

A model at the level of the foraging trip for the indirect effects of krill (*Euphausia superba*) fisheries on krill predators

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Abstract

We present a model at the level of the foraging trip for the effects of a fishery on krill (*Euphausia superba*) predators, using the Adelie penguin (*Pygoscelis adeliae*) as a model organism. The model involves: (i) the description of the biomass and spatial distribution of krill; (ii) the effects of the fishery on the krill; (iii) the description of penguin breeding; and (iv) the indirect effects of the fishery on penguin reproduction and survival. The objective is to make relative comparisons of penguin reproductive success and adult survival in the absence or presence of a fishery. The biomass of krill appropriate for the predators (and the fishery) fluctuates from one year to the next according to an age-structured, stochastic recruitment model. Furthermore, there is a spatial-temporal structure, determined by diffusion and advection, to krill availability in relation to the location of the penguin breeding colony. Fishing is assumed to change the spatial and temporal distribution of available krill. After fledging, offspring survival depends in part upon the amount of krill delivered to them during the feeding periods. We use empirical data to estimate parental and offspring needs and a standard life history model to set the upper limits for survival. Parental survival after breeding depends upon the krill deficiency (relative to needs) that parents accumulate while feeding their young. A sensitivity analysis of the breeding model shows that the predictions are robust for parameters about which little is known, to the functional forms relating krill abundance to offspring and parent survival, and to the rules that parents use to allocate krill to their offspring. We evaluate expected reproductive success (offspring survival) and expected parental survival as functions of the amount of krill captured by the fishing fleet. Over the range of catch in our study, the reductions in reproductive success are essentially linear functions of krill catch with slope 1.5 and reductions in adult survival are also linear functions of krill catch, with but slopes less than 1. That is, reductions in reproductive success and parental survival are linear functions of krill catch, but not 1:1. The reductions in offspring and parent survival are mainly determined by how long the fishing season lasts and the capacity for harvest, rather than when fishing begins. © 1998 Elsevier Science B.V.

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1. Introduction

The development of fisheries for southern ocean krill *Euphausia superba* over the last 20–25 years prompted concern about the indirect effects of such fisheries on krill predators (e.g. McElroy, 1984; Beddington and de la Mare, 1985; Butterworth, 1986; Murphy et al., 1988; Everson, 1992; Jouventin and Weimerskirch, 1990; Young, 1990; Nicol and de la Mare, 1993; Agnew and Marin, 1994; Ichii et al., 1994; and references therein). To date, all of the models that address this question are population level models (Butterworth and Thomson, 1993; Butterworth et al., 1994; Murphy, 1995), even though indirect effects may be important at the level of the foraging trip (exit from the breeding colony to sea for foraging and return to the breeding colony), particularly during the breeding season, when predators are constrained to remain within relatively small distances of the breeding colony. Although considerable foraging data have been collected on krill predators, there are currently no models at this scale for the indirect effects of fisheries of predator reproductive success and survival.

A model for indirect effects of fisheries on predators at the level of the foraging trip involves a finer spatial scale than population level models (because it focuses on the spatial and temporal distribution of krill near the predator colonies) and a finer behavioral scale than the population level models (because it focuses on how individual predators use the krill that they find). Indirect effects are a form of ‘higher order interactions’ (Kareiva, 1994). However, almost all studies of indirect interactions focus on the population level (Adler and Morris, 1994; Billick and Case, 1994; Wootton, 1994).

In this paper, we develop a model for the indirect effects of krill fisheries on krill predators, using the life history of Adelle penguins (*Pygoscelis adeliae*) to describe the predator. We choose Adelle penguins for a number of reasons. First, they are fundamentally obligate krill predators, so that we anticipate indirect effects of harvest to be more noticeable with them than with some other predators. Second, during the breeding season they are constrained to a fixed spatial

location, so that fisheries near such locations will be more likely than not to have an effect. Third, there is considerable knowledge about their breeding biology and life history (Ainley et al., 1983; Lishman, 1985a,b; Trivelpiece et al., 1987; Davis, 1988; Culik et al., 1990; Davis and Darby, 1990; Davis and Miller, 1990; Costa, 1991; Croxall and Rothery, 1991; Culik, 1994). Fourth, the size distribution of krill eaten by Adelle penguins is virtually identical to the size distribution taken by the fishery (Croxall and Lishman, 1987) and there is an association between krill abundance and these predators (Heinemann et al., 1989; Whitehead et al., 1990; Hunt et al., 1992). Fifth, Adelle penguins have been proposed as indicator species for the Southern Ocean ecosystem (Trivelpiece et al., 1990; Wilson et al., 1990).

To use a seabird as an indicator species requires knowledge of annual adult survival, chicks fledged per nest, and chick survival as a function of food supply (Cairns, 1992). As with previous models (cf Butterworth et al., 1994), we focus on relative effects of a fishery. The objective is not to predict absolute changes in Adelle abundance as a result of the fishery, but to predict changes relative to a reference state. We choose the reference state to match as much as is known about the Adelle biology and current population information.

In the next section, we describe the overall structure of the model and justify the approach that we use. We then provide details of the three major sub-models (krill spatial and temporal distribution, fishery effects on krill, and penguin breeding), after which we provide detailed results, including sensitivity analyses of the model, and evaluation of the effects of the fishery on reproductive success and survival.

2. Structure of the model

The model has four main components: (i) the description of the spatial and temporal pattern of krill; (ii) the effects of the fishery on the krill; (iii) the description of penguin breeding; and (iv) the indirect effects of the fishery on the penguins. As with all models, there is compromise between the level of tractability and the level of biological detail.

We focus on the relative biomass (Butterworth et al., 1994) and spatial and temporal distribution (Heywood et al., 1985) of ‘appropriate’ krill, which we define as the size classes of krill that the penguins eat. In doing this, we ignore size structure and growth of krill (Siegel, 1987), swarm structure (Watkins et al., 1986; Barange et al., 1993; Miller et al., 1993), and vertical migration and other meso-scale features (Everson and Murphy, 1987). We couple previous descriptions of fishing fleet behavior (Butterworth, 1989; Mangel, 1989) with the new description of the spatial and temporal distribution of krill to determine how the fishing fleet affects the distribution of krill. In addition, we include the location of the ice-edge; this physical factor appears to have strong effects on predator survival and reproduction (Fraser et al., 1992). We assume that krill disappear under the ice (Smetacek et al., 1990R. Hewitt, personal communication), but our model is designed so that other patterns of krill advection can be included.

We focus on the penguins during the period of breeding, when they are constrained to a specific physical location. The model begins with the arrival of penguins at the breeding location and follows them through pre-breeding activity, incubation, creching and fledging of the chicks. We specify foraging requirements of the parents (Chappell et al., 1993a) and chicks (Culik, 1994) and track the energy budgets (described in detail below) of each. We leave out the details of parental behavior within foraging trips (Chappell et al., 1993b). Consequently, our model is between the population level models in the literature and a full dynamic, state variable model (Mangel and Clark, 1988; Mangel and Ludwig, 1992).

The main indirect effects that we study are the effects of the krill fishery on chick survival to fledging and post-fledging and the effects of parental state on between season survival.

3. Description of the model

We envisage a breeding colony located at the origin of a coordinate system with ice in the direction of negative x -values and ocean in the

direction of positive x -values. We specify the density of appropriate krill (i.e. krill of the right size for the penguins to feed upon), integrate over the vertical distribution. These krill are transported by physical processes towards the ice edge, at which point they disappear under the ice and, although present, are not available to the penguins. The nominal spatial scale is in units of km. The nominal measure of the density of krill is kg/penguin trip. The nominal time scale is $t = 1 - 100$ days (Ainley et al., 1983), in which $t = 1$ is the first day that the penguin could establish breeding colonies.

3.1. The krill biomass distribution

As in other models investigating the indirect effects of krill fisheries on predators, we assume that in a given year the total biomass of appropriate krill is drawn from a frequency distribution. We used the age-structured population model of Butterworth et al. (1994) to generate the long-term frequency distribution of biomass of appropriate krill (Fig. 1). Because we focus on the relative effects of the fishery, it is sufficient to use relative measures of biomass. Hence we set (Table 1)

$$b_i = i\text{th biomass level in the current year} \quad (1)$$

with $i = 1$ to $i_{\max} = 20$. The units of b_i are kg krill/trip; that is, b_i is the maximum amount of krill available to the predator on each foraging trip. We set $b_i = i - .5$.

The i th biomass level occurs with frequency f_i , so that

$$\sum_{i=1}^{i_{\max}} f_i = 1 \quad (2)$$

and the average biomass per trip is

$$\sum_{i=1}^{i_{\max}} b_i f_i = 4.7 \text{ kg/trip} \quad (3)$$

3.2. The spatial distribution of krill

We assume that the spatial distribution of krill is determined by diffusion and advection (Okubo, 1980). We also assume that there is uncertainty in the timing of the arrival of krill.

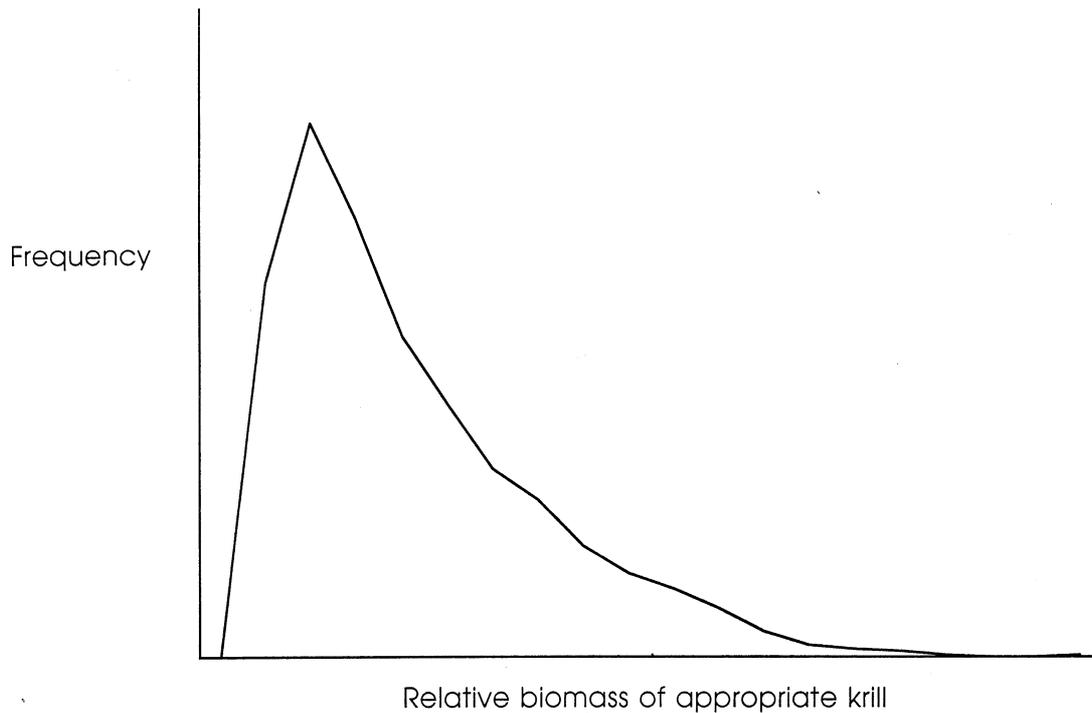


Fig. 1. Frequency distribution of krill biomass generated by the model of Butterworth et al. (1994). Because we focus on relative effects, it is sufficient to use scaled values for the biomass. See Table 2 for numerical values.

We set

$$k(t, x|x_0)$$

= density of appropriate krill at distance x from the colony on day t in the season, given that the peak of the density on day 0 occurs at distance x_0 from the colony (4)

The advection–diffusion description means that one choice of functional form for $k(t, x|x_0)$ is

$$k(t, x|x_0) = \frac{1}{\sqrt{2\pi\sigma_k^2}} \exp\left(\frac{-(x - x_0 - v_k t)^2}{2\sigma_k^2}\right) \quad (5)$$

Note that at $t = 0$, $k(x, 0|x_0)$ is a Gaussian distribution centered at x_0 (hence the diffusion description) and that for $t > 0$ the shape of the distribution is maintained but that the center is located at $x_0 + v_k t$ (hence the advection description)

We allow three values of $x_0 = 50, 90$ or 130 , corresponding to early, normal or late arrival of

krill, and assume that each of these is equally likely with probability $1/3$. We also assume that $v_k < 0$, so that advection causes krill to move towards the breeding colony (R. Hewitt, personal communication).

Combining Eqs. (1) and (5), the relative biomass of appropriate krill at distance x from the colony on day t is $b_i k(t, x|x_0)$ with probability $f_i/3$, for $x_0 = 50, 90$ or 130 (for simplicity, we index these by $m = 1-3$) and $i = 1-i_{\max}$.

3.3. The effect of fishing on the distribution of krill

We let $k_f(t, x|x_0)$ denote the density of appropriate krill at distance x and day t , given x_0 , when fishing occurs (Table 2). Suppose that fishing starts on day t_f . Then for days previous to and including t_f

$$k_f(t, x|x_0) = k(t, x|x_0) \quad (6)$$

Table 1
Symbols and their interpretation for the krill distributional model

Symbol in text	Interpretation	Base case value
b_i	i th level of krill biomass from the krill population simulation	
f_i	Frequency of the i th level of biomass	
x_0	Location of the peak of the krill distribution on day 1 of the breeding season	
$k(t, x x_0(m))$	Density of appropriate krill on day t in the breeding season in the absence of fishing at location x when arrival timing is category m	
v_k	Krill speed	−1.75
σ_k	Standard deviation of krill distribution function	50
x_{\max}	Maximum spatial extent considered in the model	200

We assume that the fishing fleet estimates the relative biomass of appropriate krill (e.g. from surveys; Butterworth et al., 1994). The fleet approaches the colony from the large x direction, and begins to fish when the relative biomass of appropriate krill exceeds a threshold level B_{\min} (Butterworth, 1989; Mangel, 1989). In particular, if the biomass in a particular year is b_i , the threshold level is

$$B_{\min} = k_s b_i k_{\max} \tag{7}$$

where k_s is the fraction of maximum relative krill biomass required for fishing to start and k_{\max} is the maximum value of $k(t, x|x_0)$, so that $b_i k_{\max}$ is the maximum value of appropriate krill in a year when the biomass level is b_i . Fishing continues at a certain spot until a stopping biomass B_{stop} is reached. We set

$$B_{\text{stop}} = k_q b_i k_{\max} \tag{8}$$

where k_q is the fraction of the maximum relative biomass at which point fishing stops because it is no longer economical. The catch by the fishing vessels will depend upon the timing of krill arrival and by the relative biomass of krill. Hence we set

$$C_{m,i} = \text{total krill catch of the fleet when the arrival is } x_0(m) \text{ and biomass is } b_i \tag{9}$$

The location of the fishing fleet at the first day, t_f , of fishing is determined as the largest value of x that satisfies Eq. (7). At this time, the total biomass of appropriate krill, which also depends upon i and m , is

$$K_{m,i} = \sum_{x=1}^{x_{\max}} b_i k_f(t_f, x|x_0) \tag{10}$$

Fishing includes with a daily harvest limit and a maximum quota determined from a limit on fishing mortality. The harvest on day t , $H(t)$, is the minimum of the capacity of the krill vessels (c_v) and the biomass of appropriate krill that is available at the location of the fleet

$$H(t) = \min(c_v, b_i k_f(t, x_{\text{fleet}}|x_0)) \tag{11}$$

where $\min(A, B)$ denotes the minimum value of A and B .

The accumulated catch is updated according to

$$C(t) = C(t-1) + H(t) \tag{12}$$

We assume that a seasonal quota Q_s is imposed, so that $C(t)$ cannot exceed Q_s and that fishing reduces the density of appropriate krill at a certain point, but not the biomass intensity of the remaining krill. This situation can be viewed as krill aggregating into a large number of swarms in a region and the fleet removing individual swarms, but leaving the remaining swarms at identical density (Mangel, 1989). Thus, if the harvest is $H(t)$ when the biomass is b_i , after fishing the density of appropriate krill in location x_{fleet} is $k_f(t, x_{\text{fleet}}|x_0(m)) - H/b_i$.

Subsequent to fishing on a given day, the krill are transported by the physical flow. Since the only source of movement is advection, krill that are located at spatial point x on day t were located at spatial point $x - v_k$ on day $t - 1$. Consequently

$$k_f(t, x|x_0) = k_f(t-1, x - v_k|x_0) \tag{13}$$

Table 2
Symbols and their interpretation for the fishing model

Symbol in text	Interpretation	Base case value
$k_f(t, x x_0(m))$	Density of appropriate krill on day t in the breeding season when fishing occurs at location x when arrival timing is category m	
k_s	Fraction of maximum krill concentration at which the fleet will start fishing on krill	0.15
k_q	Fraction of maximum krill concentration at which the fleet will stop fishing krill in that location	0
S	Length of the fishing season	30
t_f	Day the fleet starts fishing	10
x_c	The distance of closest approach of the fleet to the colonies	6
k_{dmax}	Maximum fishing mortality	0.15
B_{min}	Minimum relative biomass of krill needed before the fleet starts fishing	
k_{max}	Maximum value (over space and time) of the density of appropriate krill	
B_{stop}	Value of relative biomass at which fishing in a particular location stops	
$C_{m,i}(t)$	Total krill catch of the fleet up to day t when the arrival is $x_0(m)$ and biomass is b_i	
x_{fleet}	Spatial location of the fleet	
$K_{m,i}$	Total biomass of appropriate krill at the time that fishing commences	
$H(t)$	Harvest of krill by the fleet on day t .	
c_v	Daily capacity of the fleet 10	
v_{fleet}	Nominal movement (km/day) of the fleet after fishing	-1
Q_s	Seasonal quota on krill harvest	100000
x_{ice}	Location of the ice edge	4

After the krill are moved, the fishing fleet moves. The fleet is assumed to move v_{fleet} km towards the breeding colony, unless the biomass of appropriate krill at the new location is less than B_{min} . If that happens, the fleet continues to move towards the colony until the biomass of appropriate krill exceeds B_{min} .

Fishing stops if: (i) the fishing season length has been met; (ii) the seasonal quota Q_s is reached; (iii) fishing mortality has reached the maximum limit (i.e. another form of the quota); or (iv) the fleet has reached the distance of closest approach.

After the fishing season ends, the spatial distribution of krill is updated (using Eq. (13)) and the breeding model continues until the offspring fledge.

3.4. Breeding model

3.4.1. Offspring requirements

The model focuses on parental foraging to meet offspring requirements for growth of a single

chick, as described by Culik (1994), who provides the daily requirements of an offspring as a function of age. Following Culik, we assume that Adelie fledge their young at 54 days and define (Table 3)

$r(s)$ = daily requirement of a penguin offspring of age s

$F(s)$ = cumulative requirement of a penguin offspring up to day s (14)

Variations in krill availability will interact with breeding effort by an inability to meet the cumulative requirement. We assume that if on any day the total delivered krill falls below a critical value of the cumulative requirement (60% in our runs), the offspring dies (Fig. 2).

3.4.2. Krill deficits

The timing of the events during the breeding cycle is given in Fig. 3. We measure the state of the parents and offspring in terms of the krill

Table 3
Symbols and their interpretation for the penguin breeding model

Symbol in text	Interpretation	Base case value
τ_p	Time at which incubation starts	
τ_h	Time from the start of nest building to hatching	
τ_{pn}	Time from start of nest-building to start of incubation	10
τ_n	Length of incubation period days	34
S_f	Age at fledging	54
s_{creche}	Age at which creching begins	25
$r(s)$	Daily requirement of a penguin offspring of age s	
K_p	Parental daily requirement of krill (kg)	1
K_e	Maximum amount of krill a parent can catch and/or carry in one day	1000
$F(s)$	Cumulative requirement of a penguin offspring up to day s	
$D_p(t)$	Parental deficit at time t between the time of arrival on the breeding grounds and incubation	
$D_{n1}(t)$ or $D_{n2}(t)$	Deficit of parent $j = '1'$ or $'2'$ at time t during incubation	
$D_1(s)$ or $D_2(s)$	Deficit of parent $j = '1'$ or $'2'$ at time t while feeding offspring	
$D_{off}(s)$	Offspring deficit when the offspring is age s	
x^*	Distance from the colony containing the maximum density of appropriate krill	
$k^*(t, x^* x_0(m))$	Density of krill at x^*	
x_{def}	Distance from the colony (if such a distance exists) at which the deficit can be eliminated	
-	Length of incubation shift $q = 1, 2,$ or 3	14, 14, 6
S_{f1} or S_{f2}	Total number of days that parent 1 or 2 spent at sea during the incubation period	
T_{s1} or T_{s2}	Time in hours that parent 1 or 2 spent at sea during the incubation period	
x_{feed}	Distance from the colony at which the parent actually feeds	
E_{krill}	Krill amount that exceeds the daily need of parent and offspring	
E_{off}	Amount of excess krill applied toward offspring's deficit	
g_o	Maximum percentage of offspring's daily need given to offspring if parent and/or offspring deficits will increase	0.9
G_{off}	Amount of krill given to offspring if parent and/or offspring deficits will increase	
\max_r	Maximum range that an adult penguin can travel in 12 h	25
d_c	Critical deficit level of offspring	0.4
μ_p	Accumulated parental mortality	
$\mu_1(s)$ or $\mu_2(s)$	Accumulated mortality of parent 1 or 2 when the offspring is age s	
m_p	Mortality rate of parents while foraging	0
$\sigma_1(i, m, \tau_p)$ or $\sigma_2(i, m, \tau_p)$	Seasonal survival of parent 1 or 2 when krill biomass is b_i , arrival timing is $x_0(m)$ and breeding starts at τ_p	
$\sigma_{off}(i, m, \tau_p)$	Seasonal survival of the offspring when krill biomass is b_i , arrival timing is $x_0(m)$ and breeding starts at τ_p	
x_{off}	Parameter characterizing between season offspring mortality	0.16
x_p	Parameter characterizing between season parental mortality	0.03
m_m	Mortality multiplier for parents	0.01
m_{moff}	Mortality multiplier for offspring	0.16
ERS (τ_p)	Expected survival of offspring with breeding time breed (τ_p)	
$S_{parent}(\tau_p)$	Expected survival of parent with breeding time breed (τ_p)	

deficit at all points in the breeding cycle (Table 3). The offspring deficit is determined by the difference between deliveries of krill by the parents and the offspring requirements given by Culik (1994). During the pre-breeding and incubation periods, parental deficit is determined by the difference between the daily needs of the parents and

krill that they are able to find and consume for themselves. During the pre-creching and creching periods, the parental deficit is determined by the difference between the daily needs of the parents and the krill that they are able to find and use to either provision offspring or consume themselves. We assume that the deficits may never be nega-

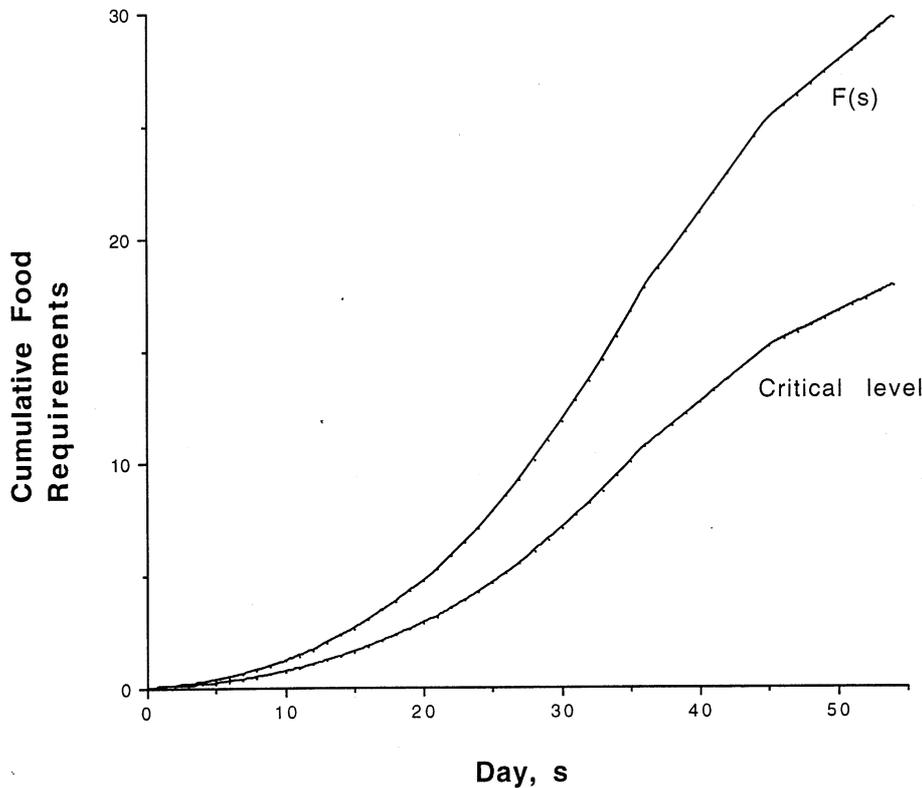


Fig. 2. The cumulative offspring requirements (kg of krill), from Culik (1994), as a function of offspring age. We also show the critical level, which in our runs is 60% of the cumulative requirement. If the krill delivery falls below the critical level, the offspring dies.

tive. That is, neither parents nor offspring may accumulate reserves relative to their krill requirements. This is easily changed, should it be desired, but provides the most conservative approach.

We assume that parents arrive at the breeding colony with deficits equal to zero. In principle, breeding initiation could be a facultative behavior, depending upon the level of parental deficit. To avoid this level of complexity in the model, we allow only three breeding options: adults initiate the breeding (described below in detail) at $\tau_p = 1$ (early breeding); at $\tau_p = 10$ (late breeding); or do not breed ($\tau_p = -1$). We then compute expected offspring survival for the early and late breeding options and expected parental survival for all three breeding options. Our choice is a compromise that allows us to consider some variation in

breeding, including not breeding, without the additional complexity of an optimization step concerning initiation of breeding. Similarly, although each foraging trip consists of many dives (Chappell et al., 1993b), as a simplification, we do not consider behavior at the level of the individual dive.

We assume that before incubation starts both parents have identical states, so that a single variable can be used to index their deficit

$$D_p(t) = \text{parental deficit at time } t \text{ between the time of arrival on the breeding grounds and offspring hatching} \quad (15)$$

Once incubation begins, because parents alternate time at sea with time at the nest (Fig. 3), we require state variables for each parent,

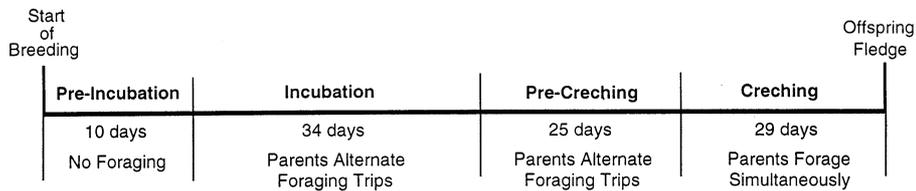


Fig. 3. The time line for a breeding penguin pair, once the breeding period starts. The name of the particular period is above the line; the corresponding length and parental foraging pattern of that period are below the line. The breeding pattern and period lengths are from Ainley et al. (1983), Lishman (1985b), Davis and Miller (1990). Superimposed upon this time line is that of the fishing fleet, which begins fishing on day t_f and fishes until the quota is reached or the season length is reached. During the incubation and pre-creching periods, parents alternate and make one trip per day; during creching both parents make one trip per day, so that the offspring receive the resources of two trips per day.

$D_{n1}(t)$ = deficit of parent ‘1’ at time t during incubation

$D_{n2}(t)$ = deficit of parent ‘2’ at time t during incubation (16)

and similarly, after hatching the parental deficits are

$D_1(t)$ = deficit of parent ‘1’ at time t after hatching

$D_2(t)$ = deficit of parent ‘2’ at time t after hatching (17)

The deficits given by Eqs. (15)–(17) are linked; for example, $D_{n1}(t)$ at the end of incubation is $D_1(t)$ at the beginning of feeding the offspring.

Parental reproductive success is measured by offspring survival. It, and parental survival, will depend upon foraging behavior (described below), timing of breeding, and the availability of krill. Thus, seasonal survival of parents is a function of the indices of biomass (i), arrival timing (m) and breeding initiation (τ_p). We denote them by

$\sigma_1(i, m, \tau_p)$ = seasonal survival of parent ‘1’ when krill biomass is b_i , arrival timing is $x_0(m)$ and breeding starts at τ_p

$\sigma_2(i, m, \tau_p)$ = seasonal survival of parent ‘2’ when krill biomass is b_i , arrival timing is $x_0(m)$ and breeding starts at τ_p (18)

Parental survival is computed from mortality that is accumulated during the course of incubation and foraging

$\mu_p(t)$ = accumulated parental mortality through day t (19)

For offspring, a deficit may accumulate during the pre-creching and creching period, when offspring are being fed. The deficit state variable for offspring is

$D_{off}(s)$ = offspring deficit at age s (20)

As described above, if $D_{off}(s)$ exceeds a critical percentage ($d_c = 0.4$) of $F(s)$, then the offspring is dead. As with, parental survival (Eq. (18)), offspring survival is described by

$\sigma_{off}(i, m, \tau_p)$ = seasonal survival of the offspring when krill biomass is b_i , arrival timing is $x_0(m)$ and breeding starts at τ_p . (21)

3.4.3. Foraging behavior

There is a pre-breeding period, during which the parents each have a daily krill requirement of K_p . During this period, they both feed and may reduce their deficits. We use simple allocation rules to describe the foraging behavior of the parents, who are assumed to swim out to the foraging location and then start hunting (Chappell et al., 1993a,b). They seek the spatial location that either eliminates the current krill deficit or, if there is no such place, they feed at the location with the maximum density of appropriate krill. To implement this behavior in the model, we search over distances from the ice edge to the maximum foraging range of the individual and determine the value of x , denoted by x^* , that has

maximum krill density. The density of krill at this point is denoted by $k^*(t, x^*|x_0)$. Next, we determine the closest spatial distance, x_{def} , that eliminates the parental deficit. This location satisfies the condition

$$b_i k(t, x_{\text{def}}|x_0) \geq K_p + D_p(t-1) \quad (22)$$

If there is a point closer than x^* that eliminates the deficit, the parents feed at that location and we set the feeding location $x_{\text{feed}} = x_{\text{def}}$. Otherwise the feeding location is $x_{\text{feed}} = x^*$. The parental deficit is updated according to

$$D_p(t) = D_p(t-1) + K_p - \min(K_e, b_i k^*(t, x_{\text{feed}}|x_0(m))) \quad (23)$$

where K_e is the maximum amount of krill a parent can catch and/or hold in one day. In our runs, we set K_e very large, to effectively eliminate the constraint. Future investigations, however, could easily explore the effect of K_e .

When the parents are feeding, they are subject to a mortality rate (e.g. from leopard seals) m_p . We assume that the maximum range \max_r corresponds to a foraging time of 12 h, so the foraging speed is $\max_r/12$. Consequently, a parent that forages at location x_{feed} is at sea for $x_{\text{feed}}/\max_r/12 = 12x_{\text{feed}}/\max_r$ h and its accumulated mortality is updated according to

$$\mu_p(t) = \mu_p(t-1) + m_p \frac{12x_{\text{feed}}}{\max_r} \quad (24)$$

If the parents do not breed ($\tau_p = -1$), we assume that they continue feeding and accumulating mortality as described in Eqs. (22)–(24). To compare with the breeding options (Fig. 3), at the end of the breeding season, we compute parental survival according to

$$\begin{aligned} \sigma_1(i, m, -1) &= \exp\{-m_m D_p(98) - x_p - \mu_1(98)\} \\ \sigma_2(i, m, -1) &= \exp\{-m_m D_p(98) - x_p - \mu_2(98)\} \end{aligned} \quad (25)$$

Eq. (25) gives the maximum parental survival when krill biomass is i and arrival timing is m because there is no parental effort on breeding ($\tau_p = -1$). This equation also shows how the parental deficit $D_p(98)$, background mortality (x_p)

and foraging mortality $\mu_i(98)$ affect overall parental survival. Note that we assume that log-survival is a linear function of the three sources of mortality. The parameters m_m and x_p measure the intensity of the deficit-dependent and deficit-independent sources of mortality, respectively. These two parameters may be empirically determined in the future through a combination of banding and physiological measurement. The pre-breeding period lasts τ_p days.

For parents that choose to breed, there is a period of length τ_p days prior to offspring hatching. This is further divided into pre-incubation (τ_{pn}) and incubation (τ_n) periods, such that $\tau_{pn} + \tau_n = \tau_h$ (Fig. 3).

With no foraging during the pre-incubation period (Fig. 3), parents accumulate a deficit, so that at the beginning of the incubation period ($\tau = \tau_p + \tau_{pn}$), their deficits are

$$D_p(\tau_p + \tau_{pn}) = \tau_{pn} K_p + D_p(\tau_p) \quad (26)$$

The incubation period consists of τ_n days, which we have divided into three extended incubation shifts (Davis and Miller, 1990). During each shift, one parent is foraging while the other is incubating and accumulating a deficit. Consequently, the deficits and accumulated mortality must be kept separately for each parent. Thus, the starting deficit values, following Eqs. (16) and (23), are

$$D_{n1}(\tau_p + \tau_{pn}) = D_{n2}(\tau_p + \tau_{pn}) = D_p(\tau_p + \tau_{pn}) \quad (27)$$

These separate deficits are maintained through the remainder of the breeding period.

We assume that because of the extended nature of the shifts, the foraging parent will remain at sea and not return until the end of the shift (Davis and Miller, 1990). Therefore, foraging and accumulated mortality during the incubation period follows Eqs. (22)–(24), with one important difference. Because the parent remains at sea during a shift, it may travel much further to forage than if returning to the colony each day. Thus, we allow the parent to travel up to $2\max_r$ from its current position each day, in either direction, subject to two range constraints. The first constraint is the ice edge. The second constraint is the maximum distance the individual can travel in the time remaining in the shift; this constraint exists since

the individual must be able to reach the breeding colony by the end of the shift.

The mortality that each parent accumulates during the incubation period depends on the mortality rate, m_p , and the amount of time they were foraging at sea during the incubation period. If S_{f1} and S_{f2} are the total foraging days during incubation by their partner for parent 1 and 2, respectively, the total times at sea (in hours) are

$$T_{s1} = 24S_{f1} \quad T_{s2} = 24S_{f2} \quad (28)$$

The accumulated mortality at hatching of the young are therefore

$$\mu_1(1) = \mu_p(\tau_p) + m_p T_{s1} \quad \mu_2(1) = \mu_p(\tau_p) + m_p T_{s2} \quad (29)$$

since no foraging takes place during the pre-incubation period.

Once the offspring hatch, it is helpful to think of two measures of time. The first is offspring age, which we denote by s and which ranges from 1 to 54 (at which time fledging occurs). The second is calendar time, t , which determines the dynamics of krill movement, and is related to offspring age by

$$t = s + \tau_p + \tau_h \quad (30)$$

At hatching ($s = 1$), the offspring deficit is zero, so that

$$D_{\text{off}}(1) = 0 \text{ and } D_1(1) = D_{n1}(\tau_p + \tau_h)$$

$$D_2(1) = D_{n2}(\tau_p + \tau_h) \quad (31)$$

After hatching, the feeding period begins. This consists of two parts. From $s = 1$ until creching (day 25; Fig. 3), parents alternate duty cycles of foraging and nest time, so that parent '1' forages on odd days and parent '2' forages on even days (Trivelpiece et al., 1987). When creching starts, both parents feed every day (Lishman, 1985a,b).

The foraging dynamics of either parent while feeding the offspring are similar to Eqs. (22) and (23). The determination of x^* is the same. The determination of x_{def} is different, because now both parent and offspring deficits must be cleared. Hence, using parent 1 for example, x_{def} satisfies

$$b_i k(t, x_{\text{def}} | x_0) = K_p + r(s) + D_1(s) + D_{\text{off}}(s) \quad (32)$$

where t is given by Eq. (30).

Once x^* and x_{def} are found, we update the deficits. There are four cases, according to the amount of krill found relative to the parent and offspring's daily need and deficits. The first case is the simplest, when a location exists so that the deficits and daily need for both parent and offspring can be completely satisfied (given the constraint, K_e). Therefore, considering the odd days when parent 1 is foraging,

$$D_{\text{off}}(s) = 0 \quad (33)$$

The situation for the parent is slightly more complicated. If the capacity constraint is not binding, so that K_e exceeds $D_1(s-1) + D_{\text{off}}(s-1) + r(s-1) + K_p$, the parent deficit is reset to 0

$$D_1(s) = 0 \quad (34a)$$

On the other hand, if K_e is less than the combination of deficits and requirements, then the parent deficit cannot be reset to 0 because the parent cannot handle all the krill needed to meet the requirements and reset the deficit. In that case

$$D_1(s) = D_1(s-1) + K_p - \min(K_e, b_i k^*(t, x_{\text{feed}} | x_0(m)) - D_{\text{off}}(s)) \quad (34b)$$

as in Eq. (23), with the modification of subtracting the krill given to the offspring from the krill available to the parent.

In the other three cases, the krill biomass is not sufficient to satisfy the parent and offspring daily need and deficit. We assume that if $b_i k(t, x^* | x_0) = K_p + r(s)$ (i.e. enough krill is found to eliminate the daily requirement of both the parent and the offspring), the krill is applied to the daily need and the deficits remain the same, so that

$$D_1(s) = D_1(s-1) \text{ and } D_{\text{off}}(s) = D_{\text{off}}(s-1) \quad (35)$$

The remaining two cases require assumptions about how the krill are allocated between the parent and the offspring; for these we use rules of thumb, rather than compute optimal allocations according to a dynamic state variable model (Mangel and Clark, 1988; Mangel and Ludwig, 1992). For the third case, where

$$K_p + r(s) < b_i k(t, x^* | x_0) < K_p + r(s) + D_1(s) + D_{\text{off}}(s) \quad (36)$$

some krill may be applied towards the deficits of the offspring and parent. The excess krill, E_{krill} , that remains after meeting daily requirements is

$$E_{krill} = \min(K_e, b_i k(t, x^* | x_0) - (K_p + r(s))) \quad (37)$$

We assume that the parents apply as much of the excess krill as they can toward eliminating the offspring's deficit and daily need first. The amount they give the offspring (E_{off}) is

$$E_{off} = \min(E_{krill}, D_{off}(s - 1)) \quad (38)$$

and the offspring's deficit is reduced, so that

$$D_{off}(s) = D_{off}(s - 1) - E_{off} \quad (39)$$

If $E_{off} < E_{krill}$, then the parents can apply the remainder of the excess krill to its deficit and daily need, such that the parent's updated deficit becomes

$$D_1(s) = D_1(s - 1) - (E_{krill} - E_{off}) \quad (40)$$

For the fourth krill allocation case,

$$b_i k(t, x^* | x_0) < K_p + r(s) \quad (41)$$

so that the offspring and parental deficits must both increase. We assume that if the krill found is less than a certain fraction, g_o , of the offspring's daily need $r(s)$, then all the krill is given to the offspring. If the krill found exceeds $g_o r(s)$, then the parent gives $g_o r(s)$ of the krill found to the offspring and keeps the remainder for itself. Thus, the amount of krill given to the offspring is

$$G_{off} = \min(g_o r(s), b_i k(t, x^* | x_0)) \quad (42)$$

and the deficits of the offspring and parent are updated according to

$$D_{off}(s) = D_{off}(s - 1) + r(s) - G_{off}$$

$$D_1(s) = D_1(s - 1) + K_p - (b_i k(t, x^* | x_0(m)) - G_{off}) \quad (43)$$

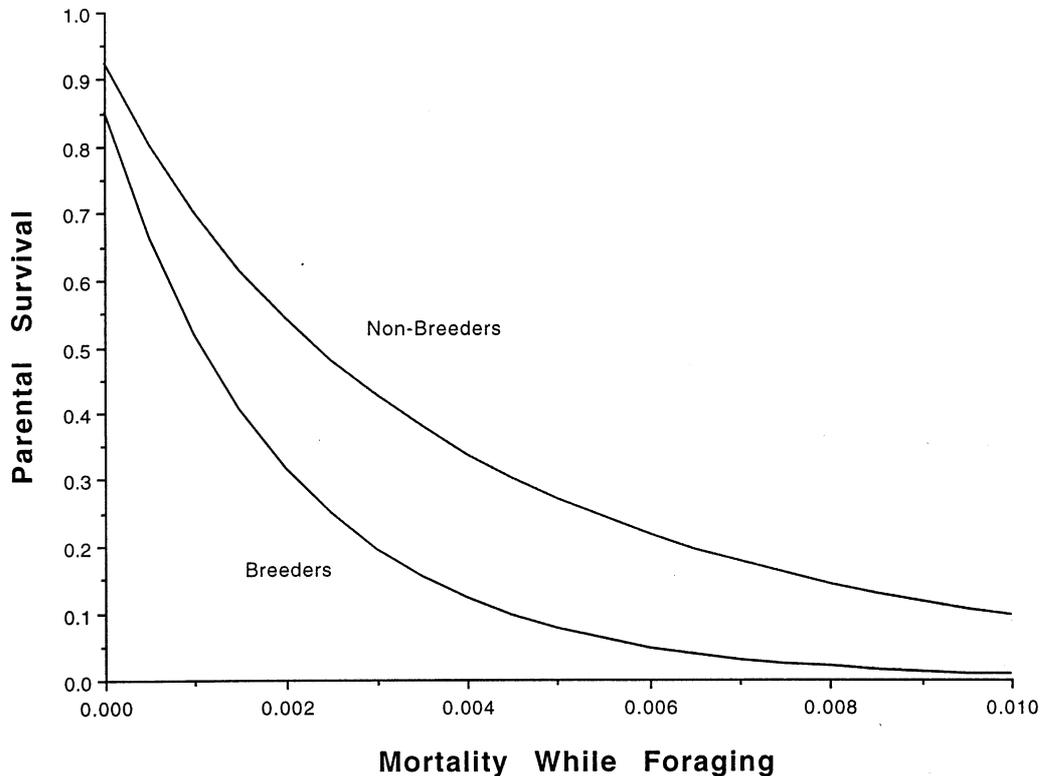


Fig. 4. Parental survival declines with increasing mortality while foraging.

As before, the parent accumulates mortality while foraging, so that in analogy to Eq. (24)

$$\mu_1(s) = \mu_1(s - 1) + m_p \left(\frac{12x_{\text{feed}}}{\max_r} \right) \quad (44)$$

During the pre-creching period, while one parent is foraging, the other parent is at the nest site and unable to forage, so its deficit increases by the adult daily requirement

$$D_2(s) = D_2(s - 1) + K_p \quad (45)$$

On even days, parent 2 forages and feeds the offspring according to Eqs. (32)–(34) and (34b)–(44) and parent 1's deficit is updated as defined in Eq. (45).

When $s = s_{\text{creche}}$, the offspring joins a creche and both parents forage at the same time. The foraging process is similar to Eqs. (32)–(34b) except that we assume that with both parents foraging, twice the amount of krill can be captured and the daily needs and deficits of both

parents become relevant. Therefore, Eq. (32) becomes

$$2b_7k(t, x_{\text{def}}|x_0) = 2K_p + r(s) + D_1(s) + D_2(s) + D_{\text{off}}(s) \quad (46)$$

and each of the four cases of krill allocation (Eqs. (32)–(34) Eq. (34b) Eqs. (35)–(43)) incorporates the double foraging catch ($2b_7k(t, x_{\text{def}}|x_0)$) and the daily needs and deficits of both parents. The same rules of thumb apply for allocating krill to the offspring, and any krill remaining after feeding the offspring is split equally between the two parents. Each parent accumulates mortality according to Eq. (44) during the creching stage.

If the offspring dies at any point between hatching and fledging, the parents forage simultaneously. We assume that the foraging behavior, deficit updates, and mortality accumulation for these parents follow that of parents with a

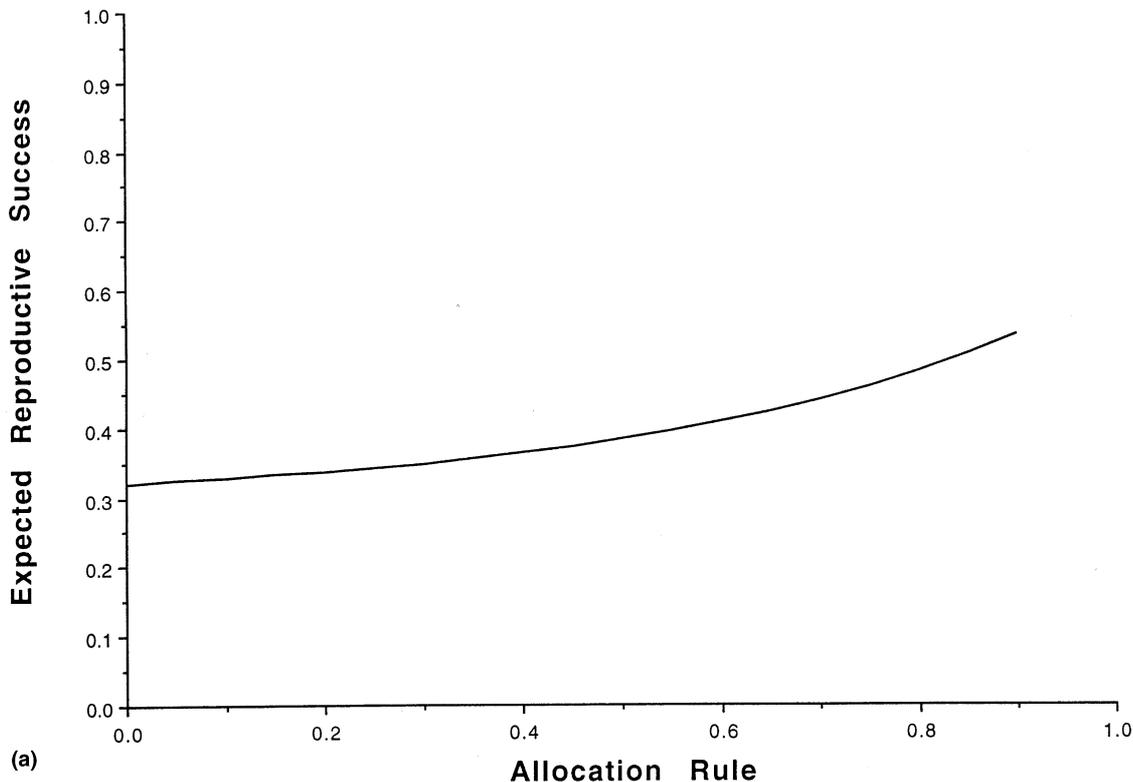


Fig. 5. The rule for the allocation g_o of krill given to offspring in times of low krill abundance has a gradual and relatively linear effect on expected reproductive success (panel a) and parental survival (panel b).

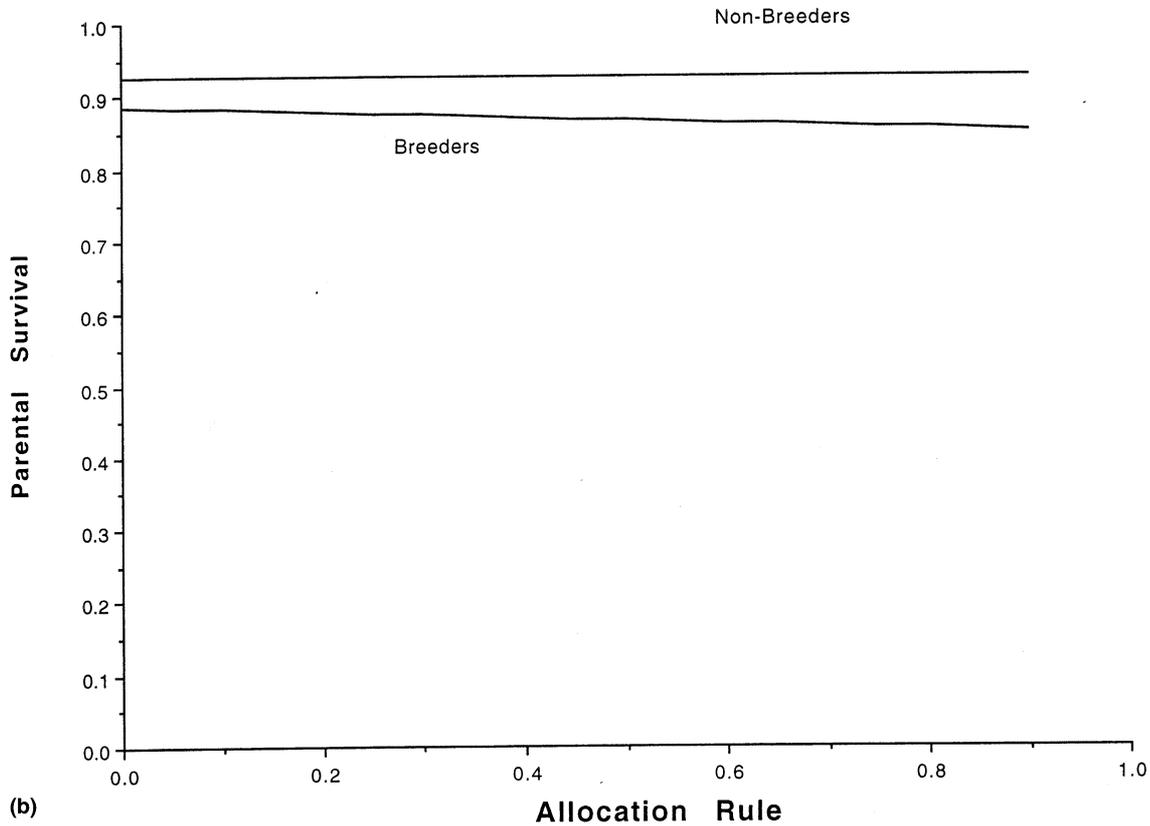


Fig. 5. (Continued).

offspring in a creche, without the need to feed an offspring.

The offspring dies if at any time before day 54 its deficit exceeds 40% of its accumulated requirement. Otherwise, it fledges on day 54, with a maximum probability of survival of 77% (Trivelpiece et al., 1987). The deficit further decreases offspring survival. Assuming a log-linear relationship between deficit and survival, we have

$$\begin{aligned} \sigma_{\text{off}}(i, m, \tau_p) &= 0 \text{ if } D_{\text{off}}(s) > 0.4F(s) \text{ for any } s \\ \sigma_{\text{off}}(i, m, \tau_p) &= 0.77 \exp(-m_{\text{moff}}D_{\text{off}}(54) - x_{\text{off}}) \\ &\quad \text{otherwise} \end{aligned} \tag{47}$$

where m_{moff} is the mortality per unit krill deficit for an offspring and x_{off} is the additional between-year mortality constant for an offspring.

The parental survival functions are analogous to Eq. (25)

$$\begin{aligned} \sigma_1(i, m, \tau_p) &= \exp(-m_m D_1(54) - x_p - \mu_1(54)) \\ \sigma_2(i, m, \tau_p) &= \exp(-m_m D_2(54) - x_p - \mu_2(54)) \end{aligned} \tag{48}$$

At the end of the breeding period, the offspring and adult survival are calculated for each krill biomass level i , krill arrival m , and breeding time τ_p . Since we use 20 biomass levels, 3 arrival timings, and 3 breeding strategies, there are 180 possible combinations of krill biomass, timing and breeding strategy. For ease of presentation, and since we are generally interested in relative comparisons, we consider average reproductive success and parental survival. In particular, the expected reproductive success, $\text{ERS}(\tau_p)$ for is the average over biomass levels and arrival times, according to

$$\text{ERS}(\tau_p) = \sum_{i=1}^{i_{\text{max}}} \sum_{m=1}^3 \frac{\sigma_{\text{off}}(i, m, t) f_i}{3} \tag{49}$$

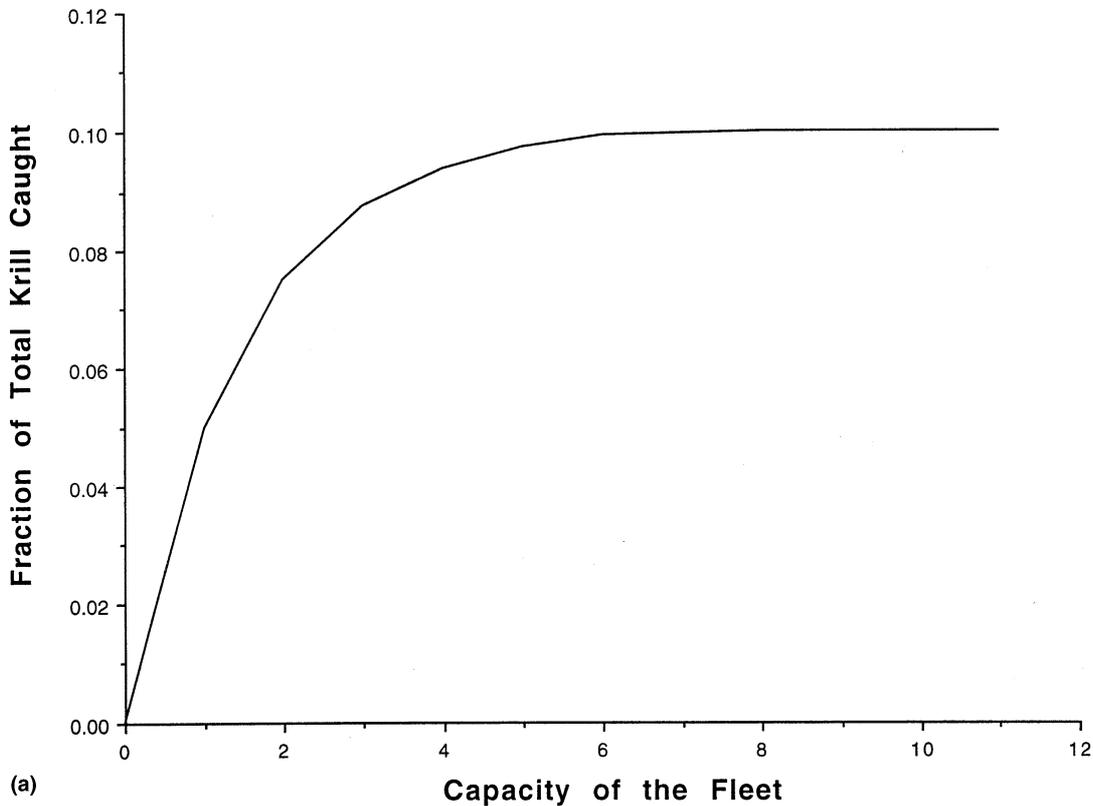


Fig. 6. The fraction of krill caught increases with daily capacity of the fleet (panel a) and the length of the season (panel b), and decreases with the day that fishing begins (panel c, for a season length of 30 and capacity of 10; a similar result—with slightly larger fractions captured—is obtained for a season of length 50). Of these factors, the day that fishing begins had the smallest total effect over the varied range.

since each krill biomass level i occurs with frequency f_i and each krill arrival m occurs with frequency $1/3$.

Expected parental survival is calculated similarly. For simplicity, we use a single number that is the average of the two parents' survival

$$S_{\text{parent}}(\tau) = \sum_{i=1}^{i_{\text{max}}} \sum_{m=1}^3 \frac{1/2(\sigma_1(i, m, \tau)f_i + \sigma_2(i, m, \tau)f_i)}{3} \quad (50)$$

4. The indirect of a krill fishery

When the fishery is included, the penguin foraging and breeding proceeds according to Eqs. (14)–(34) and (34b) Eqs. (35)–(50), with the dif-

ference that the krill distribution in these equations is given by $k_f(t, x|x_0)$ instead of $k(t, x|x_0)$.

5. Results

We begin with a sensitivity analysis of the model without fishing to pick values for the parameters in the breeding model. Then we consider the indirect effects of fishing on penguin survival and reproduction. Because parental survival and expected reproductive success of the late breeding strategy was always intermediate to the survivals and successes of the early breeding ($\tau_p = 1$) and no breeding ($\tau_p = -1$) strategies, we simplify the presentation by only comparing the results for early and no breeding.

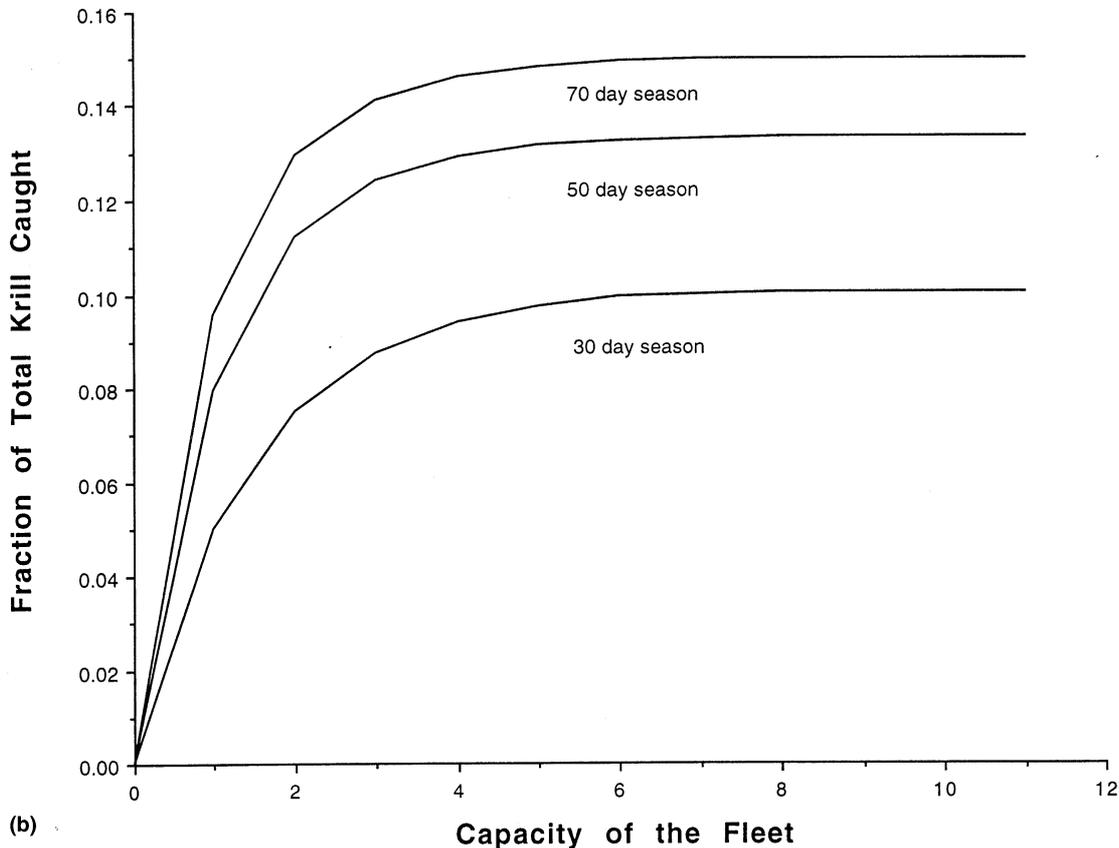


Fig. 6. (Continued).

5.1. Sensitivity analysis of the breeding model

For simplicity of presentation, we group the results concerning different parameter values. When studying the effect of varying one parameter, all others are kept at the baseline values described in the appropriate tables. For simplicity, we refer to all adults (breeders and non-breeders) as parents, understanding that non-breeders are potential parents.

We chose parameters so that the solution of the Euler–Lotka equation for population growth rate was $r = 0.01$, corresponding to a growth rate of about 1% per year or 10% per cohort.

5.1.1. The roles of x_p , x_{off} , m_m and m_{moff}

The parameters x_p and x_{off} have no effect on reproductive success and parental survival respec-

tively but parental survival depends upon x_p and expected reproductive success on x_{off} . We chose $x_p = 0.03$, $x_{off} = 0.16$, $m_m = 0.01$ and $m_{moff} = 0.16$.

5.1.2. The role of m_p

As with x_p , this parameter has no effect on expected reproductive success, but does influence parental survival (Fig. 4). We choose the value of $m_p = 0.001$ for analyses that included mortality while foraging (see below).

5.1.3. The allocation rule of thumb g_o

Both reproductive success and parental survival depend upon the allocation rule, but only weakly (Fig. 5).

In summary, the values used in the sensitivity analyses represent penguin breeding success in two cases, with predation and without predation. They

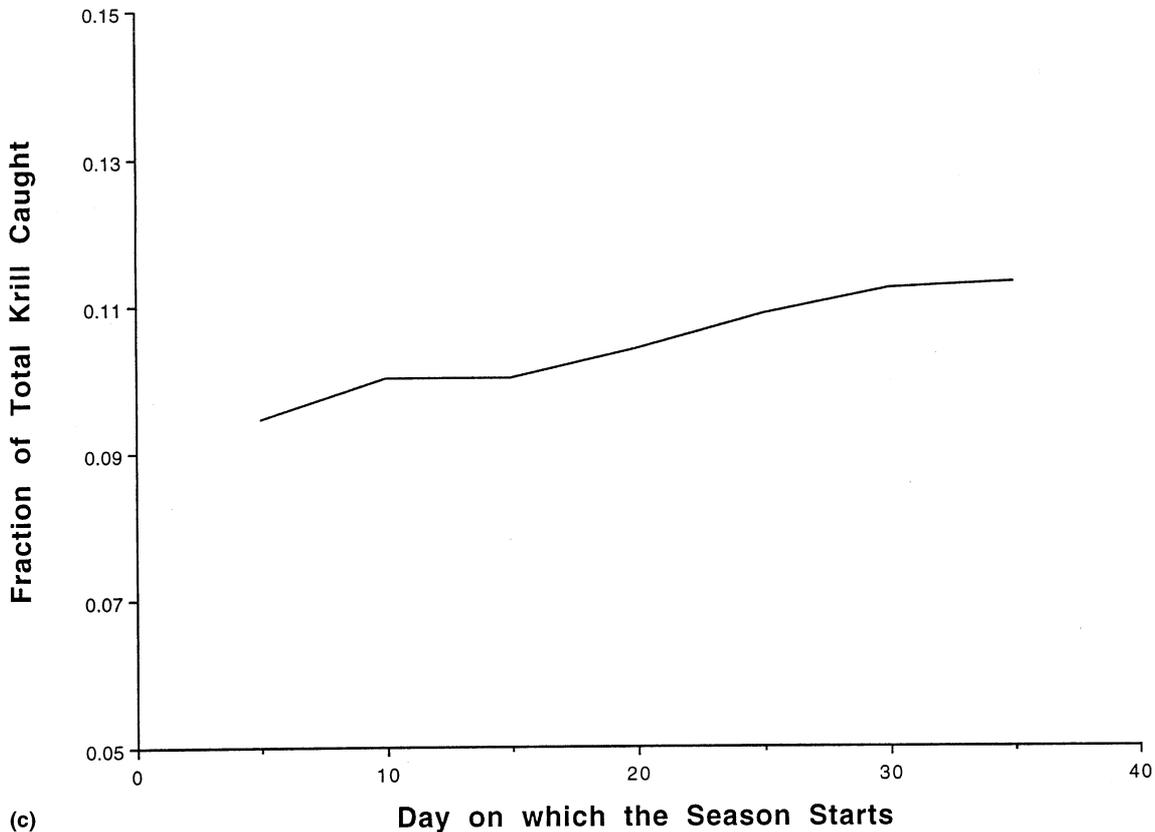


Fig. 6. (Continued).

therefore give us a baseline to compare the effects of a krill fishery on penguin breeding success. Parental survival is always highest without breeding and reproductive success is always highest with early breeding.

5.2. Sensitivity analysis of the fishing model

Krill mortality due to fishing is influenced by the capacity of the fleet, the start of the fishing season, and the length of the season. We assume a limit, k_{dmax} (0.15), on the fraction of available krill that may be harvested. As capacity increases, the total krill catch increases (Fig. 6a), and total catch is larger in longer seasons (Fig. 6b). However, total catch only depends weakly upon when the season starts (Fig. 6c).

5.3. The indirect effects of a fishery on reproductive success and survival

We now consider the effects of the krill fishery on expected reproductive success and parental survival. To do so, we use the relative measures

Relative reproductive success (RRS) =
$$\frac{\text{reproductive success in the presence of a fishery}}{\text{reproductive success in the absence of a fishery}}$$

Relative parental survival (RPS) =
$$\frac{\text{parental survival in the presence of a fishery}}{\text{parental survival in the absence of a fishery}} \quad (56)$$

Most of our results concentrate on the ‘best case’ analysis in which mortality while foraging $m_p = 0$.

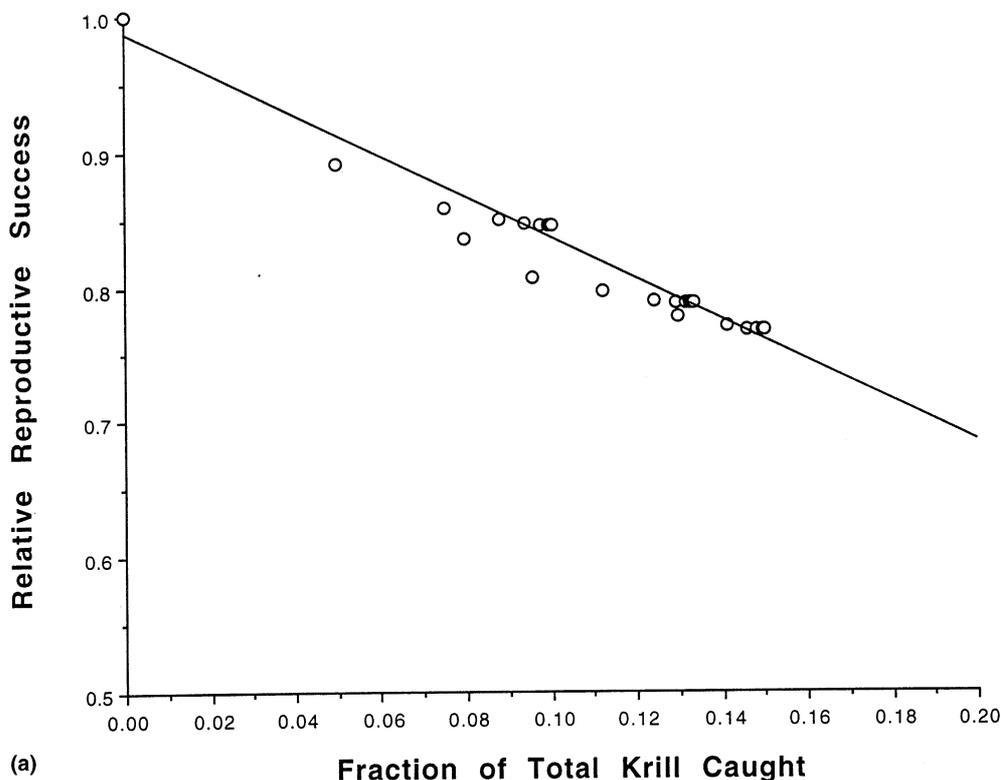


Fig. 7. Data obtained by varying fleet parameters can be combined into a regression for the relationships between relative reproductive success (panel a) and relative parental survival (panel b)

Both RRS and RPS decrease with increasing season length and increasing quotas. We varied these and then combined all of the data into a composite regression (Fig. 7). We find that relative reproductive success is

$$RRS = 1 - 1.51 (\text{fraction captured}) \tag{57}$$

and that the relative parental survivals for breeders and non-breeders are

$$RPS_b = 1 - 0.65 (\text{fraction captured})$$

$$RPS_{nb} = 1 - 0.49 (\text{fraction captured}) \tag{58}$$

When there is additional mortality during foraging (i.e. $m_p > 0$), parental survival decreases, regardless of whether the fishery operates or not. There is no effect on reproductive success, because of the structure of the model. We can summarize the effect in terms of the ratio of Relative Parental Survival with foraging mortal-

ity to that without (Fig. 8), using $m_p = 0.001$. The nonlinearity of these curves shows that there is an interaction between fishing pressure and foraging mortality on total survival.

6. Discussion

The linear terms in Eqs. (57) and (58) show that the relationship between krill harvest and life history measures is not 1:1. Reproductive success declines at a rate 50% greater than the rate at which krill are caught, but parental survival (breeder and non-breeders) declines at a rate less than that at which krill are caught.

The results in Fig. 8 suggest that krill harvest and mortality while foraging may interact in complex ways. When more is known about mortality rates at sea, it will be worthwhile to investigate this interaction in greater detail.

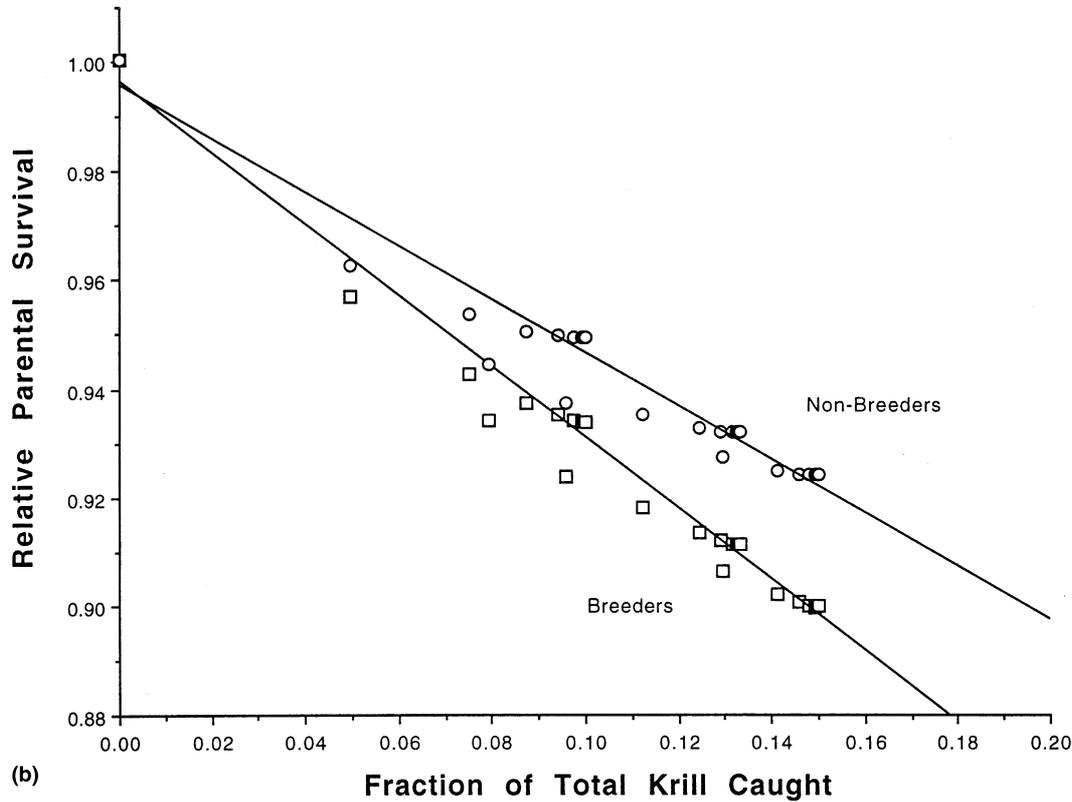


Fig. 7. (Continued).

There are three important directions for subsequent work. First, the one dimensional krill field can be replaced by a two dimensional krill field

$$k(t, x, y|x_0, y_0) = \text{density of appropriate krill at point } (x, y) \text{ from the colony on day } t \text{ in the season, given that the peak of the density on day 0 occurs at point } (x_0, y_0) \text{ from the colony} \quad (59)$$

By using a two dimensional field, we will be able to superimpose current structures that are measured by colleagues on the krill distribution. Two possibilities are Gaussian and Negative Binomial random fields as descriptions of the krill distribution. The first is a mixture of Gaussian distributions mixed across peak locations. The second is a version of the ‘patches-within-patches’ model that one of us developed some years ago (Mangel, 1989) in which certain spa-

tial points are foci for the initial location of krill swarms, which then have a negative binomial distribution around the foci. Once this is developed, colleagues will be able to import measured krill distributions and advection patterns from particular areas in the southern ocean and use the model to predict the indirect effects of krill fisheries on the predators.

Second, it is possible that post-fledging offspring mortality depends upon krill biomass. To take this into account, one could modify the second expression in Eq. (47) to

$$0.77 \exp\left(-m_{\text{off}}D_{\text{off}}(54) - x_{\text{off}} - \frac{q_b}{B}\right) \quad (60)$$

where B is krill biomass in the current season and q_b is a parameter connecting it to offspring post-fledging survival.

Third, one could add facultative fledging. Facultative fledging might occur, for example,

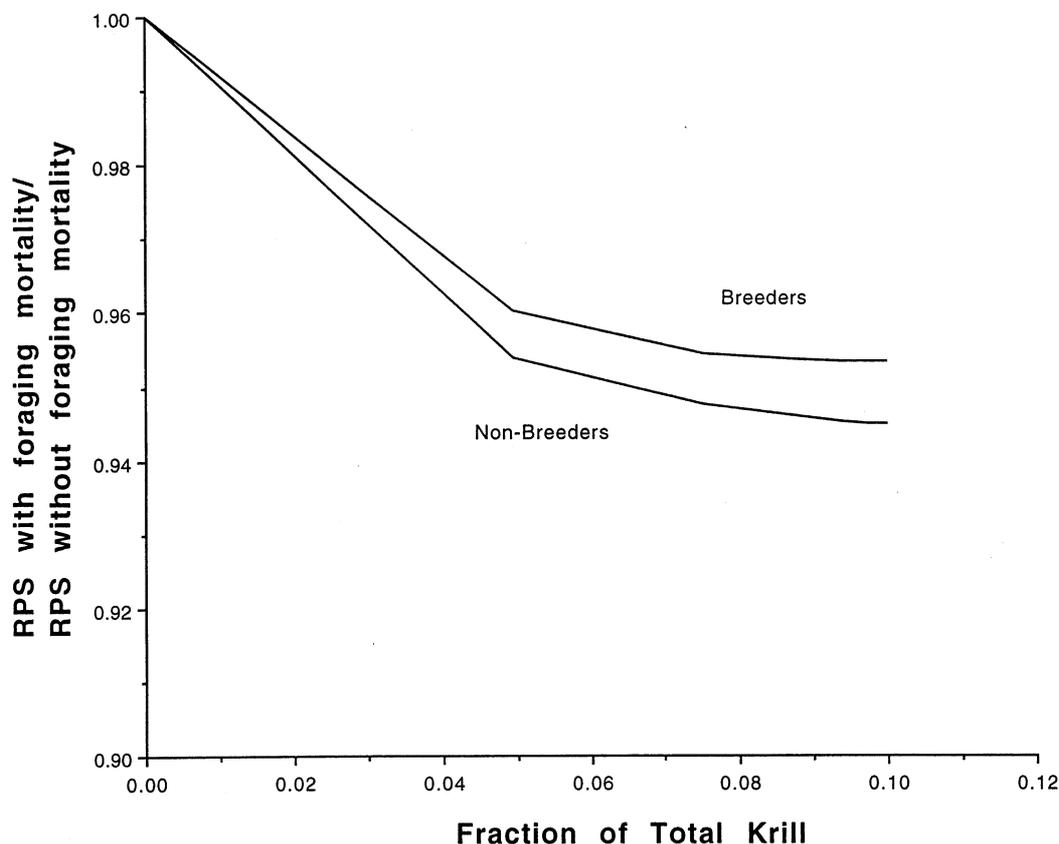


Fig. 8. When there is foraging mortality ($m_p > 0$), relative parental survival is less than relative parental survival in the absence of foraging mortality and depends upon the krill capture. The results here are for a season of length 30 days and $m_p = 0.001$.

whenever the offspring had received greater than 80% of the cumulate need required for fledging at day 54.

However, even without these additions, the model indicates the need of accurately assessing both the maximum yearly survival of adults and offspring and the fraction of krill available to the predators that the fishery takes. With this information, it will be possible to move from relative comparisons to absolute predictions.

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