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# Could whales have maintained a high abundance of krill?

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## ABSTRACT

**Question:** Several million large whales were killed between 1900 and 1970. All these whales preyed on krill (*Euphausia superba*). Why has krill population abundance declined after the elimination of their primary predator?

**Hypothesis:** Krill have changed their behaviour due to the absence of whales and this change in behaviour has resulted in a decrease in krill abundance.

**Methods:** I reproduced a computer model of krill life history. I then extended the model as an individual-based model to show the effects of habitat choice on individual lifetime reproductive success and abundance.

**Conclusions:** In the context of our current understanding of krill physiology, predator-invoked behaviour may lead to increased population abundance and, without the predator, natural selection may favour behaviour that would lead to lower abundance. This reverses the predictions of mass balance ecosystem models.

*Keywords:* computer model, IBM, regime change.

## INTRODUCTION

Krill abundance in the Southern Ocean either did or did not increase dramatically as a result of the removal of 2 million whales within 100 years (Clapham and Baker, 2001). A large surplus of krill had been predicted (Mackintosh, 1973; Laws, 1977; Smetacek and Nicol, 2005). Other predictions included a large increase in other predators of krill; for instance, a yearly increase of 300 million penguins was hypothesized (Sladen cited in Ozawa and Sato, 1967). If, however, the abundance of krill did not increase dramatically and neither did any of its other predators, this would represent a paradox.

The first challenge is to ascertain if there is a paradox to be addressed. The case cannot be proved either way as sufficiently accurate data are not available. Nevertheless, evidence strongly justifies the assumption of a paradox. Based on the average whale's diet, before 1900 whales ate 175–190 million tonnes of krill a year, and by 1987 whales ate less than

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43 million tonnes (Mackintosh, 1973, 1974; Ross and Quetin, 1988). Contrast this to the best estimate of total post-whaling krill biomass: 'Extrapolations from acoustic measurements of krill abundance indicate a krill biomass of between 60 and 155 million tonnes' (Smetacek and Nicol, 2005). Krill abundance has been notoriously difficult to measure, there may have been a long-term decline (Atkinson *et al.*, 2004), and these estimates therefore might be wrong. Nevertheless, the measurements are the result of decades of international collaborative projects specifically aimed at surveying the abundance of krill with equipment specifically designed for the purpose (Everson, 2000). We are relatively certain about the dead whales (Clapham and Baker, 2001). So, with caveats and qualifications accepted, the present highest best guess of the standing stock of krill would be insufficient to feed the whale population before human exploitation. This critical point is the basis for the assertion of a paradox in this study. We are unable to detect, at the highest bounds of our error estimate, enough standing stock of krill to supply the lowest estimate of consumption of the whales that we know were killed. This is in stark opposition to the conventional view that release of predatory pressure results in population increase: 'In looking at nature, it is most necessary to keep the foregoing considerations always in mind . . . Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount' (Darwin, 1860).

The paradox is compounded by other factors. First, in addition to the krill required to feed the whales that we know had been eliminated, we would need to account for the consumption of all the other krill predators in the Southern Ocean: seals, birds, penguins, fish, and squid. These together were thought to consume about the same amount of krill as the whales (Ross and Quetin, 1988). Second, the fur seal population was severely reduced by humans at about the same time commercial whaling started, further and substantially reducing the predatory pressure on krill (Reid and Croxall, 2001). Third, the ecosystem was dominated by long-lived, large, and specialized predators, which is typical of a mature ecosystem exhibiting characteristics of stability and symbiosis (Odum, 1969). This can only theoretically have been true if krill abundance exhibited a high minimum level over evolutionarily relevant time-scales. Thus we would need to account for sufficient uneaten krill for the long-term continuance of a high minimum abundance.

Where we do have contemporary scientific reports, they also appear to support the assumption of a paradoxical decline in the krill population following the end of whaling. A virtual absence of krill was reported around South Georgia during the 1977–78 season and again in 1983 and 1990–91, when this area (Atlantic Sector) had previously been reported to be stable and productive for whaling (Siegel and Loeb, 1995). A synthesis of whale catch data and krill sightings throughout the 1920s and 1930s repeatedly reports the South Georgia area was an area of continuously higher than average abundance of krill (Mackintosh, 1973), confirmed in later surveys (Ozawa and Sato, 1967), and does not mention any abnormally low years. The reports are unequivocal. For instance, '[krill patches] seen continuously over an area estimated to be at least 150 square miles' observed during 1931, or a scientific deck log entry in the same year: 'krill (suspected) imparting a dull plum hue to the green water around. The patch extended toward South Georgia as far as the eye could see' (Marr, 1962). Later studies suggested that the reports of penguin and albatross chicks dying and the virtual absence of krill was viewed as 'unexpected' between 1977 and 1991 (especially when considering the predicted increases in penguin abundance cited above), but could be potentially explained by weather changes and 'normal phenomena' of stock fluctuations and high spatial variation (Siegel and Loeb, 1995).

The paradox may be answered by a comparable increase in the abundance of an alternative predator. The only krill predator to show a potentially significant increase in abundance was the crabeater seal (*Lobodon carcinophagus*) (these seals were not favoured by sealers) but no firm details are known (Reid and Croxall, 2001) and their abundance is also difficult to measure (Green *et al.*, 1995).

Given the above it is reasonable to suggest that the krill population has not dramatically increased in abundance, to an extent that would be expected after the removal of its predominant predator, and neither have any of the other krill predators increased to such an extent. In fact, given the above it seems reasonable to strongly suggest that the krill abundance has decreased rather than increased. Some suggest that all this can be accounted for by conventional predator–prey interaction (Mori and Butterworth, 2004); however, let us proceed here on the basis that there is a paradox to be answered.

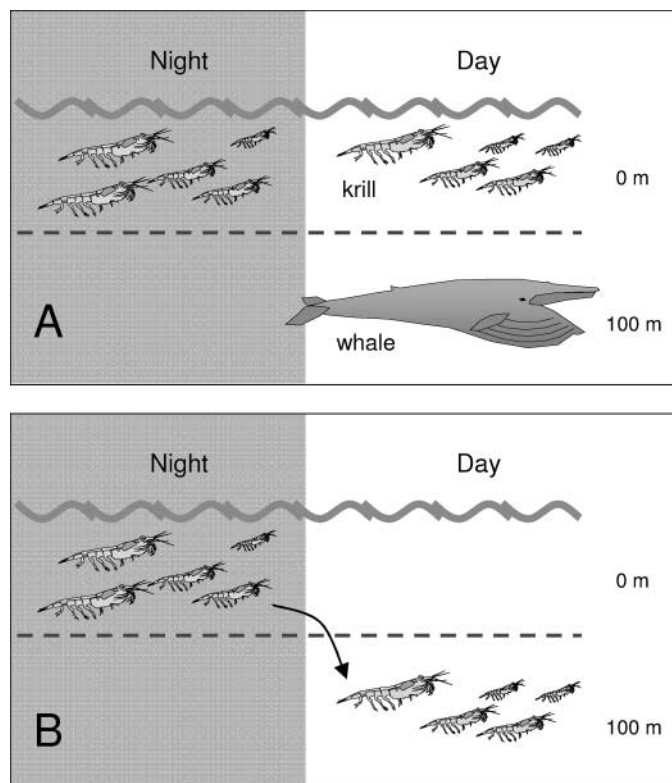
The second challenge relates to defining the normal behaviour of krill. In particular, this relates to daily migrations of krill from deep habitat during daylight to surface habitat at night. It is usually assumed that this is normal behaviour (Everson, 2000). However, this could be an oversimplification and there is no general agreement in the literature about whether krill generally migrate or not, and given they do, why they do (Godlewska, 1996; Everson, 2000). There is, however, consensus that they don't seem to be doing what they used to do. Again, very large schools of krill on the surface during daylight were reported by whaling vessels and scientific expeditions ['constant records of krill in sight day after day', 'thick with [krill] like pea soup', and 'immense pastures' (Mackintosh, 1973)], and early scientific observers from the whaling nations mapped surface schools (Arseniev, 1958; Marr, 1962; Ozawa and Sato, 1967) and strongly concluded that krill only inhabited the top 10 m and rarely went below 40 m (Marr, 1962). Early scientific observers did not ignore the possibility of diurnal vertical migrations, and in fact recorded this behaviour for developmental stages of krill, but concluded that, by adolescence, the krill remained continuously on the surface (Fraser, 1936). This is definitely not the case now; there are no observations of large schools of krill on the surface during the daylight reported in modern scientific literature (Godlewska, 1996). A post-whaling krill fishery operates in the same areas whaling had (Ichii, 2000). This fishery peaked in 1990–91 at 400,000 tonnes, accounting for 13% of the world catch of crustaceans (Nicol, 1991), and continues at approximately 125,000 tonnes per year (SC-CAMLR, 2005). Sonar, echo sounders, and knowledge of previous abundance have been the only ways in which krill have been found by the fishery during daylight after the end of whaling (Ichii, 2000). The only time krill are reported to be observable by the fishery at the surface is in twilight after sunset in one particular area (Kemp and Wilkes Land) (Ichii, 2000).

Krill show a variety of migration modes correlated to chlorophyll (food availability), their size, and seasonal changes (Godlewska, 1996). Krill also show variation in migration apparently due to the presence of particular predators (Everson, 2000). For example, krill's migration, from the surface at night to deep in the day, can be reversed in shelf waters where fish are major deep daytime predators (Godlewska, 1996). Godlewska (1996) hypothesized that the process of krill vertical migrations could result from the extinction of whales. She suggests this is an evolutionary change and uses the cases of Cyclopoida (*Cyclops abyssorum*) and introduced fish in mountain lakes as an example of similar evolved migratory behaviour (Gliwicz, 1986). If Godlewska's hypothesis were true, what would it imply about the abundance of krill?

## METHODS

To address this question, I reproduced a comprehensive model of krill life history from the literature, only making small changes to the survivability in two scenarios (Alonzo and Mangel, 2001) (Table 1). All krill spent the night at the surface, but in one scenario (A) they spent the day at the surface and in the other (B) they spent the day at a depth of 100 m (Fig. 1). Scenario A is designed to model the case when whales were present and implies that the deep habitat was ‘very risky’ for the krill; this is not explicitly modelled but implied by the fact that krill spend no time here in this case. Scenario B models the case when whales were no longer present and the deep habitat had become safe in comparison to the surface and thus krill spend their time in the deep habitat during the day. The surface habitat is warmer with more food, and I increased the risk to krill while living here compared with the deep cold habitat. Thus the model contrasted a high-risk, die young, grow fast scenario with a low-risk, live long, grow slow scenario (Table 2).

There has been substantial theoretical work on risk-sensitive foraging (Schoener, 1971; Stephens and Krebs, 1986; Mangel and Clark, 1988), which helps to explain diurnal migration strategies of aquatic life (Hall *et al.*, 1979; Gliwicz, 1986; Mangel and Clark, 1988). Dynamic programming models have shown how the optimum foraging strategy depends on the trade-off between current food



**Fig. 1.** Sketch diagram of the two habitat scenarios in the model of krill. Scenario A is surface at night and surface at day, while B is surface at night and 100 m deep during the day. The whales are hypothesized to be the reason for the change, assumed to be there in A but not in B.

**Table 1.** Components used in the calculation of growth for model krill

Component	Relation	Equation	Notes and original reference
Length-weight allometry	$W(L) = 10^{3.3874 \log L - 2.7531}$	1	Alonzo and Mangel (2001) contained a typographical error due to using the base of natural logarithm (e) rather than 10 on the right-hand side of equation (1). $L$ = length (mm), $W$ = wet weight (g)
Metabolic costs (as a function of habitat)	$C(H, L, t) = e^{-0.2512 + 0.8 \ln W(L) + 0.049 T(H, t)}$	2	Original reference: Ikeda (1985). Ikeda used dry weight rather than wet weight for derivation of this expression. Alonzo and Mangel's (2001) analysis was used for consistency.
Total metabolic costs	$C(H_s, L, t) = (1 - \tau)C(H_s, L, t) + (\tau)C(H_d, L, t)$	3	$T(H, t)$ = temperature in habitat $H$ at time $t$ ; $T(H_s, t)$ for surface temperature = 2°C, $T(H_d, t)$ for deep habitat = 0°C $C(H_s, L, t)$ = metabolic costs in habitat $H_s$ (deep) at length $L$ and at time $t$ ; $\tau$ = proportion of time that is day ( $\tau = 0.5$ in this study); $H_s$ = surface habitat
Food availability	$P$ (surface habitat $P = 1$ , deep habitat $P = 0.7$ )	4	Food availability. In this study, this parameter was changed to reflect greater food availability in the surface habitat
Assimilation rate	$A = 0.9$	5	Alonzo and Mangel (2001)
Filtration rate	$f = 4.64 W^{0.8}$ (in ml · h <sup>-1</sup> )	6	Holm-Hansen and Huntley (1984)
Temperature dependence of feeding rate	Feeding $\propto [T(H, t) - T_{\min}] / [T(H, t) + T_0]$	7	Where $T_0 = 10$ and determines the speed at which the relationship asymptotes and $T_{\min} = -5$ , the temperature at which feeding will be zero (Alonzo and Mangel, 2001)
Travel time	$M_s(H, L) = D(H)(0.002 \times L)$	8	$M_s(H, L)$ = movement time in seconds to travel to the surface for a krill of length $L$ (mm) in habitat $H$ . The suggestion is that krill swim 2 body lengths per second Habitat $H_d$ (deep) was at 100 m, and $D$ is the distance to the surface in metres
Proportion of feeding time remaining after travel	$M_p(H, L) = ((1 - \tau) - [M_s(H, L)(24 \times 60 \times 60)](1 - \tau))$	9	$M_p(H, L)$ = proportion of total time available for feeding after travel (to the surface) from habitat $H$ for a krill of length $L$
Size dependence of food intake	Feeding $\propto 1/(1 + \gamma W^{0.8})$	10	Antarctic krill growth trajectories asymptote below 60 mm (Ikeda, 1985; Mauchline, 1980) and $\gamma = 0.005$ so that the function asymptotes as expected

**Table 2.** Summary of differences between the habitats

Resources and risks	Surface habitat (risky)	Deep habitat (safe)
Temperature	High ( $T = 2^\circ\text{C}$ )	Low ( $T = 0^\circ\text{C}$ )
Food availability	High ( $P = 1$ )	Low ( $P = 0.7$ )
Predation (per week)	High (survival = 97.7%)	Low (survival = 99%)

*Note:* Symbols as in Table 1. The deep habitat is modelled as being in use only when whales had gone (scenario B). It is the implicit assumption that when whales were there, the deep habitat was 'very risky' during the day (which is not explicitly modelled here), and thus the krill would always use the surface habitat (scenario A).

intake, predation risk, and the expected future reproduction that may be risked by entering a dangerous habitat (Mangel and Clark, 1988). Risk-sensitive foraging focuses on the individual's most likely responses to risk based on its individual lifetime reproductive success, and the fundamental idea behind risk-sensitive foraging is that organisms will trade off a decrease in mean fitness for a decrease in the variance of fitness (Mangel and Clark, 1988). Here is an individual-based model that extends the theory from individual to a small population, in which each individual acts in a way consistent with the theory of risk-sensitive foraging. The aim is to explore the net effect of risk-sensitive foraging on abundance for an organism with a complicated life history like krill has.

The model of Alonzo and Mangel (2001) was used as the basis for growth and habitat selection. Their model of krill was based on calculations of growth derived from food intake and metabolic costs. The present model started with an array of 1000 krill, with ages in proportion to the survivorship for krill suggested by Alonzo and Mangel (2001). I ran the model for 10 years, in one-week steps.

### Components of growth

The calculations for components of growth were reproduced from Alonzo and Mangel (2001). Total food intake ( $F$ ) for a krill of length  $L$  in habitat  $H$  at time  $t$  combines relationships for food availability (equation 4, Table 1), assimilation rate (equation 5, Table 1), filtration rate (equation 6, Table 1), temperature dependence (equation 7, Table 1), travel time (equation 8, Table 1), feeding time (equation 9, Table 1), and size dependence (equation 10, Table 1):

$$F(H, L, t) = \frac{M_p(H, L) \cdot P \cdot A \cdot 4.64 \cdot W(L)^{0.8} \cdot [T(S, t) - T_{\min}]}{[1 + \gamma \cdot W(L)^{0.8}] [T(S, t) + T_o]} \quad (11)$$

Growth per time step ( $\Delta L$ ) is calculated using total food intake from equation (11), and subtracting total metabolic costs (equation 3, Table 1).

$$\Delta L(H, L, t) = K[F(H, L, t) - C(H, L, t)] \quad (12)$$

$$L(t+1) = L(t) + \Delta L(H, L, t) \quad (13)$$

where  $K$  is a constant (Alonzo and Mangel, 2001).

### Survival

All krill that died were assumed to have been killed by predators. Each week the krill numbers were reduced using the calculations for predation dependent on habitat use. For instance, a krill in scenario B (deep in day) had a 99% chance of survival each week, while a krill using the surface in the day had a 97.7% chance of survival each week (Table 2). Survival was decreased to 85% per week in both scenarios for krill that had reached the age of 6 years (Alonzo and Mangel, 2001).

### Fecundity

Once reproductive, the fecundity of a krill increased linearly. I used the following equation (Siegel, 1985; Alonzo and Mangel, 2001):

$$R(L) = -7396.8 + 245.7L \quad (14)$$

As each year ended, fecundity for the surviving krill was calculated and new recruits aged 1 year old were added, dependent on the total population fecundity at the end of the previous year (the total population fecundity was the sum of the fecundities for each living individual in the population). The minimum size for reproduction was 38 mm from Alonzo and Mangel (2001) and Mauchline (1980). Here  $L$  is length in millimetres and  $R(L)$  is the fecundity of a krill. Following Alonzo and Mangel (2001), the fecundity for krill at any other date than the year end was equal to its length (while it was over the 38 mm threshold). These values were used in the weekly evaluation of cumulative fecundity.

Krill are recruited into the model each year at 1 year old and length 18 mm [this is the estimated size of a 1-year-old juvenile under good feeding conditions (Alonzo and Mangel, 2001)]. Annual recruitment of 1-year-old krill was related to the previous year's population fecundity by a linear function:

$$N_{(n)} = \mu \cdot R_{(n-1)} \quad (15)$$

where  $N_{(n)}$  is the number of recruits at year  $n$  and  $R_{(n-1)}$  is the population fecundity of all the survivors at the end of the previous year.  $\mu$  (the fecundity-recruitment constant) was arbitrary and was set by preliminary analysis so as to produce a relatively stable population using scenario B (deep in day) as a reference baseline to contrast with scenario A (surface in day). I used a single value of  $\mu = 0.00067$  to convert fecundity figures to recruitment in both habitats.

The fecundity was the same for both scenario choices and thus the result of the model – a contrast between the two habitat usage scenarios – was insensitive to this value.

### Operation

I used the model to investigate two scenarios: (A) with an initial population of 1000 krill living entirely in the surface habitat, and (B) with the initial population of 1000 using the deep habitat in the day and moving to the surface habitat at night. After 10 years I calculated the average age at death, average weight at death, and average cumulative fecundity at death for every krill that had died (all that died were assumed to have died due to predation). Ten replicates of each scenario were run.

### Sensitivity analysis

The model results are robust to large variation in the parameters chosen. But a detailed sensitivity analysis of the model to the large number of input parameters is not included in this paper to avoid complexity, as the results and discussion are not dependent on the sensitivity of the model. It was also felt that it might give a false impression of accuracy or precision inappropriate for a theoretical model.

### Suggested enhancement to krill life-history model

The value  $\gamma$  in the original model was used to limit the growth of krill to 60 mm in maximum growth conditions (Alonzo and Mangel, 2001) (Table 1). This value changed the point of inflection in the growth versus length relationship, which represented the change of resources between somatic growth and gonads. In optimal conditions this point of inflection was at 38 mm, the threshold of fecundity; however, a constant value of  $\gamma$  made this inflection point move to lower lengths in other (less than optimal) conditions. This is evident in Alonzo and Mangel's (2001) figure 2(b). I believe it is logical that this inflection point would be similar in all habitats, reflecting a similar switch of resources away from somatic growth at a similar life-history stage. This would require a variable value of  $\gamma$  dependent on habitat. I ran the model in this study with variable  $\gamma$  between habitat scenarios and an appropriately varied predation balance and the results were unchanged; therefore, I used a constant  $\gamma$  value, but this could be important if this study or the original model were used again.

## RESULTS

The population in scenario A (surface in day, before whaling) increased in abundance during the simulation from 1000 to approximately 1300, whereas the population in scenario B (deep in day, after whaling) remained approximately stable in abundance (Table 3). The krill population before whaling was killed in significantly greater numbers, and delivered over twice the biomass, than the population after whaling. The krill before whaling died significantly younger and heavier than those after whaling. Crucially, however, the mean individual cumulative fecundity was lower before whaling (surface in day) than after whaling (deep in day). Since there is a fixed relationship for fecundity to recruitment in this

**Table 3.** Model results for different scenarios for all krill killed during a 10-year simulation (initial population  $1000 \pm 1$  standard deviation of 5 replicates)

Key statistics	Scenario A (surface at all times)	Scenario B (surface at night, 100 m at day)
Total weight killed (kg)	$3.3 \pm 0.2$	$1.29 \pm 0.05$
Mean cumulative fecundity at death	$2363 \pm 29$	$2940 \pm 19$
Mean weight at death (mg)	$480 \pm 7$	$307 \pm 4$
Mean age at death (weeks)	$99.5 \pm 0.6$	$145 \pm 0.6$
Total number killed	$6810 \pm 547$	$4211 \pm 182$
Final population number	$1301 \pm 185$	$941 \pm 81$

*Note:* All krill are assumed to have died through predation.

model, individual cumulative fecundity is equivalent to lifetime reproductive success, which would drive evolutionary selection (Alonzo and Mangel, 2001).

The model is designed to contrast the situation when whales were present with when they were not. The model assumes individual krill select the option in each scenario that would maximize their individual lifetime reproductive success – a consequence of natural selection. If a population of krill had the opportunity to use either scenario A or B, the model demonstrates that they would use scenario B. This is due to individual higher lifetime reproductive success, which would drive natural selection for krill that exhibited this behaviour. This is an analogy to the situation when whales are gone; krill migrate to the deep habitat during the day. The alternative scenario is designed to model the situation when whales were present. In this case, it is assumed whales made the deep habitat during the day prohibitively risky. This is not modelled explicitly; it is unnecessary because in this case the krill are naturally selected to use the surface habitat. If this was the case, all other things being equal (the most parsimonious assumption), the population of krill would increase overall and the krill killed and eaten would increase. The reasoning follows that now whales are gone, krill are selected to use the deep habitat during the day; consequently, their abundance is lower and less are killed and eaten.

## DISCUSSION

I suggest that when whales were around, krill spent the day and night at the surface and now whales are absent, krill migrate to depth during the day (Fig. 1). The model highlights a hypothesis for the decline in the population abundance of krill caused by this change in behaviour. The model shows that the alterations in habitat use, prompted by a change in the balance of risk, are well within our current understanding of a krill's physiological capacity to grow and reproduce. This study shows how Godlewski's (1996) hypothesis of a change in migratory behaviour may have resulted in a reduction in the population abundance of krill. Crucially, this study puts the answer in the context of known physiology, reproduction, habitat use, response to risk, and evolutionary theory.

The change in the balance of risk that drives the result appears most likely to be due to whales being visual predators with a visual advantage over krill related to depth. The balance of risk suggests whales were a much greater proportional threat to krill at depth during the day than they were at the surface during the day. It is possible, but controversial, that baleen whales use sonar (Beamish and Mitchell, 1971; Clark, 2004) in combination with eyesight. Sonar may be less accurate at the surface – somewhat similarly to human sonar (Gerlotto *et al.*, 2004; Godlewski, 1996). Alternatively, whales might hear the krill feeding or moving and use accurate aural detection (Marr, 1962), which may be similarly disturbed by proximity of the surface. This coupled with the fact that krill are more capable of avoiding whales in good light at the surface may have contributed to a lower risk at the surface than the deep when whales were around (Hamner and Hamner, 2000). Virtually all studies of krill mention their capability at avoiding capture in nets towed behind ships during daylight (Fraser, 1936; Marr, 1962; Ozawa and Sato, 1967; Everson, 2000; Hamner and Hamner, 2000; Nicol *et al.*, 2000; Smetacek and Nicol, 2005) and this activity is thought to be visually stimulated, with the result that trawls have been attempted at night and with larger and camouflaged nets (Nicol, 2000). The surface habitat during the day will always carry a higher risk of predation by flying birds and penguins in contrast to the deep habitat. A benefit of the model is its simplicity, which gives it the generality required to answer a big ecosystem question (Odenbaugh, 2005), but this is also its weakness in that it cannot

be used to elucidate specific information about the behaviour and risk balance of one predator over another, where models based on game theory are more appropriate (Alonzo *et al.*, 2003).

There may be other factors, such as seasonal variation or sea ice cover (Mackintosh, 1973; Kawaguchi and Satake, 1994; Smetacek and Nicol, 2005), that affect the abundance of krill and completely overwhelm the signal outlined here. Nevertheless, this study shows that our current best guess of krill physiology would suggest it is possible that the removal of a predator could lead to a behavioural change in krill, by conferring individual evolutionary advantage, and that this might lead to a decrease in krill abundance. Thus the model not only shows what a much simpler theoretical model could show regarding risk, growth, fecundity, and reproduction, but crucially places it in the context of our best current knowledge of habitats and physiology of krill, which is derived from a wide range of observations and experiments over many years (Alonzo and Mangel, 2001).

The potential of positive feedback between predator and prey is not a new idea, nor is the concept of the removal of an apex predator causing wide-scale ecosystem change, regime shift, and even collapse (Springer *et al.*, 2003; Collie *et al.*, 2004). Several recent studies have highlighted the biologically important emergent effects of multiple predators on prey species by focusing on the risk balances under different situations (Vance-Chalcraft and Soluk, 2005; Griffen, 2006). Furthermore, earlier studies highlighted the potentially enhanced regulatory effects on prey abundance of multiple predators with various different functional and numerical responses (Holling, 1959a, 1959b), which is important in this case as the abundance of krill appears now to be variable (Siegel and Loeb, 1995). Other studies have confirmed that in many cases there are linear aggregate effects of multiple predators, even when the predators have a combination of direct and indirect effects (Schmitz and Sokol-Hessner, 2002).

## Conclusion

Scientific reports from the early part of last century make for grim reading: ‘The sight of those whales and birds . . . will for ever remain one of the most vivid of my Antarctic recollections. Whales’ backs and beaks were seen at close intervals quite near the ship, and from horizon to horizon . . . The sea was swarming with *Euphausia*’ (Bruce, 1915). It is difficult not to subjectively form the view that the Antarctic ecosystem once supported a much higher abundance of whales, krill, seals, and birds than it does now.

## ACKNOWLEDGEMENTS

Chris Wilcox, Marc Mangel, Alistair Hobday, Jeff Dambacher, Stephen Nicol, So Kawaguchi, Andrew Constable, and Mark Hindell have all helped me in putting this study together.

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