An ecosystem-based approach to management: using individual behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging

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Summary

1. Changes in species' abundance and distributions caused by human disturbances can have indirect effects on other species in a community. Although ecosystem approaches to management are becoming increasingly prevalent, they require a fuller understanding of how individual behaviour determines interactions within and between species.
2. Ecological interactions involving krill are of major importance to many species within the Antarctic. Despite extensive knowledge of the ecosystem that they occupy, there is still incomplete understanding of the links between species and the effect of environmental conditions on these interactions. In this study, we extended a behavioural model used previously to understand the interactions between penguins and krill to determine the indirect effect of krill fisheries on penguin foraging success and behaviour in adjacent breeding sites.
3. Increased fishing pressure offshore is predicted to reduce penguin food intake. Given the documented links between krill and penguins, this also leads to a prediction of decreased penguin survival and reproduction. Krill behaviour is predicted to cause stronger effects of krill fisheries than explained solely by the percentage of biomass removed. Environmental conditions that decrease krill growth rates or cause krill to spend time in deeper water are also predicted to increase the magnitude of the effect of fishing on penguin success. We show that changes in penguin foraging behaviour can be used to assess the impact of local fisheries on penguin reproductive success.
4. *Synthesis and applications*. These results demonstrate that an understanding of predator–prey interactions, indirect effects between species, and individual behaviour is imperative to our ability to manage populations. We describe a general method to use what is known about ecological and evolutionary processes with species-specific information to predict the response of organisms to novel situations. We further show how individual behaviour can be used to assess the impact of human disturbance on ecosystems.

Key-words: behavioural plasticity, habitat selection, species interactions

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Introduction

Interactions between species influence population dynamics and cause indirect ecological effects. Traditionally management has focused on single species (King 1995; Quinn & Deriso 1999; Haddon 2001; Jennings,

Kaiser & Reynolds 2001). However, changes in the abundance and size or spatial distribution of a single species can have cascading effects on a wide variety of other species (Yodzis 1994; Estes 1996; Croll & Tershy 1998; Estes *et al.* 1998; Mangel & Switzer 1998; Nicol & Endo 1999; Gill, Norris & Sutherland 2001; Marin & Delgado 2001; Lester & Harmsen 2002; Ormerod 2002) so that community interactions should ideally be considered even when managing individual species. As a result, ecosystem approaches to management are becoming increasingly prevalent (Constable

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et al. 2000; Boyd & Murray 2001; Schneider 2001; Ormerod 2002). At the heart of an ecosystem approach must be an understanding of the interactions between the species of interest and how these interactions are influenced directly and indirectly by environmental conditions, the abundance and distribution of each species, and interactions with non-target species. However, to a great extent ecosystem approaches to management have not considered how individual behaviour and behavioural plasticity affects species' interactions.

Managers and ecologists alike have trouble knowing how to apply these general ideas to their specific systems because community interactions can be extremely complex and better management tools are required. A general theoretical framework now exists for examining the effect of behavioural and evolutionary interactions within and between species on ecological patterns (Alonzo 2002). We have demonstrated how this approach can be used to increase understanding of interactions between predators and prey when applied to a specific system (Alonzo, Switzer & Mangel 2003). In this paper, we demonstrate how this general method can be applied to a specific system to address a specific management problem.

Antarctic krill *Euphausia superba* Dana plays an extremely important role in the Antarctic. Most organisms in the Antarctic are one or two trophic levels away from krill. They are one of the most abundant food sources for a variety of species, and many species rely on them almost entirely (Croxall *et al.* 1985; Miller & Hampton 1989; Trivelpiece *et al.* 1990; Smith *et al.* 1995; Hill *et al.* 1996; Reid *et al.* 1996; Loeb *et al.* 1997; Croll & Tershy 1998; Mangel & Switzer 1998; Nicol & Endo 1999; Constable *et al.* 2000; Boyd & Murray 2001; Charrassin & Bost 2001; Marin & Delgado 2001; Boyd 2002). As a result, understanding krill and their ecological interactions is of utmost importance to our understanding of most Antarctic species.

There has been concern that commercial krill fisheries in the Antarctic may have indirect effects on krill predators (Ichii, Naganobu & Ogisima 1996; Croll & Tershy 1998; Mangel & Switzer 1998; Boyd & Murray 2001; Marin & Delgado 2001). The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) requires an ecosystem approach to managing the Antarctic fisheries (Constable *et al.* 2000). With increasing interest in krill fisheries and concern about managing the ecosystem as a whole, a mechanistic and predictive understanding of their links with other species is imperative.

Antarctic penguin species are land-based during their reproductive period and many of them rely on krill to feed both themselves and their offspring during this time (Trivelpiece, Trivelpiece & Volkman 1984; Trivelpiece *et al.* 1986; Trivelpiece, Trivelpiece & Volkman 1987; Davis & Darby 1990; Trivelpiece *et al.* 1990; Hill *et al.* 1996; Reid *et al.* 1996; Croll & Tershy 1998; Mangel & Switzer 1998; Boyd & Murray 2001; Charrassin & Bost 2001; Marin & Delgado 2001).

During the breeding season, penguins are central place foragers, returning to their nesting sites between foraging trips (Davis & Darby 1990; Mangel & Switzer 1998). Clear links have been shown between krill abundance and penguin survival and reproduction (Trivelpiece, Trivelpiece & Volkman 1984; Croxall *et al.* 1985; Trivelpiece *et al.* 1986; Trivelpiece, Trivelpiece & Volkman 1987; Trivelpiece *et al.* 1990; Reid *et al.* 1996; Loeb *et al.* 1997; Boyd & Murray 2001; Charrassin & Bost 2001). Evidence also exists that the distribution of penguins between inshore and offshore regions is correlated with krill abundance patterns (T. Ichii, personal communication). Thus, penguin foraging behaviour is plastic and depends on krill distributions. As a result, we would expect both penguin behaviour and penguin food availability during reproduction to be impacted by fishery-induced changes in local krill abundance.

Due to their importance in the Antarctic ecosystem, krill are relatively well studied and much is known about their physiology, reproduction and patterns of distribution (Marr 1962; Mackintosh 1972; Mauchline 1980; Miller & Hampton 1989). Diel vertical migration, group formation and distribution of Antarctic krill (Mauchline 1980; Morris, Ward & Clarke 1983; Morris *et al.* 1984; Hamner & Hamner 2000; Ritz 2000) will depend on individual size, time during the season, environmental conditions (such as phytoplankton abundance and water temperature) and predation risk (Quetin & Ross 1992; Quetin *et al.* 1996; Ross, Quetin & Lascara 1996; Ross, Quetin & Haberman 1998; Alonzo & Mangel 2001; Alonzo, Switzer & Mangel 2003). Krill distributions can only be understood by considering the size and situation-dependent migration pattern of individuals. For example, if krill move into deeper and less accessible water, penguins may experience decreased feeding rates even in the absence of a decrease in overall krill biomass. Therefore, krill behaviour could lead to a decrease in penguin food intake that is even greater than expected by the amount of krill biomass removed.

Life-history and behavioural models can help predict a species' response to novel situations (Mangel & Switzer 1998; Pettifor *et al.* 2000; Stillman *et al.* 2000; Alonzo & Mangel 2001; Forde 2002). Penguin foraging patterns and krill behaviour are not well studied. However, it is possible to use general knowledge of habitat selection (Brown 1990; Mangel 1990; Rosenzweig 1991; Brown 1998), foraging behaviour (Krebs *et al.* 1977; Pyke, Pulliam & Charnov 1977; Krebs, Kacelnik & Taylor 1978; Cowie & Krebs 1979; Schoener 1987; Mangel & Clark 1988; McNamara, Merad & Houston 1991; Newman 1991; Houston, McNamara & Hutchinson 1993; Bouskila 1995; Charnov & Parker 1995; Houston 1996; Houston & McNamara 1997; Luttbeg & Schmitz 2000; Stillman *et al.* 2000) and interactions between predators and prey (Sih *et al.* 1985; Kacelnik, Krebs & Berstein 1992; Sih 1998; Lima 2002) in combination with the extensive knowledge of krill and penguin biology (Marr 1962; Mauchline 1980; Trivelpiece,

Trivelpiece & Volkman 1984; Trivelpiece *et al.* 1986; Trivelpiece, Trivelpiece & Volkman 1987; Davis & Darby 1990; Trivelpiece *et al.* 1990; Hill *et al.* 1996; Reid *et al.* 1996; Croll & Tershy 1998; Mangel & Switzer 1998; Nicol & Endo 1999; Charrassin & Bost 2001; Marin & Delgado 2001) to increase our understanding of their interspecific links and predict their response to fishing.

In a previous paper (Alonzo, Switzer & Mangel 2003) we focused on the effect of long-term evolutionary interactions between predators and prey on the behaviour and distribution of penguins and krill. Here we show how this same approach can be used to examine the predicted impact of increasing krill fishing pressure on the foraging success and spatial distribution of penguins. We considered how local environmental conditions will affect the behaviour and growth of krill, and thus penguin foraging behaviour in the presence of fishing. We focused on predicting the relationship between fishing pressure and penguin predicted food intake rates under different environmental scenarios to assess indirect effects. Furthermore, we show how penguin behaviour can be used to assess the impact of krill fisheries on both species.

Methods

We will first briefly describe the basic elements of the model of krill and penguin behaviour (Alonzo, Switzer & Mangel 2003). We will then describe the fisheries model that uses these behavioural patterns.

THE MODEL OF KRILL AND PENGUIN BEHAVIOUR

Krill select a daytime vertical habitat and at night they either migrate to the surface to feed or remain in their daytime habitat and do not feed (Mauchline 1980; Morris *et al.* 1983, 1984). Penguins forage for krill either inshore or offshore depending on the distribution and abundance of krill (T. Ichii, personal communication). We assume that the krill and penguin behavioural 'rules' have evolved to maximize their long-term expected reproductive success (Mangel & Clark 1988; Clark & Mangel 2000; Alonzo 2002; Alonzo, Switzer

& Mangel 2003). We also assume penguins respond to the local abundance of krill and krill respond to local environmental conditions (T. Ichii, personal communication; Trivelpiece *et al.* 1986; Davis & Darby 1990; Trivelpiece *et al.* 1990; Quetin *et al.* 1996; Mangel & Switzer 1998; Charrassin & Bost 2001). The model searches for the krill and penguin behavioural patterns at which no individual can increase its expected reproductive success by changing behaviour (Alonzo, Switzer & Mangel 2003). A krill's behaviour affects its growth, survival and vertical distribution (Alonzo & Mangel 2001; Alonzo, Switzer & Mangel 2003). The distribution and growth of krill affects penguin foraging behaviour (Alonzo, Switzer & Mangel 2003). Penguin behaviour affects krill mortality (due to predation) and penguin foraging success (Alonzo & Mangel 2001; Alonzo, Switzer & Mangel 2003).

Spatial and temporal structure of the model

We consider three vertical habitats (surface, shallow and deep) combined with two horizontal regions (inshore and offshore; Fig. 1). For computational tractability, we assume that the continuous distribution of habitat range can be roughly classified into the six resulting categories. We assume also that penguins can move between inshore and offshore and that krill only move vertically but do not move between regions. These initial simplifications could be extended in future analyses. We assume a starting abundance of krill inshore and offshore; krill behaviour, survival and growth then determine the distribution and abundance of krill in each of the vertical habitats. We consider a 16-week period during which the penguins are land-based and reproducing (Trivelpiece, Trivelpiece & Volkman 1984, 1987; Davis & Darby 1990; Ichii, Naganobu & Ogisima 1996; Croll & Tershy 1998; Mangel & Switzer 1998). We assume that a penguin's ability to catch krill decreases with depth (Trivelpiece *et al.* 1986; Trivelpiece, Trivelpiece & Volkman 1987). Therefore, krill that select deeper habitats are less accessible to foraging penguins. However, krill in deeper habitats must travel further to the surface to feed.
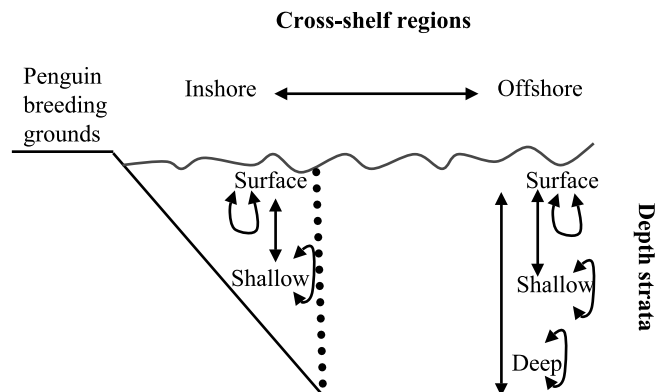
Cross-shelf regions

Fig. 1. Spatial structure of the model. See text for details.

Krill growth and behaviour

We calculate expected krill growth per week (Alonzo, Switzer & Mangel 2003). Growth rate depends on the current size of the krill, water temperature, vertical habitat, phytoplankton abundance and krill feeding behaviour (Alonzo & Mangel 2001). Growth is determined by the difference between metabolic costs and food intake (Atkinson 1994). Total metabolic costs increase with individual size (Ikeda 1985). Higher water temperatures also lead to higher metabolic costs (Ikeda 1985). However, food intake rates also increase with water temperature and individual size (Holm-Hansen & Huntley 1984; Alonzo & Mangel 2001). Phytoplankton abundance increases krill growth rates (Boyd, Heyraud & Boyd 1984; Ikeda & Thomas 1987). Krill reach a maximum size of 60 mm and we only consider individuals above 12 mm minimum size (Mauchline 1980; Ikeda, Dixon & Kirkwood 1985). Travel costs decrease with krill size and increase with distance (Alonzo & Mangel 2001). As a result, larger krill may grow more if they spend the day in deep (and colder) waters while smaller krill may grow more if they remain in warmer surface waters during they day (Alonzo & Mangel 2001).

Krill behaviour has two components. First, krill select a daytime habitat (surface, shallow or deep). Secondly, krill either feed at the surface at night or remain in their present habitat without feeding. Krill growth thus depends on behaviour. Fitness is measured as the expected reproductive success at the end of the 16 weeks. This is determined by survival through the time period (determined by predation risk), size at the end of the period (determined by growth) and the probability of surviving to reproduction after the period under consideration. Thus, krill may trade-off survival and growth because the probability of predation at the surface is higher than in deeper waters. We use the model to find the krill behaviour that maximizes individual expected reproductive success (Alonzo, Switzer & Mangel 2003). Krill feeding behaviour and habitat selection depend on individual size and time in the year. Usually, small krill are predicted to remain at the surface and larger krill to be found in deeper waters. However, predation risk affects this pattern, with more krill predicted to be in deeper waters when predation risk is higher at the surface (Alonzo & Mangel 2001; Alonzo, Switzer & Mangel 2003).

Penguin foraging behaviour

Penguins may forage both inshore and offshore, where their intake rates depend on competition from other penguins, the abundance and distribution of krill, the metabolic costs associated with foraging in each region, and their ability to forage at depth. We assume that penguin intake rates decrease linearly with competition from other penguins and increase linearly with available krill biomass. Thus, we assume that prey switching does not occur and that krill are not suffi-

ciently abundant that other factors significantly constrain penguin consumption rates. The availability of krill depends on their vertical distribution and the ability of penguins to forage at depth. We assume penguins distribute themselves with respect to their expected foraging success inshore and offshore in a way that leads to the maximum expected foraging success given krill distribution and abundance (Alonzo, Switzer & Mangel 2003). We focus on foraging behaviour during the reproductive season because it is during this time that penguin fitness is most clearly linked to krill distribution and abundance and indirect effects of fisheries (Brodin, Olsson & Clark 1998). We assume that penguin foraging behaviour is determined by their need to obtain food for themselves and their offspring. Thus penguin fitness and predicted behaviour will be directly linked to food intake. Although this may ignore much of the biology of penguins in general (Davis & Darby 1990), it clearly captures the link between krill and penguins through the food and time available for reproduction.

THE KRILL FISHERIES MODEL WITH PENGUIN AND KRILL BEHAVIOUR

We use the model to predict krill and penguin behaviour (habitat selection or foraging) in the absence of fishing. We then determine the effect of a reduction in krill abundance due to fishing on the distribution of both krill and penguins. We assume that penguins respond to the change in krill distributions and thus adjust their foraging behaviour (proportion of time spent inshore or offshore). We also assume that krill respond to the current environmental conditions and expected predation risk. This is equivalent to assuming that over evolutionary time predation has shaped the vertical habitat selection behaviour of krill but that they do not change their diel vertical migration behaviour immediately in response to penguin behavioural changes. Fishing is assumed to occur only offshore. We consider both the case where fishing takes krill of all sizes and the case where only larger krill (above 35 mm) are taken. We also examine two patterns of fishing: (i) the case where fishing occurs during the penguin reproductive season; and (ii) the case where fishing only occurs prior to the reproductive season.

We start by assuming that the abundance of krill prior to fishing is equal inshore and offshore and is sufficiently high without fishing that penguin predation only slightly depletes krill. We also assume for simplicity that krill are uniformly distributed among size classes at the beginning of the time period under consideration. However, the distribution has little effect on the qualitative predictions we report here. We then allow fishing to reduce the distribution of krill offshore by a certain percentage of available biomass equally across all size classes affected by fishing. For the continuous fishing case, we examine the range from 1% to 10% of the available krill biomass removed per week. For the case where fishing only occurs prior to penguin

reproduction, we examine the removal of from 10% to 50% available krill biomass.

For each week under consideration, we first use the pattern of behaviour predicted by the model without fishing (see above; Alonzo, Switzer & Mangel 2003) to predict the distribution and abundance of krill (Fig. 2). Given this size and spatial distribution of krill, we determine the predicted reduction in krill abundance due to fishing. We then calculate the proportion of penguins that are predicted to be found offshore (as described above) and determine their expected foraging success. We measure relative penguin success as the percentage of food they would have obtained in the absence of fishing. Penguin predation then reduces the abundance of krill both inshore and offshore. This reduced size and spatial distribution of krill is used to predict krill behaviour and size and spatial distributions in the next time period. We repeat these calculations throughout the entire 16-week period under consideration (Fig. 2).

In Alonzo, Switzer & Mangel (2003), we examined the model and specific parameters in great detail. In this analysis we focus on the impact of fishing pressure and environmental conditions on penguin foraging success. For more information on the effect of other aspects of the model on krill and penguin behaviour see Alonzo, Switzer & Mangel (2003). We examine the impact of decreasing phytoplankton from 100% to 50% of the maximum growth conditions and consider the effect of varying water temperature with depth within the range from –2 to 2 °C in 1-°C increments assuming that water temperature decreases with depth ($T_{surface} \leq T_{shallow} \leq T_{deep}$).
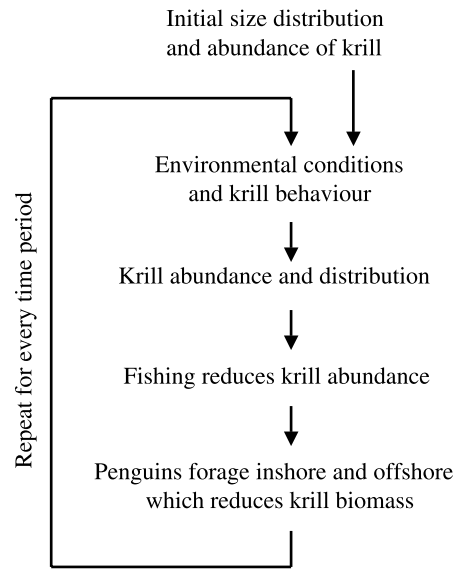

Fig. 2. Structure of the fishing model. See text for details.

Results

Basic patterns without fishing

The results of the model without fishing are described in detail elsewhere (Alonzo, Switzer & Mangel 2003). In the absence of fishing, krill are predicted to be found feeding at the surface at night both inshore and off-shore (Fig. 3). During the day most krill are predicted to be in shallow water inshore and deep water offshore
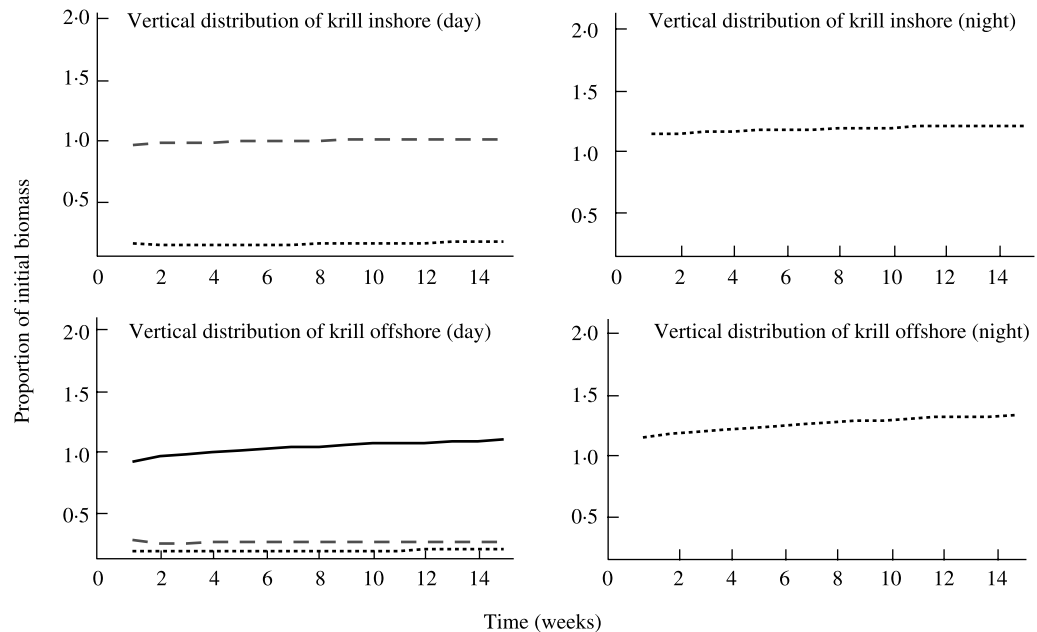
Fig. 3. Predicted spatial and temporal distribution of krill without fishing. The proportions of krill in surface (dotted lines), shallow (dashed lines) and deep water (solid lines) are shown. The absence of one of these lines indicates that krill are not predicted to be found in this habitat.

(to decrease the risk of predation by penguins; Fig. 3). However, small krill are expected to remain at the surface during the day in both regions (Fig. 3). When krill are equally abundant inshore and offshore, slightly more penguins are predicted to be found inshore (Fig. 4). This occurs both because foraging offshore increases the cost of foraging (and thus decreases energy intake) and because krill are more accessible inshore in shallower water. The proportion of penguins inshore is predicted to decrease slightly through time as some krill are depleted inshore (Fig. 4). However, the depletion of krill by penguins in the absence of fishing is predicted to be very weak. Penguin feeding rates are predicted to remain high both inshore and offshore in the absence of fishing.

GENERAL PATTERNS WITH FISHING

The relative vertical distribution of krill is not predicted to change in the presence of fishing. Abundance, however, is predicted to decrease in all vertical habitats offshore, and depletion of krill by penguins both inshore and offshore is predicted to be stronger in the presence of fishing. As a result of these underlying patterns, penguin food intake is predicted to decrease (Fig. 5) and
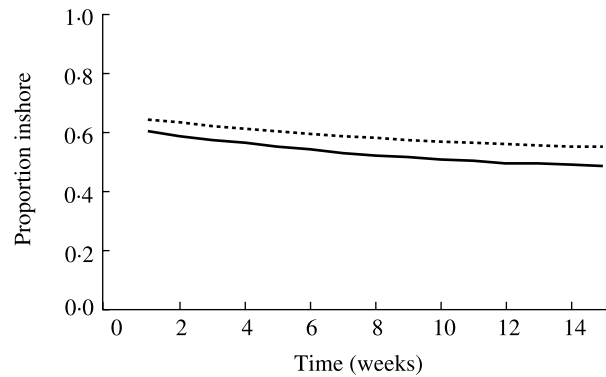

Fig. 4. The spatial and temporal distribution of penguins without fishing. The dotted line represents the pattern during the day and the solid lines patterns at night.
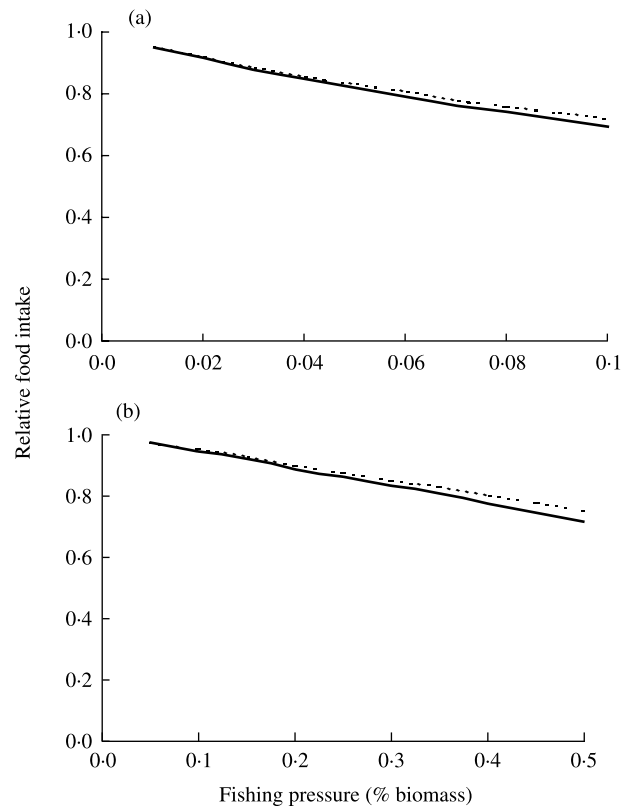
Fig. 5. Relative decrease in weekly penguin food intake with fishing for when (a) fishing occurs throughout or (b) fishing occurs only before the reproductive period. Solid lines represent the case where all size classes are fished and the dotted line gives the predictions for the case where only krill above 35 mm length are fished.

the proportion of penguins found inshore is predicted to decrease (Fig. 6) as fishing pressure increases because fishing only reduces krill biomass offshore.

As fishing pressure increases and krill abundance offshore declines, penguin food intake is predicted to decrease as well (Fig. 5). Although behavioural plasticity could easily cause non-linearities, the predicted decline in intake rates is roughly linear. Furthermore, the proportion of penguins predicted to be found inshore increases as depletion (due to fishing) increases (Fig. 6). Although the reduction in penguin consumption rate with increased fishing pressure is roughly linear (Fig. 5), the rate at which intake rates decline is greater than expected by biomass removed alone and depends on environmental conditions (Figs 7 and 8).

Whether fishing occurs prior to or during the breeding season has little effect on the predicted pattern of penguin foraging success or distribution (Figs 5 and 6).
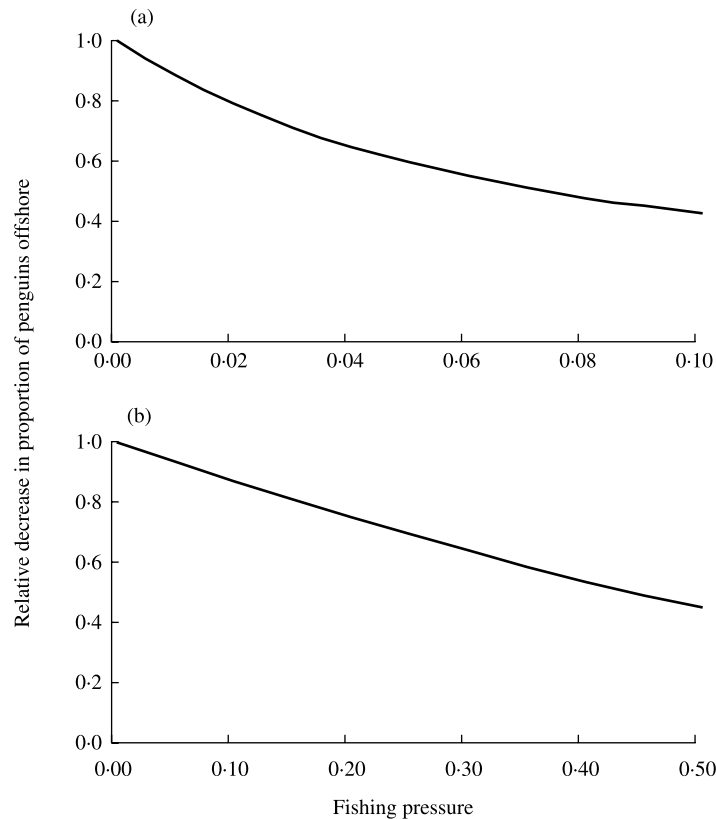

Fig. 6. Relative decrease in the proportion of penguins offshore with fishing. Results are shown for when (a) fishing occurs throughout or (b) only occurs before the reproductive season on all krill of all sizes.
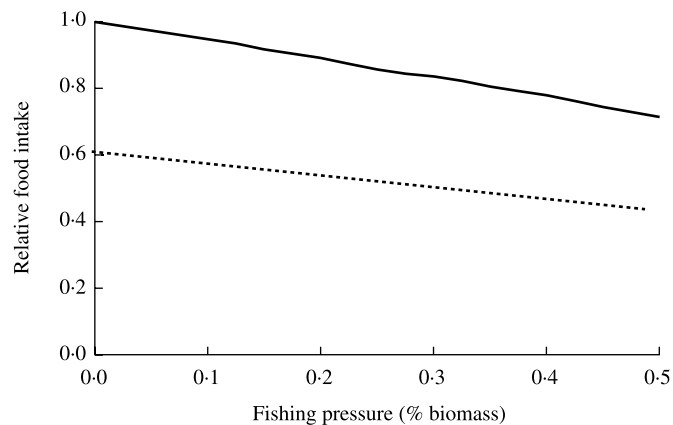

Fig. 7. Effects of phytoplankton abundance on penguin foraging success. Predicted weekly relative food intake rates of penguins are given for maximum phytoplankton abundance (solid line) and when phytoplankton is decreased by 50% (dotted line). Results shown are for the case where all krill size classes are fished and fishing occurs prior to the reproductive season. Although a 50% reduction on krill biomass offshore represents a 25% reduction in total krill biomass at the highest fishing pressure, the reduction in penguin consumption rate is approximately 30% in both cases.
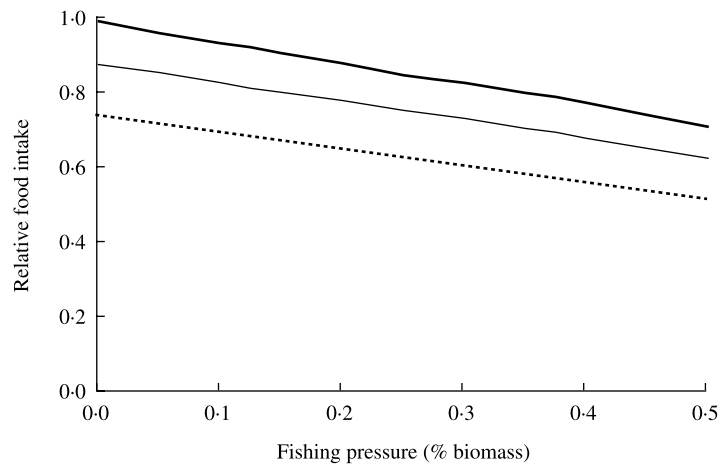
Fig. 8. Effects of water temperature on penguin foraging success. Predicted weekly relative food intake rates of penguins are given for three temperature regimes: $T_{surface} = 2$, $T_{shallow} = 0$, $T_{deep} = -2$ (thick line); $T_{surface} = 0$, $T_{shallow} = 0$, $T_{deep} = 0$ (thin line); $T_{surface} = -2$, $T_{shallow} = -2$, $T_{deep} = -2$ (dotted line). Results shown are for the case where all krill size classes are fished and fishing occurs prior to the reproductive season. Although a 50% reduction on krill biomass offshore represents a 25% reduction in total krill biomass at the highest fishing pressure, the reduction in penguin consumption rate is approximately 30% in all three cases.

Fishing during the reproductive period does amplify the effects of depletion as well as cause a decrease in food intake rates through time and a corresponding decrease in the proportion of penguins found inshore through the reproductive period. However, whether fishing occurs during or prior to penguin reproduction is predicted to have little effect on penguin intake rates. Whether krill of all sizes or only larger krill are taken by fishing also has little effect on the predicted penguin food intake rates, because large krill contribute more biomass per individual krill. However, this assumes that penguin intake rates are affected by the amount of krill biomass available rather than by krill size.

Environmental conditions that affect krill behaviour and growth are predicted to affect penguin food intake rates (Figs 7 and 8). As phytoplankton abundance decreases, penguin intake rates are predicted to decrease as well, and relatively more penguins are predicted to be found inshore. Similarly, when water temperature decreases krill growth, krill available biomass decreases and the predicted depletion of krill by penguins increases. As a result, penguin intake rates are predicted to decrease more for the same level of fishing pressure (Fig. 8) and more penguins are predicted to be found inshore than in better krill growth conditions.

Discussion

Reducing the abundance of krill near penguins that are land-based for reproduction is predicted to reduce penguin food intake rates. Given the documented links between krill abundance and penguin survival and reproduction, this also leads to a prediction of decreased adult survival and reproduction. However, krill behaviour is predicted to cause stronger effects of krill fisheries than explained solely by the percentage of biomass removed. This prediction is mainly caused by krill in deeper waters being less accessible to diving penguins. Furthermore, krill growth during the period under consideration is also important. For example, when fishing only occurred prior to the time period under consideration, a 50% reduction in biomass offshore is consistent with a 25% reduction of biomass both inshore and offshore. Thus, we would expect from biomass alone that penguin feeding rates would drop by 25% or less because of the decreased cost of foraging inshore. However, our model predicts a 30% drop in penguin food intake per week under good growth conditions for krill. The effect of krill fisheries on penguins is predicted to be even greater under conditions (low water temperature or reduced phytoplankton abundance) that decrease krill growth and increase the proportion of krill predicted to be found in deep water (and thus be less accessible to penguins). Thus, krill behaviour can have important effects on the impact of krill fisheries on penguin survival and reproduction.

We predict that the proportion of penguins found offshore will decrease as krill fisheries offshore increase. The exact number of penguins found inshore and offshore will depend on a variety of factors including the abundance of krill both inshore and offshore, the size distribution of krill, the cost of travelling offshore to forage, the total number of penguins foraging, and local environmental conditions. However, the relative change in the proportion of penguins found offshore (e.g. Fig. 6) is relatively unaffected by fishing patterns, environmental conditions, penguin foraging ability at depth or initial krill abundance. As a result, it may be possible to use changes in the behaviour of penguins to determine relative effects of the fisheries on penguin foraging success. However, before using penguin foraging behaviour as an indicator of the effect of fisheries on penguins, we must first understand what normal penguin foraging patterns look like in the absence of fishing. Although this will require some effort, it may be easier to accomplish than good estimates

of krill spatial distribution patterns. It is also true that although the relative effect may be the same in different years, the absolute effect of fishing on penguins will be higher in years of low krill abundance and growth or years in which krill are found mainly in deeper waters.

In our model, we have assumed that only krill biomass and distribution affect penguin food intake rates. As a result, the fishing pattern and size distribution of krill were not predicted to have strong effects on penguin food intake. However, in some circumstances penguins have been found to feed more on larger krill (Reid *et al.* 1996). This may indicate that penguins forage more efficiently or preferentially on larger krill. If this is true and krill fisheries take larger krill or if krill growth rates decrease, our model would underestimate the impact of the krill fisheries on penguin foraging success. We have also assumed that penguins forage to maximize their intake rates. Although patterns of penguin foraging behaviour are more consistent with rate-maximizing than survival-maximizing behaviour of penguins (Alonzo, Switzer & Mangel 2003), penguin behaviour may be influenced by other factors such as reproductive demands and survival. None the less, we would still expect penguin food intake rates to decrease as krill fisheries increase. However, our ability to manage the krill fisheries and their impact on penguins would be greatly increased by further studies of penguin foraging patterns and success.

Our results demonstrate that an understanding of the behaviour of organisms and the effect of behaviour on interactions between species can increase our ability to explain and predict the impact of human-induced disturbances such as fishing on the entire community (see also Gill, Norris & Sutherland 2001). For example, we predict that knowing the amount of prey biomass removed will not be sufficient to predict the reduction in a penguin's consumption rate. Instead, understanding how individual behaviour within a species affects interactions between species is necessary to make reliable predictions. Our method can be used to develop ecosystem approaches to management, where we utilize what is known about a particular system and interactions between species in general to predict how specific species will respond to novel situations. There has also been interest in using top predators as ecosystem monitors. In theory, the survival and reproduction of top predators will be indicative of the ecosystem as a whole. However, most top predators are long-lived, large-bodied organisms compared with their prey. As a result, the population dynamics of these species may be too slow to respond to changes in the abundance of their prey to be used as ecosystem monitors. We suggest instead that the predator behaviour may represent a better monitor of ecosystem changes.

Acknowledgements

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