

Whales maintained a high abundance of krill; both are ecosystem engineers in the Southern Ocean

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ABSTRACT: Krill abundance was predicted to rise after the end of commercial whaling in the Southern Ocean due to the release of predatory pressure from 2 million whales that were killed between 1915 and 1970, but contrary to expectations, there has been a substantial decline in abundance of krill since the end of whaling. I presented a model 7 yr ago which explained how krill behaviour, in response to the threat of predation by whales, may provide an answer to this paradox. The original model contained a speculative link: a mechanism by which krill could detect the presence of whales over a wide area, and therefore could behave in response to a credible threat. Recently, iron has been implicated in a positive feedback cycle between whales, krill and primary production. The cycle depends on the buoyant faeces of whales fertilising surface layers. This is both a plausible way for krill to detect whales over a wide area and an explanation for enhanced feeding at the surface, but this was not incorporated in the original model. Thus, nutrient retention and behavioural control are probably an example of niche construction and ecosystem engineering by both krill and whales. In this paper I revisit and update the simple model of krill mentioned above. The model is calibrated against known system states and is used to imply the ecosystem level changes caused by commercial whaling. This improved model may explain the reduction in krill abundance after the end of commercial whaling. Untested hypotheses which can be falsified in designed experiments are listed.

KEY WORDS: Individual-based model · Ecosystem model · Cetacean

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INTRODUCTION

The model presented in this paper has been developed assuming the validity of the following basic statements about the Antarctic ecosystem:

- (1) Krill *Euphausia superba* abundance in the Southern Ocean used to be enough to support the whales (and other krill predators) that existed before exploitation and was close to its pristine ecosystem carrying capacity.
- (2) Krill abundance is now lower than it was before the start of commercial whaling.
- (3) Godlewski's hypothesis is true: krill have changed their habitat use because of the lack of whales (more correctly, the lack of the perceived risk of predation from whales).

- (4) Whales enhance the surface feeding opportunity for krill through nutrient recycling.

The aim of this study is to show how a simple model that encompasses these assumptions leads to a prediction about the current state of the ecosystem, and likely future scenarios, which is more plausible than other models that have been presented to date. The first statement is hopefully uncontested given that the ecosystem has existed long enough for the participants to have evolved and that it is not contradicted by any observation or theory; it also follows the ecological theory around mature ecosystems (Odum 1969). Evidence to support the subsequent statements is outlined below. The most important contribution of this study is to provide evidence to support these basic assumptions.

Krill abundance is now lower than before commercial whaling started

Commercial whaling removed 2 million large baleen whales from the Antarctic marine ecosystem in less than 70 yr, starting around 1900 (Clapham & Baker 2001). These included blue whales *Balaenoptera musculus*, fin whales *B. physalus*, sei whales *B. borealis*, humpback whales *Megaptera novaengliae*, and Antarctic minke whales *B. bonaerensis*, hereinafter referred to collectively as 'whales'. These whales were almost entirely sustained by krill. It was assumed that the krill population would increase tremendously as a result of the release in predatory pressure due to commercial whaling (Laws 1977, Ballance et al. 2006). This effect of predatory release was expected to have been exacerbated by the commercial harvesting of fur seals *Arctocephalus gazelle* and ground fish, both krill predators, which occurred around the beginning and throughout the period of whaling, respectively (Ballance et al. 2006, Kock et al. 2007). The krill population has not increased, and rather the opposite is true. It is difficult to be certain about krill abundance in the Antarctic marine ecosystem due to its size and inaccessibility; nevertheless, after 10 yr of searching, with equipment specifically designed for the purpose (Everson 2000), scientists were unable to find enough krill to feed the whales that were known to have been killed. Nicol et al. (2000) calculated krill population abundance around the year 2000 to be between 60 and 155 million t. This figure was later revised to 133 million t global biomass (Atkinson et al. 2009). Stomach contents of >500 whales were used to estimate that, before 1900, whales consumed a total of 175 to 190 million t of krill per year (Mackintosh 1973, 1974, Ross & Quetin 1988) and this was used to infer that the difference between total whale consumption of krill before and after whaling was 147 million t (Laws 1977). This estimate was made under the assumption that there were 975 000 whales in the pristine state (Laws 1977) whereas now, with the benefit of Russian catch records which were not previously available, the best estimate is 1.697 million (Christensen 2006). So, using the Laws (1977) multipliers (his Table 2) on Christensen's (2006) population estimates (her Table 3), the difference in krill consumed by whales before and after whaling is now estimated at 276 million t. This observed feeding requirement for the whales that are known to have been killed is more than twice the observed global standing stock of krill (133 million t mentioned above). Whales, however, are not the only predators of krill: in 1985 it was estimated

that 470 million t of krill were eaten each year by whales, seabirds, seals, squid and fish (Ross & Quetin 1988). This estimate of 470 million t required to maintain the system after exploitation of whales should be compared with the present best modeled estimate of 342 to 536 million t per year gross larval production (in 2000) and the consequent estimate of 128 to 470 million t per year available to predators (Atkinson et al. 2009). The entire additional requirement of the whales, if they existed now in their pristine abundance, for ca. 276 million t of krill, would be unavailable at the higher bound of present modelled production estimates. Hence, the production of krill must have fallen by at least this amount between the start and finish of commercial whaling (a decrease of 50% at the lowest proportional estimate). A huge surplus of krill, and a tremendous rise in the abundance of other predators of krill (compensatory predation) was expected (Ballance et al. 2006), but the opposite has happened. Krill abundance has fallen, and continues to fall (Atkinson et al. 2004). There have been moderate changes in the abundance of other krill predators; the fur seal population recovered very strongly until around 1985 and has since declined, crabeater seals (*Lobodon carcinophaga* or *carcinophagus*) have shown no long-term changes, and most avian predators have declined in abundance (Ballance et al. 2006). These changes do not provide an adequate compensatory predator-based explanation for the changes in krill abundance (Ballance et al. 2006). The logical hypothesis is that presently observed krill abundance is a fraction of what was required to maintain the ecosystem before whaling.

Godlewski's hypothesis of krill behavioural changes

Godlewski (1996) presented the results of sonar-based krill surveys and suggested that krill had changed their behaviour after the end of commercial whaling. She suggested that krill had spent most days at the surface before the end of whaling, but after whaling spent the daylight hours at 100 m to 200 m depth and migrated each night to the surface (Godlewski 1996). During the early period of whaling, observers consistently reported a high abundance of krill and constant occurrence of surface schools day after day (Marr 1964, Mackintosh 1973). Surface schools of krill were described as being thick like pea-soup, and extending continuously like immense pastures over areas as large as 150 square miles

(Marr 1964, Mackintosh 1973). Such was the importance, regularity and clear association with whaling, that daylight surface schools of krill were mapped across the entire area of commercial whaling by observers from each of the main whaling countries (Arsenev 1958, Marr 1964, Ozawa & Sato 1967). Early scientists did not ignore the possibility of vertical migrations; they searched for, and occasionally recorded, this behaviour for adult and developmental stages of krill (Mackintosh 1934, Hardy & Gunther 1936, Fraser 1937, Marr 1964). During the early period of whaling, Mackintosh (1934) sampled the vertical position of krill and concluded that for the majority of day and night they stayed near the surface, especially when in schools with only a minor degree of diurnal variation. Marr (1964) reported that krill only inhabited depths within 10 to 40 m of the surface, day and night. This conclusion was derived from a literature review and a comprehensive survey based on net hauls. (Like more recent studies, this study accounted for the fact that krill are adept at avoiding nets at the surface in daylight; Marr 1964, Nicol et al. 2010). After the end of commercial whaling, there were no records of krill seen at the surface in daylight despite continued observation. At this time, a commercial krill fishery was developing and it would have been convenient for the fishers to see krill at the surface. However, sonar, echo sounders and knowledge of previous abundance were the only ways in which krill were found by the commercial krill fishery during daylight (Ichii 2000). No large surface schools were recorded as visible at the surface in daylight in the scientific literature between 1970 and 2000. Vertical daily migration is now considered standard behaviour for krill (Everson 2000). Typical scientific samples during this period were taken between the surface and 160 m in depth using sonar for school location (Ross & Quetin 1983). Where super swarms were reported in daylight in this period after whaling (e.g. Higginbottom & Hosie 1989, Godlewska 1996) they were detected with sonar; no krill were seen at the surface. Thus there is strong evidence to suggest Godlewska's hypothesis is more a fact established through observation rather than a hypothesis.

Whales enhance surface prey abundance for krill through iron recycling and fertilisation

Krill fertilise the ocean *in situ* with their excrement as they feed; a high krill biomass causes enhanced primary production in Antarctic waters (Lehette et al. 2012). Krill bodies also contain high levels of iron rel-

ative to the surrounding waters, and thus the population of krill represents a carrier for a significant proportion of all the iron flux present in the surface ocean of this region (Tovar-Sanchez et al. 2007). Whale bodies and whale faecal material are similarly rich in iron (Smetacek 2008). Whale faeces are buoyant and fluid with a high water content, and whales have been photographed defecating at the surface (Smetacek 2008). This implies an iron and nutrient storage and recycling mechanism that leads to a positive feedback in the food chain between the abundance of primary production, krill and whales (Smetacek 2008, Nicol et al. 2010). Krill may also have engineered their environment and enhanced primary production through turbulence (Kerr 2006, Smetacek 2008, Willis 2013). Turbulence can be a greater determinant of phytoplankton growth than either salinity or temperature (Margalef 1978). Turbulence as a determinant of phytoplankton growth was largely overlooked until the energetic strength of turbulence caused by fish and krill schools was found to be on the same scale as that caused by wind and waves (Huntley & Zhou 2004). It was found that this turbulence is unlikely to contribute to overall ocean mixing in the same way as wind, due to the comparatively short mixing scales (Visser 2007). However, turbulence with such energy and short mixing characteristics is a very rare event in the ocean outside of swimming animal schools (Jimenez 1997). Krill-induced turbulence may constitute ecosystem engineering through at least 3 mechanisms: (1) by directly enhancing plankton productivity (Margalef 1978), (2) by facilitating the sorting of prey sizes and types by krill, which allows krill to engineer the size and age composition of their prey (Willis 2013), and (3) by mixing the surface ocean to redistribute physical substances (nutrients) and properties such as salinity and temperature (Kerr 2006). The impact of krill-induced turbulence on primary production as a type of ecosystem engineering, or energy fertilisation, process may well be significant. Retention of nutrients and complex symbiotic interactions are also consistent with the characteristics of a mature ecosystem (Odum 1969). It is also interesting to consider the higher density caused by compression of the krill population into the top 10 m as opposed to the deeper zone between 10 and 200 m. Mackintosh (1934) suggested krill form denser schools when at the surface. Compression and higher density patches would potentially lead to more accurate targeting of fertilisation of nutrients by whales and would enhance the effects of turbulence caused by the swimming action of krill (Willis 2013). In sum-

mary, there is a nutrient retention and recycling mechanism which includes whales, krill and primary production.

Ecosystem implication of the iron cycle

The existence of a nutrient and fertilisation mechanism induced by whales and krill in the food chain implies that the throughput of the entire Antarctic ecosystem has been reduced due to decreased nutrient retention caused by commercial whaling. This means that the carrying capacity of krill is variable and is dependent on the abundance of whales, among other factors. In terms of the theory of krill behaviour and abundance, outlined in this study, the theory of an iron cycle provides 2 important explanations: (1) the mechanism by which krill are aware of whales and thus are able to react to the threat of predation could be odour in faeces, and (2) the iron cycle linked through whales and krill defecation at the surface coupled with high turbulence, temperature and sunlight would provide a good explanation for higher availability of food for krill at the surface in daylight. In an earlier study (Willis 2007), and the original model of krill on which it was based (Alonzo & Mangel 2001), the preferential conditions of the near-surface habitat relating to higher prey availability for krill were assumed to be present whether or not whales were around.

Niche construction and ecosystem engineering

The basic questions of this study are (1) whether whales and krill are mutual niche constructors which engineer their environment and (2) whether this has a significant impact on the abundances of both species which that environment supports. The niche construction theory explicitly recognises environmental modifications (ecosystem engineering when abiotic) by organisms and their legacy over time (Odling-Smee et al. 2013). Ecosystem engineering is not a new concept. Darwin (1881) showed that worms were ecosystem engineers on geological scales. Nevertheless it is often overlooked in standard behavioural ecological theory (for instance Krebs & Davies 1993). Standard theory, although recognising the physical environment as a source of selection, tends to focus on the interactions of phenotypes in different species, for example in food webs (Odling-Smee et al. 2013). The model presented in this paper may support niche construction theory by

giving a quantitative numerical example of the population impact resulting from individual reproductive success caused by niche construction. Ecosystem engineering and niche construction as evolutionary processes are possibly overlooked because they are assumed to be of relatively minor impact and to happen over time scales much shorter than evolutionary time scales (Odling-Smee et al. 2013). This is particularly true of pelagic marine science where the ecosystem approach has tended to focus exclusively on the food-web interactions of species, and concepts such as mass-balance between species (Pauly et al. 2000). The theory around fisheries management has given minimal regard to even the ecosystem level of standard ecological theory and is generally based on single species exploitation (for instance Hilborn & Hilborn 2012). This lack of theoretical treatment is challenged by the fact that pelagic marine species can directly influence their physical environment, especially through turbulence as mentioned above, and through nutrient retention (Smetacek 2008). The scale of niche constructor influences may be profound (Laland et al. 1999), and it is certainly not outside the range of possibilities that marine animals may impact their physical environment or even the climate (Kerr 2006).

Mutualism and niche construction

Mutualism is important (Hay et al. 2004). Odum (1969) summarised the importance of parasitism, predation, commensalism, mutualism and other forms of symbiosis as a defining character of mature ecosystems. It is not clear if the relationship between whales and krill is simply mutualistic, in which both cooperate to gain net survival or net reproductive benefit, or is better described as manipulative (Krebs & Davies 1993) or exploitative mutualism in a similar way to which human farming exploits other species (Smetacek 2008). For instance whales may influence krill to a mode of behaviour which, on average, increases the abundance of krill, whereas individual krill may increase their reproductive success by alternative strategies in the absence of whales (Willis 2007). Therefore niche construction is perhaps a better fundamental concept with which to start than mutualism because it encompasses both the wide range of possibilities in which 2 species interact with each other, as well as the range of ways they interact with other species and their physical environment. Indeed, the way in which krill and their prey interact is also likely to be just as complex (Kawaguchi &

Takahashi 1996). While mutualisms are fundamental to all ecosystems, the dynamic balances between exploitation, cooperation, benefits and disadvantages are often very challenging to understand from an evolutionary perspective (reviewed in Herre et al. 1999).

The model in this study

I have employed a krill life-history model which was developed to target the behavioural choices (i.e. between deep and shallow habitats) made by krill under different predation pressures (Alonzo & Mangel 2001). This model was previously used for a similar task (Willis 2007) but here is extended to target ecosystem-level changes. The environmental cycles are based on Laws (1977) depiction of the annual cycles of krill, whales and seals. I have used Christensen's (2006) whale population estimates to model changes caused by human exploitation. The object of this study was to capture the basic patterns involved in the ecosystem throughout the period of whaling to provide a rational explanation for the apparent changes in krill abundance that is consistent with (or at least not falsified by) contemporary reports, contemporary data, and generally accepted ecological theory. I have chosen to use an individual-based modelling (IBM) approach, because these models are usually simpler to understand than population models based on differential equations (a comprehensive introduction to, and review of, IBMs in ecology is in DeAngelis & Gross 2009).

METHODS

Design of the model

The fundamental driver of the model is individual lifetime reproductive success of krill in a simple model based on the balance of risks and availability of nutrients. The model is calibrated to 2 overall scenarios: (1) whales present, and (2) whales absent. There are 2 krill habitat options: (1) surface all the time, and (2) surface at night, deep in day (standard diurnal vertical migration [DVM]). At each time step, krill feed, grow and develop fecundity and are subject to predation risk, and may die (Fig. 1). The fecundity and growth of each krill using various zones (surface or deep) is calculated using a set of physiological parameters derived from earlier scientific studies (summarised in Willis 2007 and also pre-

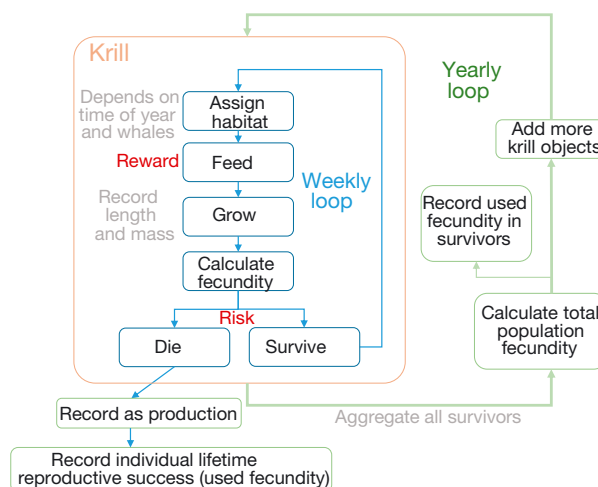


Fig. 1. Flowchart of steps (functions in programming terms) that occur during the running of the model in this study. Model krill ($n = 1000$) are introduced and every model week they feed, grow and allocate fecundity. Each week they are also subject to risk of predation, and some die. Those that do not die contribute to the population additions in the annual loop. All the fecundity in the population is added together and used to determine how many new recruits appear. When a model krill dies, it is recorded how much fecundity it actually used in procreation. This is its individual lifetime reproductive success, which is the driver for evolution through natural selection

sented in Alonzo & Mangel 2001). Variables such as feeding rate, length of day, temperature at depth, and energy expenditure when moving between surface and deep, are used to calculate weekly growth and allocation of fecundity (Fig. 1). The equations used in this model for these calculations are summarised in Table 1 of Willis (2007). The changes in habitat use throughout the year are predefined based on Laws's cartoon of the annual cycles of the Antarctic ecosystem (Laws 1977) and daylight proportion is calculated on a weekly basis using a standard mathematical model of sun elevation (NOAA Sunrise/Sunset calculator, www.esrl.noaa.gov/) (Fig. 2). Each year, in the annual loop (Fig. 1), the total population fecundity is used to determine the number of new recruits to the model. As the model progresses, the abundance of krill changes (determined by risks and population fecundity) along with the overall biomass of krill, and the 'production' which is the sum of biomass of krill which die at each time step and are assumed to be eaten by predators (Fig. 1). The sum of all surviving individual fecundity in the population each year determines the number of new entrants recruited into the population. Fecundity used in this spawning process is therefore a direct measure of individual lifetime reproductive success. Thus the

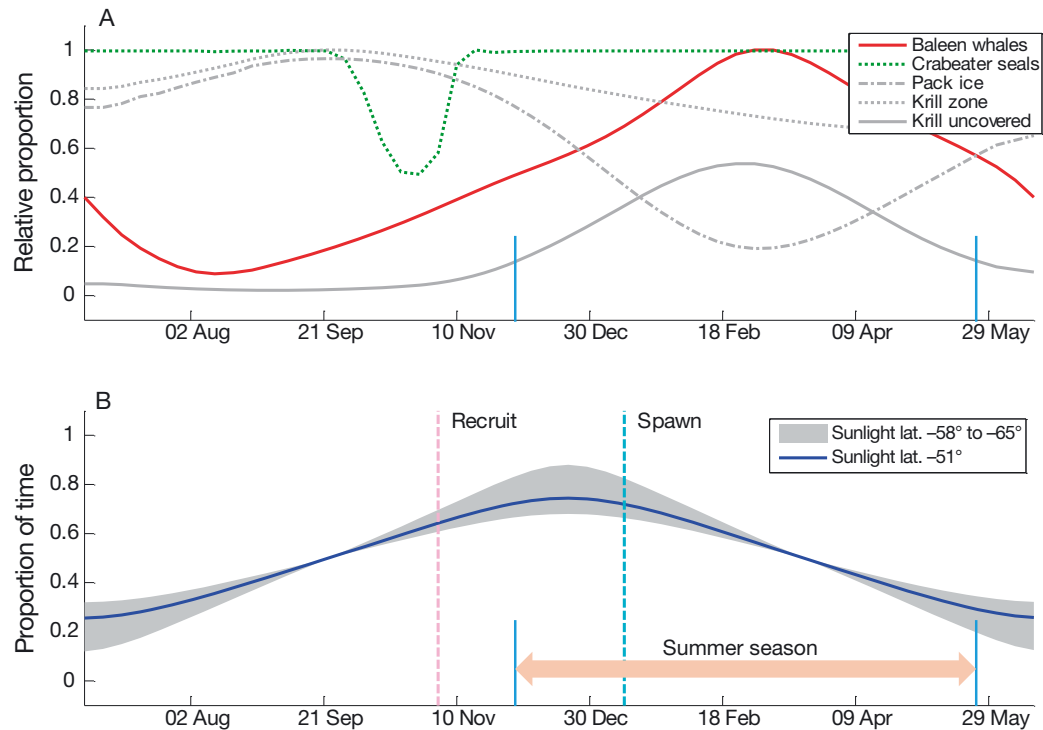


Fig. 2. Annual cycles in the Antarctic ecosystem used in the model. (A) lines are derived from Laws' (1977) cartoon of the ecosystem and show (proportionally) when the pack ice recedes and when whales (red line) and krill (grey solid line) feeding activity occurs. The pack ice cover as a proportion of maximum in any one year (grey dot-dash line) subtracted from the total potential area for krill (dotted grey line) is used to estimate the changes to the area in which krill become available throughout the year (solid grey line). Green line is crabeater seal feeding as a proportion of maximum feeding from Laws (1977). (B) The proportional length of daylight is shown for various latitudes (the latitude indicated by the central blue dashed line was used in this study). The summer season was defined in this model as when the krill activity was above 1.15, and weekly time for recruitment and spawning (calculation of used fecundity) are shown as vertical dashed lines. Note that the summer season for whales is characterised by an almost continual decline in daylight. This suggests that the starting time for whale feeding is critical to their success, as they are thought to be visual predators

model aims to explore the balance between risk, growth, and fecundity in various habitat selections under various risk assumptions, all in the context of what is known about krill physiology. The model is written in a MATLAB® (Mathworks) or GNU Octave compatible script and is available by contacting the corresponding author.

The model can be represented in a flowchart (Fig. 1) and as pseudocode, as follows:

1. Initialise krill
2. Burn-in krill population using a calibrated steady-state population (50 yr)
3. Initialise habitat parameters including presence of whales
4. Loop through 5200 steps (52 wk in each of 100 yr)
 - a. Update environmental parameters based on time of year
 - b. Update whale presence parameters based on year
 - c. Krill behave (choose habitat selections for week, based on presence of whales)

- d. Krill feed (dependent on habitat use)
- e. Krill grow (dependent on existing size and food gained)
- f. If week is spawning week (Fig.2)
 - i. Calculate fecundity
 - ii. Record used fecundity for each individual (lifetime reproductive success)
- g. If week is recruitment week (Fig. 2)
 - i. Recruit new krill (based on total fecundity the year before)
- h. Krill die (of predation dependent on habitat risks)—record details
5. End loop
6. Output results

Use of the model

The model is used here in 2 ways; (1) the risk balance of the habitats is calibrated to produce a result

that is consistent with what is known about the behaviour of krill pre- and post-whaling, and (2) the calibrated model is used to estimate the changes in the abundance of krill before, during and after whaling. Since risk is not associated with any physiological characteristic it is a free variable in the model and any value is equally plausible, in itself, in any habitat. The same values as in Willis (2007) were used for relative food availability, but now the enhanced feeding availability in the surface layers is only represented in the scenario with whales present. All other values are similar, representing no difference in food availability between scenarios and habitats and thus no implied knowledge. Therefore the 4 risk variables (summer surface and summer deep in each scenario [whales and no whales]) are the tuning variables of the model.

Initialisation and model running

The model time step is 1 wk and the usual run length is 150 yr (Fig. 1). The model was initialised with 1000 model krill. The physiological parameters of krill and their life history, including the energy assimilation from food, and the energetic requirements of growth and fecundity at various temperatures, under various lighting conditions, and under different travelling regimes are all held constant and are all similar to earlier studies based on field and lab observations (Alonzo & Mangel 2001). Reward is a proportional instantaneous feeding rate between 0 and 1 which is used to define the comparative feeding opportunity for krill between locations. Risk is a survival probability between 0 and 1. Krill can die each week; those that die are recorded as 'production' and thus all are assumed to have died through predation. New krill are added (as age 1 juvenile recruits) at an annual interval and the number of new recruits is based on a linear function of population fecundity. So the number of krill in the model changes throughout the model run. The summer season is defined as when Laws (1977) (normalised) cartoon of krill activity is greater than 0.15 and spawning and recruitment weeks were likewise chosen to be approximately at the appropriate time of year (Fig. 2).

Calibration

There are 2 scenarios on which the model can be calibrated; (1) pre-whaling and (2) post-whaling.

The assumed characteristics of these states are as follows:

Pre-whaling state

- Roughly stable populations of krill and whales
- Population abundances close to the system carrying capacity
- Krill abundance adequate to support pristine whale population and populations of seals, flying birds, penguins, squid and fish (approx. 700 million t).
- Krill are selected to use the surface zone in daylight, therefore individual lifetime reproductive success (termed 'used fecundity' in the model) is expected to be higher for surface users.

Post-whaling state

- Stability is not assumed
- Population biomass of krill was around 150 million t at some point
- Krill are selected to use the deep zone in daylight, therefore 'used fecundity' higher for deep users in daylight.

Operation

In the operation phase the model is run for 150 yr. The first 50 yr are a 'burn in' period designed to allow the model to stabilise. Since the model employs a feedback mechanism to maintain a population of krill (based on fecundity as described above) it is initialised with an estimated value of total population fecundity. As the model progresses past the first few years the influence of the initial estimated fecundity is eliminated and the model reaches an independent steady state dependent only on the risk parameters. The operation stage of the model then progresses from Year 50 to Year 150 and is designed to model the impact of commercial whaling between 1900 and 2000. The abundance of whales in each year is calculated as a proportion that ranges between 1 (pristine) and 0 (complete extinction) and is based on the total biomass of the 5 main species of whale in this study. The proportion is applied to the krill population to determine if a krill is in an environment with or without whales for the summer season. For example, if there are 1200 krill at the start of a year, and, that year, whale population biomass is at 50% of pristine, on average (actual allocation is determined using a

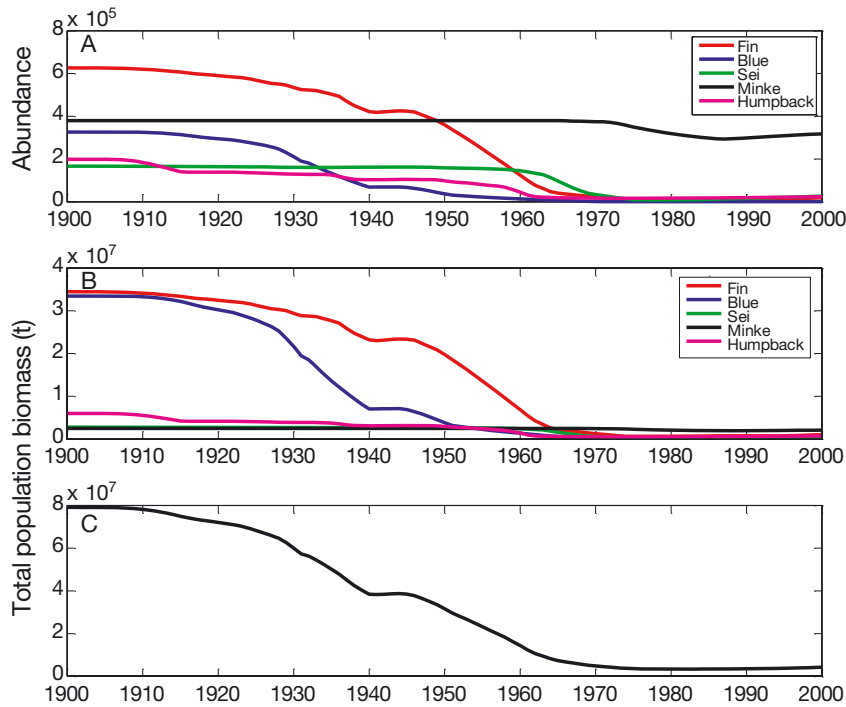


Fig. 3. Abundance, biomass and total population biomass of the 5 species of whales in this study in the Southern Ocean from 1900 to 2000 from Christensen (2006). The whales are: blue *Balaenoptera musculus*, fin *B. physalus*, sei *B. borealis*, humpback *Megaptera novaengliae*, and Antarctic minke *B. bonaerensis*. The abundance values from (A) Christensen (2006) have been multiplied by the average whale mass from the same study to calculate (B) species biomass, and these are summed to produce (C) the total whale biomass. Total whale biomass as a proportion of the maximum is used in this study to calculate the number of krill using each habitat selection in the model

random number generator) 600 krill will be in a whale-free environment and 600 in an environment with whales. In this concept a single krill represents an isolated group of krill that either encounters or doesn't encounter whales during the year in question. Those that encounter whales use the surface habitat, and those that do not use the deep habitat (surface at night, deep in day; DVM).

Abundance of whales

The abundances of whales during the period of 1900 to 2000 in the Southern Ocean were taken from Christensen's (2006) graphs of population abundance (Fig. 3). The average adult mass of each species was used to calculate the population biomass of each species. The sum of species biomasses was used as the estimate of the total population biomass used to determine the proportional abundance of whales throughout the period in the model (Fig. 3).

RESULTS

Calibration

The results of the calibration are summarised in Tables 1 & 2, and Figs. 4 & 5.

The key result in the calibration is in the 'used cumulative fecundity' (lifetime reproductive success) (Fig. 5A). Table 1 shows how in the scenario with whales present, the used lifetime fecundity was significantly higher in the surface habitat choice, which would suggest that krill would be evolved to use this habitat when they can detect whales. With no whales the position is reversed; the used fecundity was significantly higher for the deep habitat, suggesting that krill are evolved to use the deep habitat when whales are not detected. Table 2, giving instantaneous risk (survival rates), also shows this same pattern and reversal, which is logically consistent but not necessary for a plausible calibration. That is; it is plausible that a krill would trade a higher risk for greater lifetime reproductive success, but in this parameterisation that is unnecessary. It is logically consistent

that the calibrated risk levels are also higher in both zones when whales were present.

The weekly production in the surface habitat when whales were around was 4 to 8 times as much as the production in the deep habitat when whales were not present (Fig. 4C), and the total population biomass shows a similar pattern (Fig. 4B). This pattern is dimensionally similar to the recorded changes in the real ecosystem discussed in the introduction, where 1 g of model production is equivalent to 1 million t of real krill. Individual model krill growth shows the periodic shrinkage which is thought to happen during the winter period (Alonzo & Mangel 2001) (Fig. 4D).

Operation

The results of the operation of the model are summarised in Fig. 6. The model krill abundance increased over the initial 50 yr as the whale abundance

Table 1. Model krill population parameters after 50 yr in the calibration scenario, using the 2 habitat selections (surface [all the time] and deep [surface at night, deep in day; i.e. diurnal vertical migration] during the summer season) for the 2 scenarios (whales and no whales), mean values \pm 1 SD of 5 similar runs of 1000 model krill

	Whales	No whales
Krill abundance (from an initial population of 1000)		
Surface habitat	925 \pm 164	1 \pm 1 (collapse)
Deep habitat	1 \pm 1 (collapse)	447 \pm 126
Weekly production (g)		
Surface habitat	7.1 \pm 1.2	0
Deep habitat	0	1.2 \pm 0.4
Lifetime used fecundity of a group of 300 model krill tracked from 50 yr until death (arbitrary units)		
Surface habitat	874 \pm 271	389 \pm 123
Deep habitat	400 \pm 60	792 \pm 54

Table 2. Model krill risk and reward values for surface and deep zones in calibration scenarios. Values in **bold** are those that impact the comparative results between the scenarios. Risk is expressed in annual survival proportion; thus a high value indicates a lower risk

	Whales	No whales
Risks (annual survival rates)		
Surface daylight	0.9534	0.96
Deep daylight	0.94	0.974
Night time	0.99	0.99
Under ice (winter)	0.995	0.995
Feeding opportunity (day and night time, proportion of maximum)		
Surface	1	0.7
Deep	0.7	0.7
Under ice (winter)	0.5	0.5

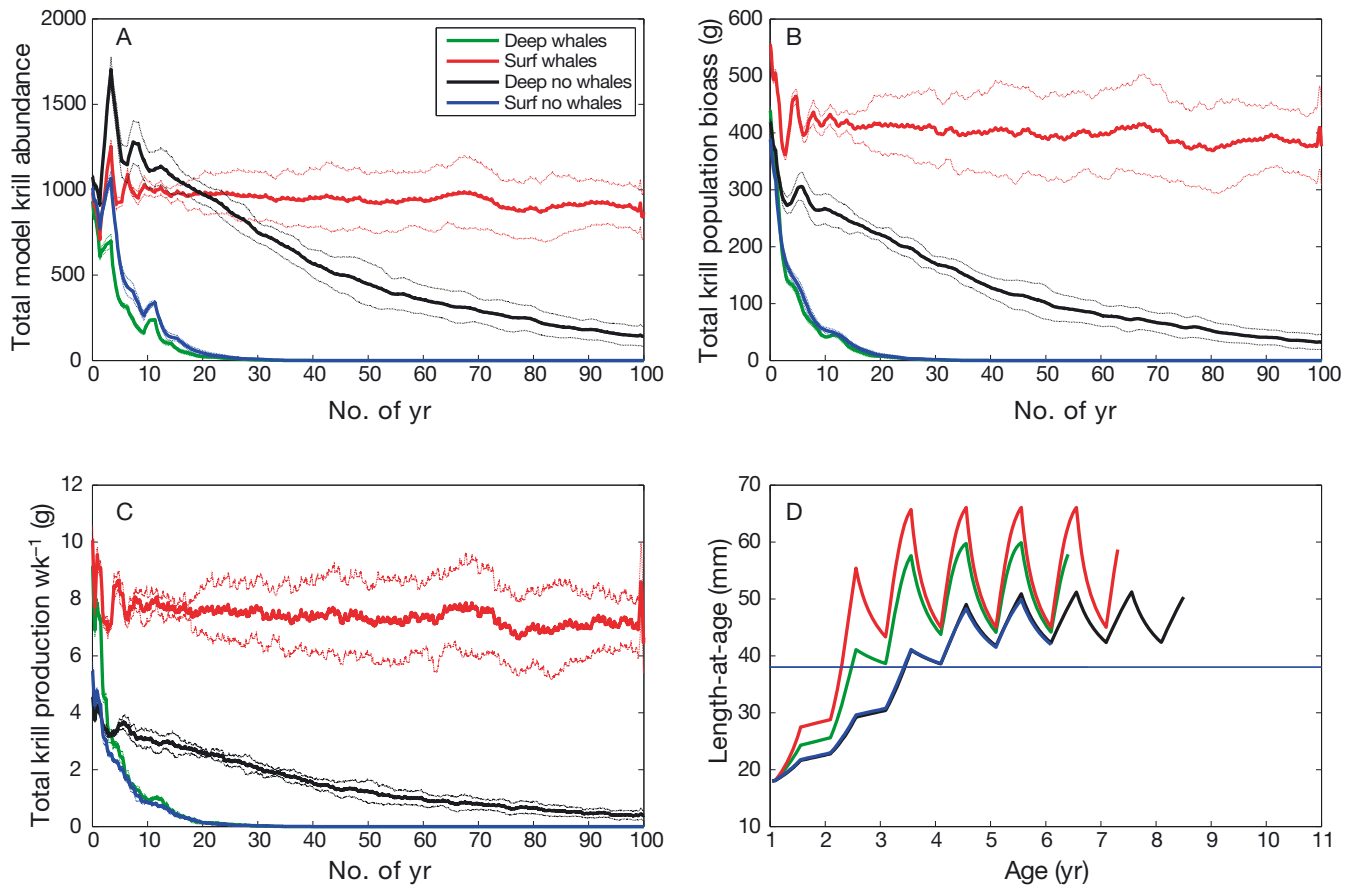


Fig. 4. Results from the model in the calibration phase, showing the various implications of the risk and reward balances in the 4 habitat scenarios through 100 yr on model run time. 'Deep' means krill are at the surface in the nighttime and deep in day; 'surf' means krill are at the surface day and night. (A) Mean (\pm SE) total krill abundance of model krill after 5 model runs, showing how abundance decreases for all scenarios except surface when whales were around. Mean \pm SE (B) krill population biomass and (C) production showing similar patterns. (D) Average length of a batch of 300 model krill after 50 yr. The lines are truncated at different points as no krill lived past these ages. Krill are thought to shrink during periods of low food, and this effect is also shown

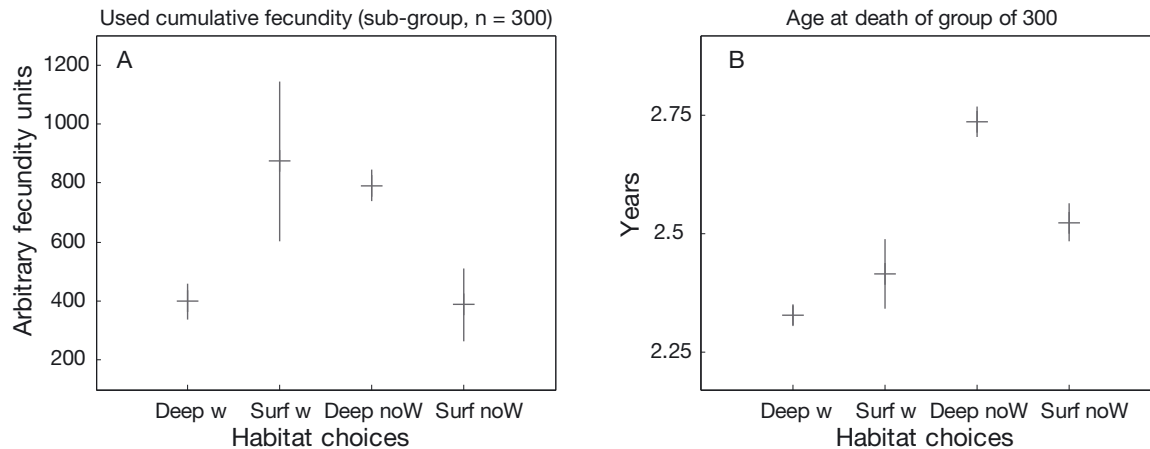


Fig. 5. Differences in (A) used cumulative fecundity (a direct measure of individual lifetime reproductive success) and (B) age at death of a sub-group that entered the krill population after 50 yr in the calibration phase, based on the presence/absence of whales in the model. The vertical lines indicate ± 1 SD of 5 replicates. (A) When whales were around (deep w and surf w), the used fecundity was significantly higher for the surface habitat, and that the position was reversed when whales were not present (deep noW, surf noW). (B) Krill live longer on average in the deep habitat when whales were not present. Hence, 'deep noW' is a live-long grow-slow habitat in contrast to 'surf w', which was a grow-fast die-young environment. This is the key result of the calibration of the model. Krill evolved to go deep when whales were not present but to stay at the surface when they were present

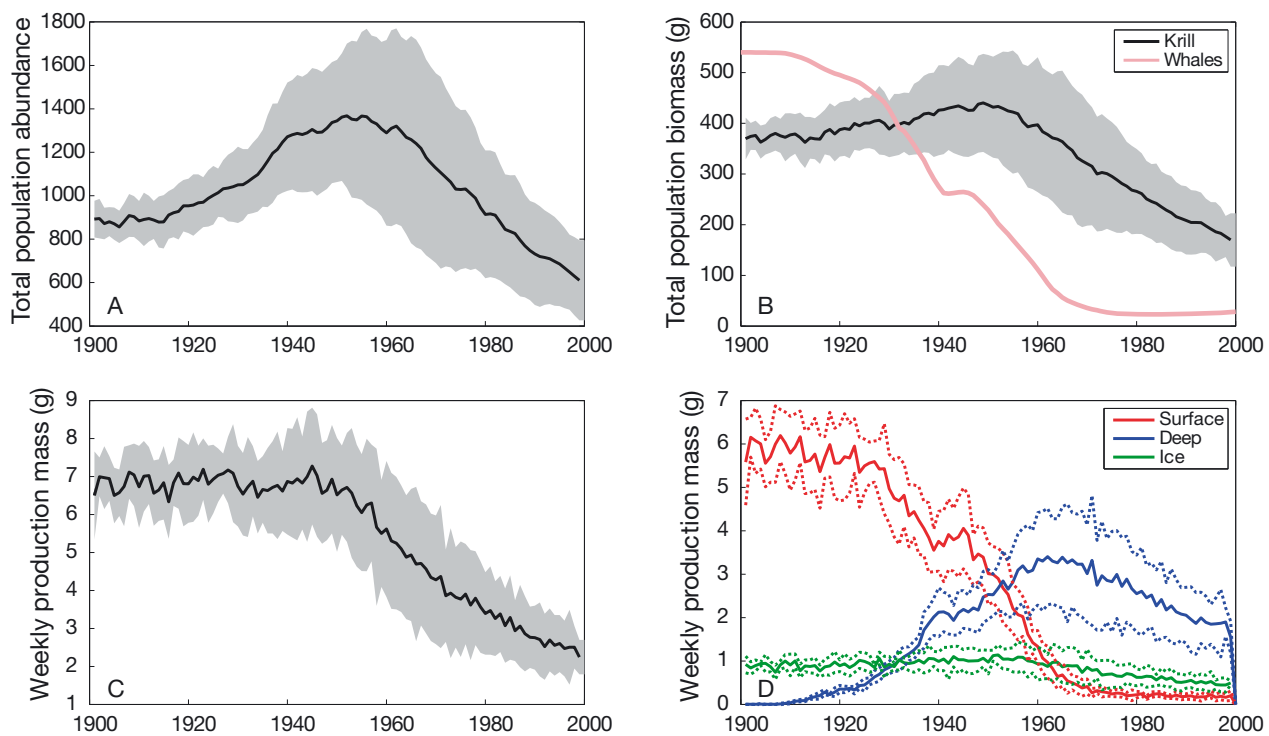


Fig. 6. The krill model in this study in relation to the proportion of whales present (in terms of biomass) throughout the period from 1900 to 2000. The whale biomass, and therefore implied presence, is external information which drives the model results. Means ± 1 SD of 5 replicates are shown. (A) The total abundance of krill increases as the decline in whales begins. (B) The population biomass of krill remains reasonably stable during this period as more krill change habitat, which is similar to (C) production. Average weekly production is shown (7 g would relate to $\sim 371 \text{ g yr}^{-1}$). By 1960, however, the abundance, biomass and production of krill all diminish in the same pattern as the abundance of whales. (D) Krill production according to habitat, showing how krill production at the surface follows a pattern very similar to the whale biomass, as krill are leaving the surface habitat in that same proportion (red line). The krill in the deep habitat builds up but begins to decline after 1970. There is no evidence from the real ecosystem which contradicts this pattern. Production during the winter when krill are under the pack ice is shown in green

fell. This is caused by the longer life of krill in the deep habitat (Fig. 5B), which causes a very slightly higher percentage of additional older krill to begin each year, and thus increase the population fecundity as spawning happens soon after the start of the new season (Fig. 2). This is supported by the relatively unchanged krill population biomass during this period (1900–1950, Fig. 6B). This effect was balanced and reversed after 50 yr as the whale population became so low as to put more krill into the deep habitat, and the pattern of population decrease in the habitat became dominant. Overall production was unchanged during the initial period, which implies that there was more food available during this period for other surface predators of krill (as whales' requirements diminished). Both whales and non-whale predators are assumed to make a numerical or behavioural response to the additional resource and so maintain the risks as constant. The production switched from availability in the surface zone to the deep zone after ca. 50 yr and finally ends up predominantly in the deep zone (Fig. 6C). Krill production in the ice remained relatively constant throughout, only slightly diminishing toward the end of the period (Fig. 6D). If under-ice production of krill is the determinant for the crabeater seal population (which are assumed to be a large proportional predator on krill in the winter) then it would explain why their population abundance has remained relatively unchanged, until a slow decline started ca. 1960.

DISCUSSION

The calibrated model shows that there are plausible balances of risk that produce results consistent with what is known about the ecosystem and krill behaviour before and after whaling. The calibrated model linked to the decrease in whales produces a reasonably consistent pattern of decreased krill abundance and biomass that has been observed in the actual system. This includes the decrease in surface production (and thus visibility of krill) matched with the decrease in whale abundance (Fig. 6). Therefore it is reasonable to assume that whales did maintain a high abundance of krill, until any of the main assumptions of this study are falsified.

The mutualism between whales and krill (expressed in terms of population abundance) is clearly shown by the model as the reduction in whales leads to a delayed response in the abundance of krill (Fig. 6A,B). The individual lifetime reproductive success of the model krill would be a plausible cause for

their likely habitat selection behaviour (Fig. 5). The instantaneous risk (Table 2) would also drive this pattern. This type of lagged response is typical of niche construction theory (Laland et al. 1999). The lagged response is an emergent property of the model and is caused by multiple factors, including simple predatory release, mixed life histories (krill developing quickly in the surface layers and subsequent years living in the less risky habitat) and the rate of decline of population abundance in the deep habitat. The decrease in population biomass of krill lags that of whales by around 20 to 40 yr (Fig. 6), which is 5 to 10× the average lifespan of krill (Fig. 5) which is indicative of the concept of niche construction providing legacy impacts to future populations beyond the lifetime of a single animal (Odling-Smee et al. 2013).

It seems counter-intuitive that whales evolved to maintain a high abundance of krill. The alternative is even more counter-intuitive. The broad implication of the importance of niche construction for mature ecosystems are often mirrored elsewhere (Laland et al. 1999, Odling-Smee et al. 2013). Regularly removing large quantities of what is essentially 99.9% grassy biomass from a domestic lawn to maintain a grass-based ecosystem is a direct analogue to the fundamental mechanism of this study. Grass and herbivores evolved in lowland ecosystems, and removal of large grass-eating herbivores leads to less grass, rather than more grass (Vera 2000). In exactly the same way, niche construction theory suggests that the removal of whales from the ecosystem to which that had evolved was bound eventually to lead to less krill, their only prey, rather than more, and any other outcome would be illogical and unexpected.

The predictive potential of the theory presented here, based on niche construction, may be no better than the previous, least daring, theory. For example, expectations of an experiment involving the reintroduction of wolves in Yellowstone National Park (Beschta & Ripple 2013) were not met. The ecosystem did not return to its previous state after the reversal of the removal of wolves. Irreversibility such as this is called hysteresis, a common ecosystem phenomenon (Mangel 2006). Species that were thought unimportant may in fact have a pivotal role; others held footholds (constructed niches) that they had previously been denied. For example, krill preferentially eat salps, which leads to potentially complex linkages between krill and their prey (Kawaguchi & Takahashi 1996). Salps and copepods both are filter feeders, like krill, and both have a far higher overall biomass in the Southern Ocean than krill (Voroniina

1998). Salps appear to have increased in abundance while krill have decreased (Atkinson et al. 2004). Prey at one life stage may be a competitor at another stage, potentially leading to a further level of niche construction which is very common in aquatic ecosystems (Hay et al. 2004). Furthermore, large mobile species which have been either invisible or at apparently low abundances may play a pivotal role; especially fish and have cephalopods which predate krill using the deep habitat and which have the potential for a rapid numerical response to environmental perturbation (Ainley et al. 2010).

Objection to Godlewski's hypothesis

The most compelling argument against Godlewski's hypothesis (i.e. that krill have changed their behaviour after the end of commercial whaling) is that it is hard to explain in terms of evolution by natural selection, particularly in light of how quickly the change is supposed to have occurred (Smetacek 2008). In response to this argument it is worth examining behaviours of closely related species, because if they have been shown to exhibit similar behaviour to that proposed for krill, it suggests that such behaviour is plausible for krill. In fact, there are many examples of Crustacea changing their daily vertical migrations in response to predatory threat. A particularly convincing example of this behavior is the variations in patterns of DVM in the water flea *Daphnia magna* when the concentration of fish odour increases or decreases (Loose & Dawidowicz 1994). High concentrations of fish odour in the environment cause an instantaneous switch to more intense DVM and less exposure to light (Loose & Dawidowicz 1994, Giske et al. 1998). There are many other examples of marine and freshwater Crustacea changing DVM in response to the perception of threat from visual predators (e.g. Stich & Lampert 1981). These similar examples have been derived from field and laboratory observations and are cued through olfaction, mechanical stimulation or vision (Stich & Lampert 1981, Gliwicz 1986, Bollens & Frost 1991, Fiksen & Giske 1995, Fiksen 1997, Fiksen & Carlotti 1998). Mackintosh (1934), Marr (1964) and Hardy & Gunther (1936) all independently concluded that most krill stayed at the surface but a minority exhibited DVM. So, an instant switch in DVM due to avoidance of whales as visual predators, cued by odour, mechanical stimulus or vision, is not only plausible; it is a very strong candidate for an explanation of DVM of krill. Arsenev (1958) explains how whales and krill

are most often observed together at the surface, but that deviations from this regularly occur (whales without krill and vice versa). Arsenev (1958) explains that it appeared that such phenomena (deviations) are only observed in the course of a single day; on the following day whales appeared where there was only krill before, and vice versa. Arsenev's (1958) observations suggest that krill will switch DVM locally within one daily migratory cycle in response to the threat of predation by whales, but also that whales do not have to be physically present to invoke the response. A similar rapid switch of DVM has been shown experimentally for the marine copepod *Acartia hudsonica*, again only due to the credible perception of predatory pressure rather than the presence of actual predators (Bollens & Frost 1991). Added to these examples of closely related species, theoretical considerations of krill physiology and habitat selection support the plausibility of Godlewski's hypothesis (Alonzo & Mangel 2001). Although Godlewski (1996) considered the behavioural change to be potentially an evolutionary change, that is not a necessary requirement of the hypothesis. The change was most likely due to behavioural plasticity of krill, however, the developing theory around rapid niche evolution would suggest either is a possibility (Kozak & Wiens 2010). So, in conclusion, it is likely that all krill regularly switched between both behavioural states in the pristine ecosystem. When the abundance of whales was high, the majority of krill remained at the surface day and night, but all krill retained the ability to switch daylight habitat based on the immediate perception of predatory threat from whales. This study examines what this conclusion implies for the changes to abundance in krill as a result of commercial whaling.

Behavioural trigger

The linkage between odour and behaviour has not been shown in krill but there is some evidence that this is a plausible hypothesis (which is worth testing). Dogs (*Canis canis*) can be trained to pilot boats to locate whale faeces from several kilometres away using smell (Rolland et al. 2006). Whale faeces are buoyant and remain at the surface for days (D. Ainley pers. comm.). In turn, krill are sensitive to olfactory cues. The highest krill olfactory sensitivity was shown to be to Newcastle Brown Ale, where experimental subjects needed to be prised off the pipette used to introduce the substances into the test apparatus (Hamner & Hamner 2000). Perhaps not coincidentally Newcastle

Brown Ale, which is a dark bottled beer, has a relatively high concentration of soluble iron (Sancho et al. 2011). Whales in the Arctic have been observed preferentially attacking krill at depth in daylight (Laidre et al. 2010) which supports the concept that deep in the day was higher risk for krill when whales were around, but which also suggests that whales are used to finding krill at depth as well as at the surface and adds credibility to the theory that krill may have evolved this behaviour as a response to the presence of whales.

Alternative explanation: a fisheries management approach

Mori & Butterworth (2004, 2006) attempted to explain the changes in krill abundance due to commercial whaling by fitting a fisheries management model to whale catch data. This is a prime example of standard ecological theory which is has been contrasted unfavourably to niche construction theory in other examples (Laland et al. 1999). Their model led them to hypothesize that a krill surplus did happen due to release of predatory pressure, and that krill abundance peaked in 1950, well before the end of whaling (which ended around 1970), and has decreased since then. Mori & Butterworth (2006) concluded that krill biomass under unexploited coexistence with whales was around 150 million t, which then gradually increased to about 700 million t during the first half of the 20th century, after which it declined again to around 200 to 300 million t around 2006. The main challenge in the Mori & Butterworth (2006) model was to explain how the high abundance of krill caused by the predator release from whaling was subsequently reduced through alternative predators. There are similarities in the suggested abundance pattern of krill in the Mori & Butterworth (2006) model and the model presented here (Fig. 4), the principle difference between the studies lies in the explanation for the decline following the peak abundance. The Mori & Butterworth (2006) model fails to provide an explanation for the observed changes in krill abundance, for 2 principal reasons; (1) the main hypothesis has been falsified, and (2) the initialisation is implausible. These points are explained in more detail in the paragraphs following. The Mori & Butterworth (2006) model was convenient for those wanting to support a fishery for krill or minke whales; it suggested that the abundance of both are higher now than they were in the pristine state.

Contrary evidence to the conventional model

Mori & Butterworth (2006) proposed that minke whales and crabeater seals increased in abundance as a result of increased krill availability between 1920 and 1950. This then is supposed to have caused compensatory predatory pressure which led to a decrease in krill abundance since 1950, even as whale abundance continued to be reduced through whaling until 1970. They confirm that their model would not fit with whales alone and so crabeater seals are employed as the additional factor which drives the krill abundance down after 1950. In order for this to be a partially plausible scenario, the population abundance of minke whales would have needed to have risen very quickly before the 1950's from a previously low level (they suggest from 300 000 to 1 200 000) and crabeater seal abundance would also have needed to grow from very low (~1 000 000) to high abundance (~20 000 000) during the last 20 yr of commercial whaling. In addition to no other evidence to suggest minke whales increased in abundance, these hypotheses have been falsified (1) through genetic studies of the minke whale population (Ruegg et al. 2010), and (2) by contemporary reports. For instance, crabeater seals, sometimes in high abundance, were reported by every major expedition that passed through the pack-ice in the southern summer before 1962 or stayed over winter in the pack ice, as a Belgian expedition did in 1898; estimated abundances were consistently between 2 and 5 million (Marr 1964). There was no mention of a 20-fold increase, and a 44 yr time series in the Antarctica Peninsula region suggests no long-term trend in crabeater abundance after 1950 (Ballance et al. 2006). In comparison, the model presented in this study suggests that krill abundance, available to predators in the deep habitat, was relatively high during the 20–40 yr around the end of commercial whaling (1940–1980) but then decreased (Fig. 6D). This may correspond to an increase in crabeater seals (which is difficult to quantify), and the population patterns of fur seals (Ballance et al. 2006) and gentoo penguins (Emslie et al. 2013).

Initialisation of the conventional model

The other difficulty with Mori & Butterworth's (2006) model was that it was based on implausible initial assumptions about the pristine state of the system. In short, they assumed too few whales eat-

ing too small an amount of krill. This then allowed for the model to fit a massive proportional increase in krill abundance to levels consistent with contemporary reports in the 1970's. Their estimate of the krill eaten by the whales which were killed during whaling was roughly 50 million t as opposed to the commonly quoted estimate of 147 million t (Laws 1977). The Mori & Butterworth (2006) estimate was an implausibly low number; whales alone weighed roughly 60 to 70 million t (see earlier analysis of Christensen 2006). Mori & Butterworth (2006) excluded 50% of fin whales and all the sei whales (although, for instance, Harrison Matthews (1938) suggested sei whales only ate krill). There is no reason, or precedent, for a separate fin whale population, rather the potential separation of feeding locations is more consistent with the theory of mature ecosystems and niche specialisation (Odum 1969). Their fitted model estimated the pristine abundance of blue and fin whales (187 000 and 235 000 respectively) to be much less than estimates in other studies; an alternative study based on a reasonable life history model estimated 327 000 and 625 000 respectively (Christensen 2006). Laws (1977) had suggested 200 000 and 400 000, without the benefit of Russian catch reports that were then not available. It is likely the pristine abundances of these species were more than these highest estimates, as has been suggested through genetic studies of other similarly exploited whales (Ruegg et al. 2013). The Mori & Butterworth (2006) model further relied on whales in the pristine state being continually starved through 'overfishing' krill. This scenario would simply have led to smaller or fewer whales over time in either a behavioural or function response to the limitation of food (Holling 1959). The concept of whales over-harvesting the krill below the maximum sustainable yield at a fraction of the carrying capacity (~30%) is an anthropomorphic concept contrary to ecological theory. Ecological theory would suggest that the amount of standing crop biomass supported by the available energy flow is expected to increase to a maximum in the mature or climax stages of an ecosystem (Odum 1969). The idea that whales were 'half-starved' as a result of overfishing the krill before the start of whaling is also falsified by contemporary reports based on stomach contents. Whales examined during the early whaling period usually had stomachs full of krill (Hardy & Gunther 1936). Mackintosh & Wheeler (1929) examined 519 blue and fin whales and all but 68

had full stomachs of krill. Ruud (1932) found that of 300 whales examined in factory ships, only 2 immature whales had empty stomachs, and all others had krill in large quantities. Mori & Butterworth (2006) make several other assumptions which are inconsistent with ecosystem ecological theory. As mentioned above, they suggest that there was a high level of interspecific competition which caused a suppression of the abundance of minke whales and crabeater seals in the pristine state; apart from the fact there is no evidence for this, and no explanation for how it might have happened (baleen whales do not attack each other or seals and vice versa), it is inconsistent with the characteristics of mature ecosystems which have high levels of niche specialisation and mutualism (Odum 1969). The only example they give to suggest this might be plausible involves 2 species of odontocetes fighting over fish hooked on a longline, again an unnatural situation, involving whales which are very different from the mysticetes discussed elsewhere in this study. On the other hand, ecosystem theory is again borne out through detailed reports of separation between minke, fin, sei and blue whales feeding times and/or places (Kemp & Bennett 1932, Marr 1956, Laws 1977, Santora et al. 2010). Mori & Butterworth (2006) also suggest a relatively high range of natural mortality for the larger whales, allowing their model to fit to large whales with a low average natural lifespan and thus quicker population turnover. They modelled large whales, some of which were the largest animals that have ever existed, as if they were smaller animals (bigger animals live longer than smaller ones; Speakman 2005). For instance, they used a limit of 0.03 to 0.06 in annual mortality for blue whales (Laws [1997] had estimated 0.027 to 0.033). A range of 0.01 to 0.03 or lower would have been more consistent with the facts (Branch et al. 2004, Ramp et al. 2006), our uncertainty, and the theory of longevity of apex predators in mature ecosystems (Odum 1969).

Other explanations: climate change

Flores et al. (2012) suggested that the long-term decline in krill abundance was the result of climate change through the reduction of sea ice and other environmental changes. Sea ice extent has been shown to be a factor in krill recruitment (Kawaguchi & Satake 1994). Later studies showed that sea ice had not reduced as Flores et al. (2012) had thought, and

rather that it had an inverse relationship to sea temperature (Shu et al. 2012). Therefore sea ice reduction is not a plausible explanation for the long-term decline in krill abundance. In general, climate change cannot yet be implicated as the major cause of krill abundance changes since the end of whaling (Trathan et al. 2012); the present study does not falsify any hypotheses derived from that theory.

Hypotheses generated by this study

The model presented here, or more correctly the modelling process, helps develop hypotheses that would be valuable to test (Table 3). The model suggests that krill respond to the threat of whales. The smell of faeces is a likely cue. Krill can change their daily migrations within a single cycle. All these

Table 3. Summary of predictions and hypotheses derived from the modelling and discussed in the text

Condition	Predictions or hypothesis
1. Surplus of krill in the deep habitat from about 1950 to (see Fig. 6).	Predators which are able to exploit krill in these areas 2000 are likely to have had higher abundance during this period, for instance: crabeater seals, fur seals, fish, squid, some penguins and other species (Ballance et al. 2006).
2. Krill population abundance has decreased since ca. 1970.	Krill population abundance may continue to decrease or be approaching a low asymptote (Atkinson et al. 2004).
3. Non-whale surface predators may have benefited from a cooperative relationship with whales.	Previous abundances of surface krill predators may provide indication of previous abundance patterns of whales.
4. Whales may have developed mutualistic relationships between species.	The abundance patterns and numbers of fin, blue, minke, sei, and similar species may have been mutually interrelated. For instance, they may have inhabited the same areas in succession throughout the summer season as day length reduced. Successively smaller feeding requirements could have maintained the nutrient retention cycle for surface krill.
5. Whales may have developed mutualistic relationships between individuals.	The abundance patterns of whales are likely to have been dispersed or grouped dependent on the availability of surface-inhabiting krill. Where krill are at the surface, whales may develop mutually beneficial fertilisation and strong aggregation behaviour, whereas whales may disperse to search for deep inhabiting krill.
6. Krill will react strongly to whale faeces.	Krill are attracted to substances rich in soluble iron (Hamner & Hamner 2000). They should react by changing their behaviour.
7. Krill on the surface in daylight indicates whales are around, will be around or were around the day before.	Observations already confirm this (Arsenev 1958) and more advanced instruments should further confirm.
8. Abundance patterns of krill will be dependent on the deposition of whale faeces.	Krill may swim laterally to areas of high concentration of whale faeces and thus congregate in patterns that are different from passively advected particles. The retention of krill in the Antarctic Peninsula Plume (Smetacek 2008) may be an example involving a major ocean feature. It is otherwise unknown how krill navigate.
9. Krill size will vary less through the annual cycle: they may now be smaller and live longer than when whales were abundant.	If winter feeding opportunity is lower than summer, then the lack of additional nutrients due to the breakage of the nutrient retention cycle means that krill body size fluctuation will be less (Fig. 5), however the lowered risk may mean krill live longer on average.
10. Whales will defecate in patterns (spatially and temporally) which will serve to preserve the patterns of maximum feeding opportunity, and maximum retention of faeces in the surface layers.	If an area is saturated (over-fertilised) or unproductive it is likely a whale will travel to an alternative location to defecate. This depends on digestive rate and swimming speed and on the whale's cognitive and sensory appreciation of the hydrodynamic environment. Top predators target Lagrangian coherent structures (Tew Kai et al. 2009) which are eddies, fronts, convergences or divergences which can serve to concentrate substances, small animals and plants at the ocean surface. Whales may sense these directly or indirectly.

behaviours have been the subject of extensive research on other closely related species, as outlined in the introduction, and much further research with krill in the laboratory and field is warranted. The fertilisation process derived from whale faeces must take some time, perhaps a few days or weeks, and there must be a process of dilution and transport related to water movements and thus weather or hydrodynamics. There is great opportunity to model the implications of fertilization and turbulence in biogeochemical ecosystem models. Mackintosh (1934) mentioned the hydrodynamic associations with whales in convergences, vortices, etc. and assumed that krill passively aggregated in these areas, but the situation is potentially more to do with the aggregation of planktonic prey of krill. There may also be local feedbacks where a group of whales fertilising the same area leads to an overall increase in feeding opportunity for krill, and whales and other predators. Whales have the choice where to deposit the fertiliser and this might lead to spatial patterns that are independent of physical processes or enhanced by them, i.e. whales may congregate or disperse to defecate, or go to certain areas such as persistent eddies or upwellings in order to make best use of the fertilisation process. There is much scope for observation and modelling of whale activity in this respect. The distribution of krill is associated with ice cover (Kawaguchi & Satake 1994) and so there may be other confounding factors.

Improvements to the model

The model is very simple and so there is an almost endless number of improvements that could be made if realism is the objective, although this may not be the best objective for such an idealised model (Odenbaugh 2005). Firstly, the model includes no limitations on resources and no density-dependent release of predation at low abundances. This does not impact the calibrated states, but does limit the model as a predictor outside these states. For instance, the model calibration suggests it is plausible that the krill population has diminished, but cannot be used in any way to aid prediction about when the decrease will be terminated through density-dependent effects, i.e. through a lower risk which should happen at some low abundance. As for other more minor potential improvements, there are a number of alternative options for linking whale abundance to krill encounter and thus krill habitat use. Rather than an annual allocation, the likelihood of presence of

whales for each krill could be re-determined on a weekly, monthly or other temporal schedule. In this case, however, it is unknown how long the period between whale fertilisation and feeding advantage takes. Presumably it takes some time (at least 1 wk) and begins a positive feedback mechanism locally and so may take several weeks or months to build up to a threshold or maximum. Presumably once it begins to build up it makes the area more attractive to other whales and so may reinforce itself for sequential groups of whales. Kemp & Bennett (1932) suggested whales of different species (fin and blue) frequented the same areas in succession. Once the positive feedback mechanism has started it seems therefore unlikely that a whale would move on from a higher feeding opportunity to speculate about feeding potential in other areas (Table 3). However, water movement, ice, competition and weather patterns may impact the effect. Or the whales may purposely fertilise and return on a schedule based around a number of locations. Since these factors are mostly unknown it seemed most parsimonious to assume linkage on an annual basis.

CONCLUSIONS

The mechanisms outlined in this study offer the potential for development of a krill fishery based on fertilisation and behavioural control of krill. It must be possible to distribute an analogue of whale faeces over small areas and bring krill to the surface, thereby causing krill abundance and production to increase in the same way humans farm, e.g. grain and cows, through a mixture of protection and aggregation with individuals compressed in artificially fertile areas. This would be a more sustainable plan than competing with recovering whale populations for a diminishing residual resource and perhaps driving the krill and whales to extinction.

Krill abundance is less than one quarter of what it used to be in the pristine ecosystem. Even in the face of high-quality unequivocal scientific evidence, this stark fact has been overlooked or obfuscated in the scientific conversation around the exploitation of krill. The precautionary approach would be to stop all krill fishing until the krill and whale population abundance pattern is clearly understood. Furthermore, the impact of whales on the ecosystem is likely to be a lot more complex than the one feedback mechanism in this study (Ainley et al. 2010). At very least, a representative spatial and temporal protected area should be implemented in order to avoid any

further confusion about the state of the ecosystem in the absence of exploitation. Maintenance of an ecologically relevant protected zone would be the minimum indication that a precautionary approach exists in action rather than solely as rhetoric. The failed protection of the Ross Sea would have been such a signal of intent (Blight et al. 2010).

Southern Ocean whale population biomass decreased during the 20th century in a strangely smooth curve (Fig. 3) only interrupted by the Second World War, demonstrating the complete futility of the size-based rules (Marr 1956) and any other management intervention. Experiences of whalers from the Arctic moving on to work in the Antarctic meant that serial depletion of whale populations on a global scale was clearly common knowledge well before the peak of whaling in the Southern Ocean (Villiers 1925). Likewise, we should accept our own limitations in the face of very strong evidence. We should admit that history suggests that a profitable krill fishery, however small it is now, is a warning of the likely expansion of the fishery until krill are commercially extinct.

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