be more than sufficient to actually drive patterns in the reverse direction than expected from environmental conditions alone. Thus simple relationships between any one variable and the distribution and abundance of krill or penguins are not predicted. Instead, a mechanistic understanding of these predator–prey interactions that takes into account life-history constraints and interactions within and between species will be required to make predictions and explain observed patterns. Although we focus on the Antarctic system and specifically on krill and penguins, the complexity of these patterns will be general to any predator–prey system where both species move among habitats that vary in conditions and risk. Further, the specific life-history constraints of the species involved may be of even greater importance than the habitat differences alone.

Our results show that understanding predator–prey interactions in general or within a specific system requires an understanding of the life histories of the species involved as well as the impact of environmental conditions on each species and the links between the species. At first this may appear to make generalization impossible. However it is clear that certain characteristics arise as being generally important. For example, if prey can escape predation in any of the available habitats, then the expected future reproduction of the prey will drive their relative distribution and thus availability to predators. Similarly, if predators increase their reproductive success most by having more energy available for reproduction, then strong links will exist between prey availability and predator distribution patterns and these links will be relatively intuitive. However, if predators are simply meeting basic energy de-

mands and increase their present and future reproductive success by minimizing the time spent foraging, then predators will be less influenced by the quantitative patterns of prey abundance. Predicting general patterns is only possible within the context of predator and prey life histories. These results clearly demonstrate that, through the application of this method, we can use what is known about individual species and ecological interactions in general to gain a greater understanding of complex interactions between species.

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