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Modeling Antarctic Marine Ecosystems

edited by
M.L.D. Palomares, P. Pruvost, T.J. Pitcher and D. Pauly

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MODELING ANTARCTIC MARINE ECOSYSTEMS

edited by
Maria Lourdes D. Palomares, Patrice Pruvost, Tony J. Pitcher and Daniel Pauly

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FISHERIES CENTRE RESEARCH REPORTS ARE ABSTRACTED IN THE FAO AQUATIC SCIENCES AND FISHERIES ABSTRACTS (ASFA)
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DIRECTOR'S FOREWORD

A map of the world with points wherever *Ecopath* models exist would be covered with such points, and Antarctica, which would have been an exception before, would be represented by the models in this report. In fact, there had been a model of Antarctica published earlier, by Astrid Jarre and others (Trophic flows in the benthic shelf community of the eastern Weddell Sea, Antarctica. p. 118-134. *In* B. Battaglia, J. Valencia and D. Walton (eds.) *Antarctic Communities: Species, Structure and Survival.* Cambridge University Press, Cambridge, 1995), based on work by P.H. Schalk and others, published in *Trophic Models of Aquatic Ecosystems* (V. Christensen and D. Pauly, eds., ICLARM Conf. Proc. 26, 1993). The various models documented here, however, will allow comparisons between subsystems and thus enable, for Antarctica, the kind of detailed comparative analysis that has long been possible for other areas.

Such comparison, having provided numerous insights for tropical and temperate systems, can be expected to do the same for Antarctic systems. Notably, it will be possible to quantify the role of pelagic-benthic coupling, assumed to play an important role in polar systems. Also, the dominance of marine mammals and birds will be amenable to comparative study, especially as Arctic systems where these homoeothermic animals dominate have also been described.

Two workshops, both sponsored by the *Sea Around Us* Project, funded by the Pew Charitable Trusts, led to this report: one held on 15-17 April 2003 at the Fisheries Centre, where various models were presented and their implications studied; and the other held on 29 September to 2 October 2003 at the Muséum National d'Histoire Naturelle in Paris, where a group of French researchers with experience in the Kerguelen Islands worked on refining an ecosystem model of the waters around that island. This workshop was proposed and followed by visits by Mr. Patrice Pruvost, working with Dr. M.L. Deng Palomares and others at the Fisheries Centre. This report, thus, is also a testimony to the collaboration between the Fisheries Centre and the Muséum National d'Histoire Naturelle.

We would also like to acknowledge cooperation between the *Sea Around Us* Project and the Renewable Resources Assessment Group (Imperial College, London, UK: Dr David Agnew) and the Falklands Islands Government (Dr John Barton) for advice and data concerning the Falklands Islands marine ecosystem and its fisheries, even if we were unable to consider all of them in the pilot models of the Falklands published in this report.

Daniel Pauly
Director, UBC Fisheries Centre
5 November 2005

ABSTRACT

This Fisheries Centre Research Report presents eleven papers that describe whole-ecosystem models of four Antarctic areas: the Antarctic Peninsula, Kerguelen Islands, Falkland Islands, and the Southern Plateau region, New Zealand. A mass-balance model, sources of data, and derivations of model parameters are detailed for each region. Dynamic simulation models for the Antarctic Peninsula and the Falklands provide preliminary explorations of critical issues in the management of their fisheries and the effects of climate. Analyses examine competition among krill-eating species, the spatial impacts of potential krill fisheries, and precautionary fishery limits established by management bodies.

INTRODUCTION

SIMULATING ANTARCTIC ECOSYSTEMS: WEAPONS OF MASS CONSTRUCTION[1]

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The ocean dynamics of the Antarctic region are thought to have a large influence on global fluxes. Living marine organisms in the Antarctic have evolved together in an intricate web of feeding relationships structured on a template of these complex ocean habitats fashioned from ice, currents and upwellings. Evidently, these food webs are robust in the face of extreme seasonal change and have survived long-term climate fluctuations since the Pleistocene. But Antarctic ecosystems have proven delicate in the face of human influences, especially commercial fishing, sealing and whaling. The almost complete removal of large whales by the 1970s must have had major effects on Antarctic food webs, while the present slow recovery of cetacean populations is taking place in the virtual absence of studies at the ecosystem level. Moreover, the ecosystem impacts of a mooted expansion of krill fisheries, driven by massive global depletion of more accessible fishery resources, are largely unknown.

While trying to gain an understanding of these changes, many national research agencies (for example the British, Chilean, German and Australian Antarctic institutes), have been working with the international management agency for the Antarctic, CCAMLR (the Convention for the Conservation of Antarctic Marine Living Resources) to try to conserve Antarctic biodiversity at the same time as setting fishery quotas that are designed to be sustainable. Many scientists consider that this agency is doing a creditable job. Indeed, CCAMLR's work is seen as a bellwether for the reconciliation of exploitation with conservation in natural healthy ecosystems. Meanwhile, the public profile of Antarctic issues, promoted by many NGOs such as WWF and Greenpeace, has never been higher. Sadly, Canada, although it has signed the CCALMR treaty, does not take up its treaty obligations to contribute to CCAMLR science and has no co-ordinated national policy or research on Antarctic issues.

At the same time, Canada is the home of a new generation of quantitative whole-ecosystem models that track trophic flows in the food web from plankton and aquatic plants, through pelagic and benthic fishes, to marine mammals and seabirds. Although in their infancy, such simulation models are becoming more widely used as management agencies move towards ecosystem-based decision-making. Whole-ecosystem simulation models are important because they represent a rational way of quantifying the trade-offs between sustainable exploitation of natural marine resources and conservation of charismatic fauna. The models can be tuned to conventional stock assessment data, and surveyed biomass estimates, and can be fitted to climate indicators. Ecosystem simulation modeling is a new science and its present state can be compared to meteorology in the 1950s – you certainly appreciate having a weather forecast, but accept that it is going to be wrong some of the time!

A major challenge faced by ecosystem modelers focussing on the Antarctic is the massive seasonal changes in abundance and diet as top predators like birds and marine mammals migrate, refuge and adapt to the extreme cold and dark. Winter darkness means almost zero primary production, while extended daylight in the austral summer leads to exceptionally high phytoplankton production. Antarctic food chains exhibit a dramatic switch on and off each year. High nutrient availability in the upwellings of the Antarctic convergence zone drives a pelagic ecosystem with exceptionally high but patchy zooplankton densities, mainly comprised of large, nutritious krill.

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[1] Cite as: Pitcher, T.J. (2005) Simulating Antarctic ecosystems and fisheries: weapons of mass construction. *In*: Palomares, M.L.D., Pruvost, P., Pitcher, T.J., Pauly, D. (eds.) Modeling Antarctic marine ecosystems. Fisheries Centre Research Reports 13(7). Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 3-4.

Emulating complex spatial features is critical to providing useful management advice, but presents a difficult challenge to whole-ecosystem modeling. Spatial features that need to be captured in whole-ecosystem simulations include under-ice winter refuges for krill and phytoplankton that initiate a rapid bloom of marine plankton in the austral spring. In fact, the under surface of sea ice provides a critical feeding niche for a number of fish and birds, such as penguins renewing their fat reserves in the early spring. Other seabirds and marine mammals specialize in feeding among pack ice (orcas), at the ice edge (elephant seals) and further at sea in the convergence zone (large baleen whales, albatross). Wide-ranging predators like leopard seals exploit a mosaic of many different ice-related habitats. But some aspects of Antarctic ecosystems are easier to deal with. For example, compared to tropical ecosystems, a much smaller number of species has to be covered in the models.

This report documents the workshop, held on 15-17 April 2003 at the Fisheries Centre through which these and related issues were explored. Also, this report documents the results of a smaller follow-up workshop, held on 29 September to 2 October 2003 at the Muséum National d'Histoire Naturelle in Paris, where a group of French researchers led by D. Pauly and M.L.D. Palomares worked on refining a model of the Kerguelen Islands, initiated by P. Pruvost.

ANTARCTIC PENINSULA

AN ECOSYSTEM SIMULATION MODEL OF THE ANTARCTIC PENINSULA[1]

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ABSTRACT

An increased fishery on Antarctic krill (*Euphausia superba*) in the Antarctic Peninsula might negatively impact a wide range of its predators, e.g., seabirds, seals and whales (Croll and Tershy, 1998; Tinan, 1998). Commercial fisheries for Antarctic krill, though fairly small-scale, may be localized into relatively small areas close to the shelf (CCAMLR, 2001). These are the same areas where many land-based predators forage at the height of their breeding season (Everson and de la Mare, 1996), making the krill fisheries as a potentially strong competitor of krill predators. This study aims to use whole-ecosystem simulation to assess the impact of fisheries for adult Antarctic krill on its predators and we present a preliminary mass-balance ecosystem model for the Antarctic peninsula with 39 functional groups, and derive parameters with which it may be used for dynamic and spatial simulations to address the krill fishery issue.

INTRODUCTION

A mass-balanced model of the Antarctic Peninsula constructed using *Ecopath* with *Ecosim* (Christensen and Walters, 2003) was presented at the *Sea Around Us* Project sponsored workshop on 'Modeling Antarctic Ecosystems' held at the Fisheries Centre, University of British Columbia, in April 2003. It took as a starting point an incomplete *Ecopath* model by Cornejo (2002), as well as a second *Ecopath* model by Jarre-Teichmann *et al.* for the Weddel Sea, the area immediately east of the peninsula. According to sources (Abbot and Benninghoff, 1990) there are a total of 120 species and 29 families present in the Antarctic region. For the purposes of this model, we have divided the species into 39 functional groups. This adds significant complexity to a 2002 partial model by Jorge Cornejo which has only 28 groups and a 1997 Weddell Sea model of Jarre-Teichmann *et al.* (1997) with 21 groups. The present model is similar to Cornejo in that it has many groups with high trophic levels, while it is also similar to Jarre-Teichmann *et al.* with regards to numerous groups at lower trophic levels.

Hence, our *Ecopath* model of the Antarctic Peninsula consists of 39 groups discussed here in detail. Fisheries operate on only 2 of these groups, i.e., adult and juvenile krill. The spatial features of the ecosystem were emphasized in an attempt to simulate near-shore fishery-predator competition for Antarctic krill, the dynamics of which are discussed in more detail by Pitcher and Erfan (this volume).

DESCRIPTION OF MODEL COMPONENTS: *ECOPATH*

Ross seal

The Ross seal (*Ommatophoca rossii)* is one of the rarest and the least studied seals in the Antarctic Peninsula. Following the Weddell Sea model, its Q/B ratio was set to 12 year^{-1} based on an average daily food intake of 10 kg per adult seal, and its P/B ratio was 'guesstimated' at 0.28 year^{-1}.

In the absence of biomass estimates, ecotrophic efficiency was set to 0.4. This led to a biomass estimate of 0.008 t·km^{-2}, a value consistent with the observation that the Ross seal is the rarest seal in the region.

Cephalopods seem to be an important component of its diet (about 57 %) although fish (about 37 %) also occurs in its diet (Barrett-Hamilton, 1901; Wilson, 1907; Brawn, 1913 cited in Knox, 1994). Following these

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[1] Cite as: Erfan, A., Pitcher, T.J. (2005) An ecosystem simulation model of the Antarctic Peninsula. *In*: Palomares, M.L.D., Pruvost, P., Pitcher, T.J., Pauly, D. (eds.) Modeling Antarctic marine ecosystems. Fisheries Centre Research Reports 13(7). Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 5-20.

observations as well as the diet composition suggested by Pauly *et al.* (1998), the diet was set to 65 % squid, 15 % fish, 5 % benthic mollusk, and 15 % krill.

Weddell seal

Weddell seals (*Leptonychotes weddellii*) are the top predators in high-Antarctic shelf waters and are frequent inhabitants of the peninsula. Their Q/B ratio was set to 12 year^{-1} based on an average daily food intake of 10 kg per adult seal and their P/B was set to 0.04 year^{-1} based on an average longevity of 25 years.

Estimates of biomass only exist for the neighboring area of the Weddell Sea, where Schalk *et al.* (1997) estimated about 0.07 t·km^{-2} and Jarre-Teichmann *et al.* (1997) estimated 0.036 t·km^{-2}. Considering that the Antarctic Peninsula is within the foraging radius of Weddell Sea mammals but is not the main habitat of the Weddell Seal, the lower estimate of 0.036 was assumed.

Analysis of the stomach contents of Weddell seals indicates that a variety of prey is taken including fish (Casaux *et al.* 1997; Dearborn 1965; Knox, 1994), squid (Clarke and Macleod 1982) and crustaceans, including krill (Bertram 1940). In McMurdo Sound, Burns *et al.* (1998) suggest a diet almost exclusively of Antarctic silverfish, *Pleuragramma antarcticum*, a small pelagic fish (70-100 %), some squid and a shallow benthic fish *Trematomus* spp. in the diet of the juveniles. Casaux *et al.* (1997) state that in the South Sheltlands, fish were the most frequent (95.7 %) and numerous prey (46.2 %), but molluscs were the most important by mass (65.8 %), mainly an octopod, *Pareledone charcoti*. Diet compositions as suggested by Pauly *et al.* (1998) are in agreement, thus enabling us to set to the composition to: 15 % cephalopods, 20 % benthic mollusks and 65 % fish (mostly small pelagics).

Crabeater seal

The Crabeater seal (*Lobodon carcinophaga*) is evidently the most common seal of the Antarctic Peninsula and the species most dependent on krill. Its Q/B value was set to 15 year^{-1} based on the estimate that it consumes 7 % of its body weight during 11 months of the year, and it weighs, on average, about 150 kg. The P/B was set at 0.08 year^{-1} assuming an average longevity of 33 years.

Crabeater seals tend to live on the ice throughout the year and they are almost exclusively counted on ice. A study covering the Amundsen-Bellingshausen Sea to the west of the Antarctic Peninsula suggests densities of 0.76 ind·km^{-2} (Gelatt and Siniff, 1999), while a study from the Weddell Sea to the east of the Peninsula reports 0.72 ind·km^{-2} (van Franker *et al.*, 1997). Assuming similar numbers for the area of interest and an average weight of 150 kg, the biomass used in the model was 0.11 t·km^{-2} which sets the Crabeater seal biomass higher than other seals in the model.

Despite its name, the main food of the Crabeater seal appears to be Antarctic krill. Following Knox (1994), Lowry *et al.* (1988) and Pauly *et al.* (1998), the diet was set to 90 % krill, 8 % pelagic fish, and 2 % squid.

Leopard seal

The Leopard seal (*Hydrurga leptonyx*) is the most vicious seal of the Antarctic and has the highest tropic level in this model after the toothed whales. While the feeding strategy of this species has been the subject of much interest, not much information is found about their physiology. A guesstimate of 5 year^{-1} was used for their Q/B ratio. The P/B ratio was estimated at 0.04 year^{-1} based on an average longevity of 26 years.

Leopard seals seem to be found in relatively small numbers in the Peninsula. Based on number counts provided by van Franker *et al.* (1997) and an assumed average body weight of 300 kg, the biomass was estimated at 0.015 t·km^{-2}. This preliminary value, however, did not conform to the mass-balance principle and was brought down to 0.010 t·km^{-2} to balance the model.

In contrast to other seal species, the Leopard seal is an opportunistic predator, taking a variety of prey, including krill, squid, fish, penguins and seals. Leopard seals are perhaps best known for their predation on penguins (Knox 1994) as described by Muller-Schwarze and Muller-Schwarze (1975), Penny and Lowry (1967) and Hunt (1973). But they are also reported to prey on at least 5 other seal species, most importantly the Crabeater seal (Bertram 1940; Laws, 1957, 1984; Gilbert and Erickson, 1977; Siniff and Bengtson, 1977; Siniff *et al.*, 1979; Knox, 1994). In view of their predatory behavior, it is perhaps surprising that Leopard seals also take substantial quantities of krill. Oritzland (1977) concluded that overall the Leopard seal takes 37 % krill in its diet, but at Palmer Station on the Antarctic Peninsula a much higher proportion was taken (87 %, Knox, 1994). In the Antarctic Peninsula area (Siniff and Stone 1985), and in South Georgia (Walker *et al.* 1998), the diet of Leopard seals changes over the year, an observation that the current model is not able to handle. Taking into account this large amount of information together with the diet composition suggested by Pauly *et al.* (1998), the diet for the Leopard seal was set to 15 % seals (Crabeaters), 15 % penguins (mostly Adélie), 5 % flying birds, 10 % squid, 20 % fish (mostly pelagics) and 35 % krill.

Antarctic fur seal

There is very little information available on the Antarctic fur seal (*Arctocephalus gazella*) in the Peninsula. The Q/B ratio and the P/B ratio were assumed to be about the same as other seals and set to 12 $year^{-1}$ and 0.08 $year^{-1}$ respectively.

In the absence of any data on density, the ecotrophic efficiency was set to 0.4 which led to a reasonable approximate biomass of 0.00375 $t \cdot km^{-2}$.

Though the diet of the Antarctic fur seal is still largely unknown, it is clear that in the region around the Peninsula during the breeding season, krill are a staple food for lactating females while fish and squid are taken by juvenile and non-breeding adults (Doidge and Croxall, 1985; North *et al.,* 1983; Knox, 1994). Reid and Arnould (1996) provide estimates of diet during the breeding season at South Georgia suggest that 88 % of the diet is krill, while *Champsocephalus gunnari* and *Lepidonotothen larseni,* small fish that both feed on krill constituted 94 % of the total fish in the diet. The diet composition in the model is mainly based on suggestions of Pauly *et al.* (1998) and set at 20 % squid, 35 % fish (mostly pelagics) and 45 % krill.

Southern elephant seal

Similar to the fur seal there is virtually no data for elephant seals (*Mirounga leonine*) in the Antarctic Peninsula. The Q/B ratio and the P/B ratio were assumed to be about the same as other seals and set to 12 $year^{-1}$ and 0.08 $year^{-1}$ respectively.

In the absence of any data on density, the ecotrophic efficiency was set to 0.4 which led to an approximate biomass of 0.00375 $t \cdot km^{-2}$.

Again, there is very little published information available on the pelagic food habits of elephant seals and most food consumption studies were conducted during molt periods, i.e., when elephant seals are ashore fasting (e.g., Laws, 1960). It appears that they depend much more heavily on squid than on krill (Clark and Macleod 1982; Rodhouse *et al.* 1992; McConnel *et al.* 1992). The diet composition in the model is mainly based on suggestions of Pauly *et al.* and set at 75 % squid, 20 % fish (mostly pelagics) and 5 % benthic molluscs.

Toothed whales

The known toothed whales of the Antarctic Peninsula are the sperm (*Physeter catodon*) and the toothed whales (suborder Odontoceti). Toothed whales are the ultimate top predators in the Antarctic Peninsula food web and are preyed upon only by their own group – a fact that made this group very hard to balance. The Q/B ratio was guesstimated at 6 $year^{-1}$ following George Cornejo (Saxby Enterprises Ltd, pers. comm.). Because of the cannibalism within the group, P/B ratio controlled ecotrophic efficiency, i.e., P/B ratio of 1 $year^{-1}$ led to a calculated EE of 0.06 which seems reasonable considering toothed whales have no predators in the system. The biomass set to 0.001 $t \cdot year^{-1}$ allowed balancing the model but has no real basis.

The toothed whales are the most eclectic group in the model, eating all species of seals, birds and fish. Their diet was set o 13 % seals, 2 % whales, 15 birds, 25 % squids and 45 % fish based on Pauly *et al.* A study by Alonso *et al.* (1999) gives some clues about the species of fish in the diet and based on these observations about a third of the fish in the diet of toothed whales appeared to be benthopelagic.

Baleen whales

Baleen whales (suborder Mysticeti) are important in the Antarctic region because they take large quantities of krill. The most important species reported is the minke whale (*Balaenoptera bonaerensis*). Again, there was not much data available on baleen whales. Their Q/B ratio was set to 11 year^{-1} and their Q/B ratio to 0.1 year^{-1}.

Ecotrophic efficiency was set to 0.001, representing the fact that baleen whales have virtually no predators in the system (except for toothed whales that might occasionally consume one). Baleen whales feed mostly on krill and some fish and their diet was set to 2 % squid, 18 % fish (mostly pelagics) and 80 % krill following Pauly *et al.* (1998). Of the krill, about a quarter was assumed to be juvenile reflecting the fact that baleen whales simply swim through swarms of krill and are not at all selective in their feeding on different sizes of the zooplankton.

Adélie penguin

The Adélie penguin (*Pygoscelis adeliae*) seems to be the most common penguin at the Antarctic Peninsula, but it is also quite a bit smaller than other penguins and has a different physiology. This justifies creating a group in the model for it alone. Q/B ratio was set to 18 year^{-1} since the smaller Adélies have higher metabolic rates than other penguins. P/B ratio was set at 0.2 year^{-1} based on an assumed longevity of 5 years.

The expected biomass is around 0.025 t·year^{-1} based on number counts by van Franker *et al.* (1997). This value was, however, too low for the mass-balance routine of *Ecopath* and was thus raised to 0.05 t·year^{-1}, still a reasonable estimate considering that the Adélie is the most common penguin in the region.

The diet of Adélie penguin seems to include more squid than the other penguins. It was set to 30 % fish, two-thirds of them pelagics, 20 % squid and 50 % krill based on papers by Kerry *et al.* (1997) and Ainley *et al.* (2001).

Penguins (other)

At this preliminary stage of model construction, little information was found about penguins and they were therefore grouped together in the model, with the exception of the Adélie penguin. The 'other penguins' group then includes emperor penguins (*Aptenodytes forsteri*), chinstrap penguins (*Pygoscelis antarctica*) and gentoo penguins (*Pygoscelis papua*). The Weddell Sea model used a Q/B ratio of 12 year^{-1} based on a food intake of 1 kg·day^{-1} for emperor penguins weighing around 30 kg (Jaree-Teicchmann *et al.* 1997). Considering that this mixed penguin group contains species that are smaller than the emperor penguin and have a higher metabolic rate, the Q/B was set to 16 year^{-1}. The P/B ratio was set to 0.1 year^{-1} based on an assumed longevity of 10 years on average for the penguins in this group.

Biomass (0.08 t·km^{-2}) was estimated from counts by van Franker *et al.* (1997) and an average individual weight of 10 kg. Because of the differences between species in this group, deciding on a diet composition was difficult. It was set to 40 % fish, about half of them pelagics, 10 % marine invertebrates and 50 % krill, some of them juveniles, based on a study by Kooyman (1998).

Flying seabirds

The majority of birds at the Antarctic Peninsula are penguins, though several species of flying seabirds are also found. While penguins dominated by biomass, flying seabirds are more numerous. Though no surveys of the birds of the specific area were consulted for constructing this model, it appears that the flying seabirds group is dominated by several species of albatrosses and petrels. Q/B and P/B ratio were guesstimated at 15 and 0.1 year^{-1}, respectively, values similar to those used for penguins. Based on number counts by van Franker *et al.* and an estimated average weight of 4 kg, the biomass of 0.03 t·km^{-2} was used in the model. The diet composition for the group is similar to penguins, i.e., 10 % squid, 10 % invertebrates, 30 % krill and 48 % non-demersal, mostly smaller fish. The final 2 % of flying seabirds' diet consists of penguins, reflecting the fact that large albatrosses occasionally hunt small penguins.

Cephalopods

Even though information on squids in the Antarctic is sparse, they were included in the model because of their importance in the diet of top predators. The P/B ratio was set to 0.5 year^{-1} and P/Q ratio was set to 0.15 year^{-1} based on a gross efficiency of 15 %. Ecotrophic efficiency was set to 95 % which resulted in *Ecopath* calculating a biomass of 1.66 t·km^{-2}. The diet was based on a study by Rodhouse and Nigmatullin (1996) and was set to 30 % fish, mostly small benthopelagics and bathypelagics, 65 % marine invertebrates, especially benthic crustaceans and cheliceratian arthropods (30 %) and 5 % cannibalism.

Pelagic fish (large and small)

The pelagic fish were divided into 2 groups based on their size, although similarities in diet were also taken into account. The large pelagic group contains Antarctic toothfish (*Dissostichus mawsoni*) and southern opah (*Lampris immaculatus*). The small pelagic group contains mackerel icefish (*Champsocephalus gunnari*), *Nansenia antarctica,* smalleye moray cod (*Muraenolepis microps*) and Antarctic silverfish (*Pleuragramma antarcticum*). Among these, the Antarctic silverfish is the most common species, often encountered in the diet of top predators.

The Q/B ratios for the 2 pelagic groups were calculated by averaging the reported Q/B compiled in FishBase (see www.fishbase.org). For large pelagics, a Q/B ratio of 1 year^{-1} was used, while for small pelagics this was set to 6 year^{-1}. In the absence of better data, P/Q ratios for large and small pelagics were set to 0.25 and 0.3 year^{-1}, respectively. Although there are no comprehensive surveys of the fish in the Antarctic Peninsula, studies by Kock *et al.* (1998 and 2000) for the Elephant Island area provid an idea of possible fish biomasses. Kock (1998) suggests biomass estimates based on bottom trawl surveys for selected species including the large pelagic Antarctic toothfish and the small pelagic mackerel icefish. Kock *et al.* (2000) presents the results of more general surveys, giving species compositions. Biomass estimates of large and small pelagic populations were obtained from these two articles, adjusted and expressed in t·km^{-2}. Both estimates were however initially low according to the mass-balance routine of *Ecopath* and were raised to 1.8 t·km^{-2} for large pelagics and 1.5 t·km^{-2} for small pelagics. Based on suggestions from FishBase (www.fishbase.org), the diet of large pelagics was set to 90 % fish and 10 % krill, and the diet of small pelagics to 3 % fish, 5 % invertebrates, 83 % krill and 9 % other zooplankton.

Demersal fish (large and small)

Demersal fish were divided into 2 groups based on size, though diet compositions were also considered. The large demersal group included yellowbelly rockcod (*Notothenia coriiceps*), blackfin icefish (*Chaenocephalus aceratus*), blunt scalyhead (*Trematomus eulepidotus*), striped rockcod (*T. hansoni*), *Gymnodraco acuticeps,* Eaton's skate (*Bathyraja eatonii*), McCain's skate (*B. maccaini*) and *Parachaenichthys charcoti.* The small demersal group includes *Artedidraco skottsbergi,* Gaudy notothen (*Lepidonotothen nudifrons*), *Pogonophryne platypogon,* and humped rockcod (*Gobionotothen gibberifrons*).

The Q/B ratios for the two demersal groups were calculated by averaging out the reported Q/B compiled in FishBase (see www.fishbase.org). For the large demersals, the Q/B ratio of 2.3 year^{-1} was used, while for small demersals this was set to 2.6 year^{-1}. Values of P/Q for large and small demersals were set to 0.20 and 0.25 year^{-1}, respectively. Though there are no comprehensive surveys of the fish in the Antarctic Peninsula, results from Kock *et al.* (1998 and 2000) for the Elephant Island area were used to provide possible fish biomass estimates. Kock (1998) reports biomass estimates based on bottom trawl surveys for selected species including the large demersal blackfin icefish and the small demersal humped rockcod. Kock *et al.* (2000) presents the results of more general surveys, giving species compositions. Biomass estimates of large and small demersal populations were obtained from these two articles, adjusted and expressed in t·km^{-2}. The estimate for large demersals was low for the mass-balance requirement and was raised 0.9 t·km^{-2}. An estimate of 1.1 t·km^{-2} for small demersal was obtained. Based on suggestions from FishBase the diet of large demersals was set to 37 % fish, 18 % invertebrates, 35 % krill and 10 % zooplankton, while the diet of small demersals was set to 90 % invertebrates and 10 % zooplankton.

Benthopelagic fish (large and small)

Benthopelagic fish were divided into two groups based on size, though diet compositions were also considered. The large benthopelagic group includes marbled rockcod (*Notothenia rossii*), grey rockcod (*Lepidonotothen squamifrons*), striped-eye notothen (*L. kempi*), *L. larseni,* spiny icefish (*Chaenodraco wilsoni*), *Coryphaenoides ferrieri,* ocellated icefish (*Chionodraco rastrospinosus*), slender escolar (*Paradiplospinus gracilis*) and *Neopagetopsis ionah.* The small benthopelagic group consists only of

Gymnoscopelus nicholsi.

The Q/B ratios for the two benthopelagic groups were calculated as the average of available Q/B ratios compiled in FishBase (see www.fishbase.org). For the large benthopelagics, the Q/B ratio of 3 year^{-1} was used, while for small benthopelagics this was set to 6.1 year^{-1}. The P/Q ratios for large and small pelagics were set to 0.28 and 0.3 year^{-1}, respectively.

Though there are no comprehensive surveys of fish in the Antarctic Peninsula the studies of Kock *et al.* (1998 and 2000) for the Elephant Island area provided biomass estimates. Kock (1998) provided biomass estimates based on bottom trawl surveys for selected species including the large benthopelagics marbled rockcod, ocellated icefish, and spiny icefish. Kock *et al.* (2000) presented results of more general surveys, giving species compositions. Biomass estimates of large and small demersal populations were obtained from these two articles, adjusted and expressed in t·km^{-2}. The biomass estimates obtained above were too low for the mass-balance requirement of the model. Large benthopelagic biomass was thus raised to 1.5 t·km^{-2}. Since there were no data available on the biomass of small benthopelagics, ecotrophic efficiency was set to 90 % which led to an *Ecopath* estimated biomass of 0.658 t·km^{-2}. Based on suggestions from FishBase, the diet of large benthopelagics was set to 18 % fish, 25 % invertebrates, 37 % krill and 10 % zooplankton, while the diet of small benthopelagics was set to 18 % invertebrates, 70 % krill and 12 % zooplankton.

Bathypelagic fish (large and small)

Bathypelagic fish were divided into two groups based on size, though diet compositions were also considered. The large bathypelagic group includes Antarctic escolar (*Paradiplospinus antarcticus*), Antarctic jonasfish (*Notolepis coatsi*), daggertooth (*Anotopterus pharaoh*), Patagonian toothfish (*Dissostichus eleginoides*), Whitson's grenadier (*Macrourus whitsoni*) and blue antimora (*Antimora rostrata*). The small bathypelagic group included *Gymnoscopelus braueri, Bathylagus antarcticus* and the Antarctic flashlight fish *Electrona antarctica,* which is the dominant mesopelagic fish of the Southern Ocean (Greely *et al.* 1999).

The Q/B ratios for the two bathypelagic groups were calculated as the average of available Q/B ratios compiled in FishBase (see www.fishbase.org). For the large bathypelagics the Q/B ratio of 3 year^{-1} was used, while for small bathypelagics this was set to 6 year^{-1}. In the absence of better data, the P/Q ratios for large and small pelagics were set to 0.2 and 0.3 year^{-1}, respectively. Since there were no data available on the biomass of either large or small bathypelgics, the ecotrophic efficiencies were set to 90 % leading to *Ecopath* calculated estimates of 2.927 t·km^{-2} for large bathypelagics and a biomass of 1.262 t·km^{-2} for small bathypelagics. Based on studies reported in FishBase, the diet of large bathypelagics were set to 20 % fish, 50 % invertebrates, 20 % krill and 10 % zooplankton, while the diet of small bathypelagics was set to 10 % invertebrates, 75 % krill and 15 % zooplankton.

Bathydemersal fish (large and small)

Bathydemersal fish were divided into two groups based on size, though diet compositions were also considered. The large bathydemersal group includes *Cryodraco antarcticus* and *Chionobathyscus dewitti.* The small bathydemersal group includes *Pachycara brachycephalum, Gymnoscopelus opisthopterus* and *Ophthalmolycus amberensi.*

The Q/B ratios for the two bathydemersal groups were calculated as the average of available Q/B ratios compiled in FishBase (see www.fishbase.org). For the large bathydemersals the Q/B ratio of 2.6 year^{-1} was used, while for small bathydemersals this was set to 6 year^{-1}. In absence of better data, the P/Q ratios for large and small pelagics were set to 0.2 and 0.3 year^{-1}, respectively. An estimate of the biomass of large bathydemersals was obtained from Arana and Vega (1999) at 0.8 t·km^{-2}. Since there were no data available on the biomass of small benthopelagics, the ecotrophic efficiency was set to 90 % which lead to an *Ecopath* calculated biomass of 0.503 t·km^{-2}. Based on suggestions from FishBase, the diet of large bathydemersals was set to 20 % fish and 80 % krill while the diet of small bathydemersal was considered to be dominated entirely by invertebrates.

Marine invertebrates

This model includes all the marine invertebrate models reported in the Jarre-Teichmann *et al.* (1997)

model of the Weddell Sea. However, due to difficulties in finding data at this stage, the model simply copies the Weddell Sea values as much as possible. As Table 1 below suggests, the P/B, Q/B and P/Q ratios were set to values from the Weddell Sea model (Jarre-Teichmann *et al.*, 1997) where available. Many of the biomasses however had to be raised from the Weddell Sea model in order to achieve the mass-balance requirement set by *Ecopath*. There could be several reasons for this, most importantly that the Weddell Sea model uses the units gC·m^{-2} which are here converted to t·km^{-2}. Considering that many of the invertebrates have high levels of carbon, the conversion probably underestimates biomasses. Following the Weddell Sea model, invertebrate diet was assumed to depend on detritus to a large degree, phytoplankton to a small degree and other invertebrates. The amount of benthic biomass in the Antarctic has been questioned by Brey and Gerdes (1997).

Table 1. Biomasses input for the invertebrate groups in the Antarctic peninsula model compared to Weddell sea values. All Ecotrophic Efficiencies (EE, bold) were estimated by the *Ecopath* mass-balance procedure.

#	Group	Biomass Weddell Sea Model	Biomass input to Ant. Peninsula Model	P/B	Q/B	P/Q	EE
23	Benthic mollusca	-	1.9	0.30	1.0	0.30	**0.950**
24	Tunicata	2.80	8.5	0.30	1.0	0.30	**0.987**
25	Porifera	4.81	6.0	0.18	0.6	0.30	**0.918**
26	Hemichordata	6.26	8.6	0.30	2.0	0.15	**0.903**
27	Lophophora and Cnidaria	7.49	18.0	0.10	1.0	0.10	**0.925**
28	Benthic crustacea and chelicerata	0.45	15.0	0.70	3.5	0.20	**0.915**
29	Polychaeta and other worms	27.51	20.0	0.60	4.0	0.15	**0.941**
30	Echinoidea	0.54	18.0	0.07	0.233	0.30	**0.825**
31	Crinoidea	6.20	8.0	0.30	1.0	0.30	**0.845**
32	Ophiuroidea	24.00	12.0	0.173	0.577	0.30	**0.282**
33	Asteroidea	20.88	20.0	0.08	0.267	0.30	**0.656**
34	Holothuroidea	?	2.22	0.20	1.10	0.182	**0.900**

Krill (larvae and adults)

Because of the interest in studying the interactions between krill and top predators, and in order to better simulate the krill production in the model, two separate groups were considered here, a larval and an adult krill group. The two groups are largely different in feeding habits, spatial and depth distribution, since young krill are planktonic while adult krill are generally considered as micro-nektonic (Nicol and Endo, 1999). The age at transition to adult group was set to 2 years, while the ratio of average adult weight to weight at transition was set to 4 years. Other parameters were left as *Ecopath* defaults. Pitcher and Erfan (this volume) discusses some problems with this approach and explores some alternatives.

The krill fishery is an important aspect of the Antarctic Peninsula ecosystem model (see Figure 1) notably because it is the only existing fishery of its kind in the region. Despite the recent studies on krill biology (Siegel, 1992; Siegel *et al.*, 1998; Lascara *et al.* 1999; Nicol and Endo, 1999; Hernandez-Leon *et al.* 2001), there is still not enough information to estimate input parameters needed for *Ecopath*. The P/B ratio for adult krill was set to 0.95 year^{-1} following Siegel (1992) who suggests a range of 0.88 to 0.96 year^{-1}. No estimate of P/B ratio for juveniles was found and so a guesstimate of 4 year^{-1} was used, based on values seen in juvenile prawns. Pitcher and Erfan (this volume) discuss scenarios in which the juvenile P/B ratio is set to 1.0 as an alternative in order to examine the robustness of conclusion to this uncertainty.

For both adult and juvenile groups, the P/Q ratio and the ecotrophic efficiencies were set to 0.5 year^{-1} and 95 %, respectively.

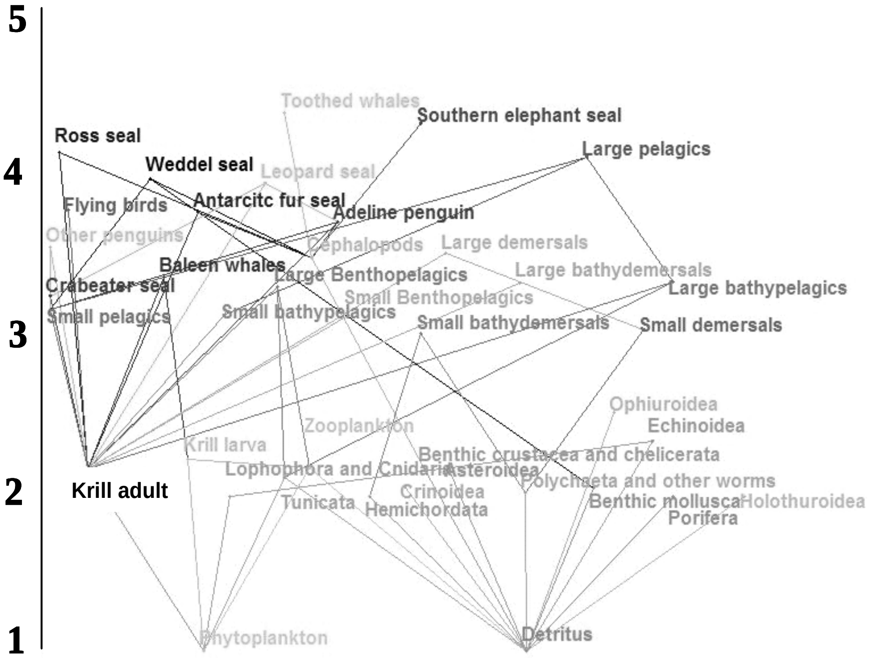

Figure 1. Food web diagram for 39 functional groups in the Antarctic peninsula *Ecopath* model, plotted against trophic level (vertical axis). Only trophic links more than 15 % of diet are shown. The pivotal position of krill in the ecosystem is apparent.

There is an ongoing debate on where biomass estimates should be based, given that krill populations are affected by seasonal and inter-annual variability. Lascara *et al.* (1999) suggest that densities off the west coast of the Antarctic peninsula range from a high of 95 g·m^{-2} during the summer to a low of 8 g·m^{-2} during the winter. Siegel (1998) calculated an instantaneous biomass of 1.16—1.65 million tonnes off the Antarctic peninsula, while he reports an additional 4.3—5.0 million tonnes passing through the survey area in the summer. Nicol and Endo (1999) report values as high as 4500 t·km^{-2} while the Antarctic krill are swarming. Furthermore, substantial mismatches between abundance of krill estimated from acoustic surveys and that estimated from predator demand (Nicol and Endo, 1999) are evident. Using a predator demand model, *Ecopath* calculated 32.2 t·km^{-2} of adult krill and 5.0 t·km^{-2} of juvenile krill. These estimates are within the annual range suggested by Lascara *et al.* (1999) and Siegel (1998) and were therefore considered as being reasonable estimates to use in the model at this stage of the work.

The diets of juvenile and adult krill were based jointly on the Weddell Sea model (Jarre-Teichmann *et al.*, 1997) and a study by Hernandez-Leon *et al.* (2001) which examined the diel cycle of gut contents of krill in the Antarctic Peninsula, suggesting that krill feed on phytoplankton during the day whereas they switch to carnivory during the night. Based on these observations the diet of juvenile krill was set to 80 % phytoplankton and 20 % zooplankton, and the diet of adult krill was set to 2.5 % juvenile krill, 2.5 % adult krill, 10 % zooplankton, 75 % phytoplankton and 10 % detritus.

Zooplankton

All the non-krill zooplankton are grouped together in a zooplankton group. This group consists largely of copepods (Boysen-Ennen *et al.*, 1991) and essentially replaces the mezzo-zooplankton group in the Weddell Sea model of Jaree-Teichmann *et al.* (1997). Similar to the invertebrates, input parameters for this group were adapted from the Weddell Sea model, i.e., P/Q ratio set to 0.4 year^{-1}, P/B to 4.5 year^{-1} and biomass to 13.4 t·km^{-2}. The zooplankton group consumes 10 % juvenile krill, 5 % zooplankton, 45 % phytoplankton, and 40 % detritus, again following the Weddell Sea model.

Phytoplankton

Boyd (2002) reviews studies on primary production in the Antarctic that have used remote sensing and perturbation experiments. Jarre-Teichmann *et al.* (1997) suggested a P/B ratio of 224 year^{-1} and a biomass range of 3.1-7.5 t·km^{-2} for Weddell Sea phytoplankton. An in-depth study of the Palmer Long Term Ecological Research (LTER) project by Smith *et al.* (1998, 2001) suggested a mean production of 1400 t·km^{-2}·year^{-1} for the highly productive coastal zone of the Antarctic peninsula, and an approximate mean production of 200 t·km^{-2}·year^{-1} for low-productivity zones. Since the area under study covers a high proportion of coastal areas (about 50 %), the average productivity for the periinsular area was estimated at 800 t·km^{-2}·year^{-1}.

Table 2. *Ecopath* model results for the Antarctic peninsula, with krill P/B at default value of 4. Parameters estimated by the mass-balance procedure in bold. TL = trophic level; B = biomass in t·km^2; P = production; Q = consumption; EE = ecotrophic efficiency; C = consumption; rates are annual.

Group name	TL	B	P/B	Q/B	EE	P/C
Ross seal	4.23	**0.008**	0.280	12.000	0.400	**0.023**
Weddel seal	4.06	0.036	0.040	12.000	**0.625**	**0.003**
Crabeater seal	3.3	0.281	0.080	15.000	**0.938**	**0.005**
Leopard seal	4.03	0.039	0.040	3.500	**0.192**	**0.011**
Antarctic fur seal	3.84	**0.019**	0.080	12.000	0.400	**0.007**
Southern elephant seal	4.42	**0.005**	0.300	11.000	0.400	**0.027**
Toothed whales	4.48	0.010	1.000	3.000	**0.030**	**0.333**
Baleen whales	3.42	0.020	0.100	4.000	**0.150**	**0.025**
Other penguins	3.61	0.080	0.200	12.000	**0.970**	**0.017**
Adeline penguin	3.78	0.060	0.500	12.000	**0.993**	**0.042**
Flying birds	3.85	0.075	0.100	10.000	**0.564**	**0.010**
Cephalopods	3.55	**0.222**	3.100	**10.333**	0.950	0.300
Large pelagics	4.20	2.000	**0.250**	1.000	**0.680**	0.250
Small pelagics	3.21	1.500	**1.500**	6.000	**0.797**	0.250
Large demersals	3.57	0.800	**0.460**	2.300	**0.828**	0.200
Small demersals	3.08	1.100	**0.650**	2.600	**0.709**	0.250
Large Benthopelagics	3.36	1.500	**0.840**	3.000	**0.418**	0.280
Small Benthopelagics	3.17	**0.524**	**1.830**	6.100	0.900	0.300
Large bathypelagics	3.39	**2.060**	**0.600**	3.000	0.900	0.200
Small bathypelagics	3.18	**0.894**	**1.800**	6.000	0.900	0.300
Large bathydemersals	3.38	0.800	**0.520**	2.600	**0.710**	0.200
Small bathydemersals	3.06	**0.440**	**1.200**	6.000	0.900	0.200
Benthic mollusca	2.05	**0.187**	3.000	**10.000**	0.900	0.300
Tunicata	2.12	7.200	0.300	1.000	**0.960**	**0.300**
Porifera	2.00	6.000	**0.180**	0.600	**0.793**	0.300
Hemichordata	2.00	6.500	0.400	2.000	**0.778**	**0.200**
Lophophora and Cnidaria	2.00	9.000	0.300	1.000	**0.524**	**0.300**
Benthic crustacea and chelicerata	2.20	6.500	1.200	3.500	**0.800**	**0.343**
Polychaeta and other worms	2.02	10.000	1.200	4.000	**0.636**	**0.300**
Echinoidea	2.36	6.500	0.200	**0.667**	**0.716**	0.300
Crinoidea	2.06	8.000	0.300	1.000	**0.733**	**0.300**
Ophiuroidea	2.54	15.000	0.173	**0.577**	**0.123**	0.300
Asteroidea	2.17	15.000	0.080	**0.267**	**0.379**	0.300
Holothuroidea	2.00	**1.111**	0.200	1.100	0.900	**0.182**
Krill larva	2.24	**4.541**	4.000	**8.000**	0.950	0.500
Krill adult	2.18	**27.215**	1.000	**2.000**	0.950	0.500
Zooplankton	2.18	13.400	4.500	**11.250**	**0.408**	0.400
Phytoplankton	1.00	7.500	239.000	-	**0.085**	-
Detritus	1.00	2.000	-	-	**0.087**	-

Using this productivity estimate and the suggested P/B ratio of 224 year^{-1}, phytoplankton biomass was estimated at 3.57 t·km^{-2}, which is also within the range suggested for the Weddell Sea.

Detritus

This model assumes that detritus is the accumulation of unassimilated biomass from ice algae and top predators, i.e., whales and large fish. Following the Weddell Sea model, detritus import was set to 50 t·km^{-2}·year^{-1}.

Fisheries

Catches reported by CCAMLR statistical bulletins indicate that in the last decade the catch in sub-area 48.1 consists solely of the Antarctic krill. Krill catches for the period 1991-2001 were averaged and entered into the model by country, i.e., Argentina, Chile, Japan, Korea, Poland, Russia, Ukraine, United Kingdom and

Uruguay. The total krill caught in the sub-area amounts to about 48,000 t·year-1. It was assumed that 10 % of these catches were juveniles.

Balancing the model

Given the assumption that species with high trophic levels are dominant in this system, and that the data available are reliable, a top-down balancing approach was adapted. This meant adjusting the biomass of prey to match the trophic demand of their predators; either by adjusting biomasses of prey from the baseline values imported from the Weddell Sea model or by allowing the model to calculate biomass by setting ecotrophic efficiencies to 95 %. Changes to baseline were accepted only if they generated reasonable results (Table 2). Table 3 shows the diet matrix, as adjusted during balancing and after preliminary diagnostic runs using *Ecosim*.

Table 3. Diet matrix giving proportional diets for the 39 functional groups in the Antarctic peninsula *Ecopath* model. Predators/grazers in vertical columns eat prey given in the rows; each predator diet sums to one.

Prey \ Predator	Ross seal	Weddel seal	Crabeater seal	Leopard seal	Antarcitc fur seal	Southern elephant sea	Toothed whales	Baleen whales	Other penguins	Adeline penguin	Flying birds	Cephalopods	Large pelagics	Small pelagics	Large demersals	Small demersals	Large Benthopelagics	Small Benthopelagics	Large bathypelagics	Small bathypelagics	Large bathydemersals	Small bathydemersals	Benthic mollusca	Tunicata	Porifera	Hemichordata	Lophophora and Cnida	Benth crus and chel	Polychaeta	Echinoidea	Crinoidea	Ophiuroidea	Asteroidea	Holothuroidea	Krill larva	Krill adult	Zooplankton
Ross seal							0.03																														
Weddel seal							0.03																														
Crabeater seal				0.15			0.02																														
Leopard seal							0.01																														
Antarcitc fur seal							0.02																														
Southern elephant seal							0.02																														
Toothed whales							0.01																														
Baleen whales							0.01																														
Other penguins				0.05			0.04				0.01																										
Adeline penguin				0.15			0.06				0.01																										
Flying birds				0.02			0.05																														
Cephalopods	0.65	0.15	0.02	0.1	0.2	0.75	0.25	0.02		0.2	0.1	0.05																									
Large pelagics		0.01	0.01	0.01	0.01		0.01	0.01	0.01	0.01	0.01		0.05		0.02				0.021																		
Small pelagics		0.19	0.07	0.09	0.09	0.05	0.07	0.09	0.19	0.21	0.12		0.225	0.03	0.02				0.031																		
Large demersals	0.02	0.05		0.01	0.03	0.02	0.02	0.01	0.02	0.01			0.05		0.05						0.025																
Small demersals	0.02	0.05		0.01	0.03	0.02	0.02	0.01	0.02	0.01			0.05		0.16						0.025																
Large Benthopelagics	0.02	0.05		0.01	0.02	0.02	0.1	0.01	0.03	0.01	0.07	0.04	0.025		0.02		0.05																				
Small Benthopelagics	0.02	0.05		0.01	0.03	0.02	0.14	0.01	0.02	0.01	0.1	0.06	0.05		0.02		0.1																				
Large bathypelagics	0.02	0.05		0.01	0.05	0.03	0.01	0.01	0.03	0.01	0.07	0.1	0.2		0.02				0.052																		
Small bathypelagics	0.02	0.05		0.01	0.03	0.02	0.02	0.01	0.03	0.01	0.1	0.1	0.2		0.02				0.103																		
Large bathydemersals	0.02	0.05		0.01	0.03	0.01	0.01	0.01	0.02	0.01			0.025		0.02		0.01				0.05																
Small bathydemersals	0.01	0.1		0.01	0.03	0.01	0.02	0.01	0.03	0.01			0.025		0.02		0.02				0.1																
Benthic mollusca	0.05	0.2				0.05	0.03								0.07	0.07																	0.02				
Tunicata																0.05	0.19		0.155														0.03				
Porifera												0.05				0.02						0.05										0.05	0.03				
Hemichordata									0.02		0.02	0.1				0.05		0.03	0.021			0.2										0.1					
Lophophora\ Cnidaria															0.01													0.01		0.25		0.01					
Benth crus and chel									0.02		0.03	0.3		0.04	0.1	0.1	0.06	0.06	0.124	0.1		0.1						0.05	0.01	0.04		0.1	0.02				
Polychaeta									0.02		0.02	0.05		0.01		0.52		0.03	0.144			0.5	0.05					0.1		0.06		0.085	0.06				
Echinoidea									0.01		0.01	0.03				0.02		0.03	0.021			0.05										0.05					
Crinoidea									0.02		0.02	0.1				0.05		0.03	0.021			0.1										0.1					
Ophiuroidea									0.01		0.01	0.02				0.02													0.005								
Asteroidea																												0.02									
Holothuroidea																													0.005								
Krill larva								0.2	0.06															0.1												0.025	0.1
Krill adult	0.15		0.9	0.35	0.45			0.6	0.44	0.5	0.3		0.1	0.83	0.35		0.37	0.7	0.206	0.76	0.8															0.025	
Zooplankton														0.09	0.1	0.1	0.2	0.12	0.103	0.14											0.05				0.2	0.1	0.05
Phytoplankton																							0.05	0.2	0.05		1		0.06		0.1	0.055			0.8	0.75	0.45
Detritus																							0.9	0.7	0.95	1		0.82	0.92	0.65	0.85	0.45	0.84	1		0.1	0.4

DESCRIPTION OF MODEL COMPONENTS: *ECOSIM*

Ecosim runs were conducted as a diagnostic tool to adjust *Ecopath* parameters, notably diet and P/B values to ensure realistic responses to zero fisheries, very large fisheries, and pulse fishing. *Ecosim* parameters provide the basis for dynamic simulations and for the spatial simulations in Ecospace. In this preliminary work, most *Ecosim* parameters were left at their default values except in the following cases:

Table 4. Vulnerability parameters for all predator/prey interactions in the Antarctic peninsula *Ecosim* model. Values have been scaled by trophic level of the prey type from 2 (bottom up) to 6 (top down). Note that values are expressed here in to the new (2004) *Ecosim* default range from 1 to infinity; in previous version this was 0-1.

Prey \ predator	Ross seal	Weddel seal	Crabeater seal	Leopard seal	Antarcitc fur seal	Southern elephant se	Toothed whales	Baleen whales	Other penguins	Adeline penguin	Flying birds	Cephalopods	Large pelagics	Small pelagics	Large demersals	Small demersals	Large Benthopelagic	Small Benthopelagic	Large bathypelagics	Small bathypelagics	Large bathydemersa	Small bathydemersa	Benthic mollusca	Tunicata	Porifera	Hemichordata	Lophophora/Cnidaria	Benth crust/chelic	Polychaeta/worms	Echinoidea	Crinoidea	Ophiuroidea	Asteroidea	Holothuroidea	Krill larva	Krill adult	Zooplankton	Phytoplankton	Detritus
Ross seal							4.65																																
Weddel seal							4.33																																
Crabeater seal				3.02			3.02																																
Leopard seal							4.05																																
Antarcitc fur seal							3.91																																
Southern elephant seal							4.99																																
Toothed whales							5.18																																
Baleen whales							3.22																																
Other penguins				3.54			3.54				3.54																												
Adeline penguin				3.32			3.32				3.32																												
Flying birds				3.91			3.91																																
Cephalopods	3.54	3.54	3.54	3.54	3.54	3.54	3.54	3.54		2	3.54	3.54																											
Large pelagics		4.49	4.49	4.49	4.49		4.49	4.49	4.49	4.49	4.49		4.49		4.49				4.49																				
Small pelagics		3.02	3.02	3.02	3.02	3.02	3.02	3.02	3.02	3.02	3.02		3.02	3.02	3.02				3.02																				
Large demersals	3.54	3.54		3.54	3.54	3.54	3.54	3.54	3.54	3.54			3.54		3.54						3.54																		
Small demersals	2.93	2.93		2.93	2.93	2.93	2.93	2.93	2.93	2.93			2.93		2.93						2.93																		
Large Benthopelagics	3.22	3.22		3.22	3.22	3.22	3.22	3.22	3.22	3.22	3.22	3.22	3.22		3.22		3.22																						
Small Benthopelagics	2.93	2.93		2.93	2.93	2.93	2.93	2.93	2.93	2.93	2.93	2.93	2.93		2.93		2.93																						
Large bathypelagics	3.22	3.22		3.22	3.22	3.22	3.22	3.22	3.22	3.22	3.22	3.22	3.22		3.22				3.22																				
Small bathypelagics	2.93	2.93		2.93	2.93	2.93	2.93	2.93	2.93	2.93	2.93	2.93	2.93		2.93				2.93																				
Large bathydemersals	3.22	3.22		3.22	3.22	3.22	3.22	3.22	3.22	3.22			3.22		3.22		3.22				3.22																		
Small bathydemersals	2.93	2.93		2.93	2.93	2.93	2.93	2.93	2.93	2.93			2.93		2.93		2.93				2.93																		
Benthic mollusca	2.07	2.07				2.07	2.07								2.07	2.07																	2.07						
Tunicata																2.07	2.07		2.07														2.07						
Porifera												2				2						2										2	2						
Hemichordata									2		2	2				2		2	2			2										2							
Lophophora/Cnidaria															2													2		2		2							
Benth crust/chelic									2.13		2.13	2.13		2.13	2.13	2.13	2.13	2.13	2.13	2.13		2.13						2.13	2.13	2.13		2.13	2.13						
Polychaeta/worms									2		2	2		2		2		2	2			2	2					2		2		2	2						
Echinoidea									2.25		2.25	2.25				2.25		2.25	2.25			2.25										2.25							
Crinoidea									2.07		2.07	2.07				2.07		2.07	2.07			2.07										2.07							
Ophiuroidea									2		2	2				2													2.45										
Asteroidea																												2.13											
Holothuroidea																													2										
Krill larva								2	2															2												2	2		
Krill adult	2.07		2.07	2.07	2.07			2.07	2.07	2.07	2.07		2.07	2.07	2.07		2.07	2.07	2.07	2.07	2.07															2			
Zooplankton														2.13	2.13	2.13	2.13	2.13	2.13	2.13											2.13				2	2.13	2.13		
Phytoplankton																							5.18	5.18	5.18		5.18		5.18		5.18	5.18			5.18	5.18	5.18	2	
Detritus																							5.18	5.18	5.18	5.18		5.18	5.18	5.18	5.18	5.18	5.18	5.18		5.18	5.18		

- simulation duration was set to 20 years;
- predator/prey vulnerabilities were set proportional to the trophic level of each prey group (Table 4), between 2 (representing bottom-up, or 'donor' control) and 6 (top-down control) (Cheung *et al.* 2002); this has proved to be a reasonable shortcut to tuning individual predator prey relationships from the default assumption that all vulnerabilities are the same (Ainsworth, in prep);
- juvenile and adult stages of krill were linked as 'split-pools', using 2 years as the age of transition to adult, and 4 as the ratio between average adult weight and average weight at the time of transition. This recruitment relationship is investigated further in Pitcher and Erfan (this volume).

DESCRIPTION OF MODEL COMPONENTS: ECOSPACE

Defining habitats

The Antarctic marine ecosystem in this model is divided into 3 zones: (1) a high-Antarctic zone, i.e., covered by ice all year long, (2) a seasonal pack-ice zone, i.e., covered by ice during some time of the year, and is ice-free during other times, and (3) an ice-free zone, i.e., the permanently open ocean (see Figure 2). This categorization corresponds roughly to the *biogeographical zones* identified by Hart (1934), Trèguer and Jacques (1992) and used by the Palmer LTER project (Smith *et al.*, 1998). In this model, the high-Antarctic zone is the zone adjacent to the land area, the seasonal pack-ice zone is adjacent to the ice, and the ice-free zone is furthest away from land.

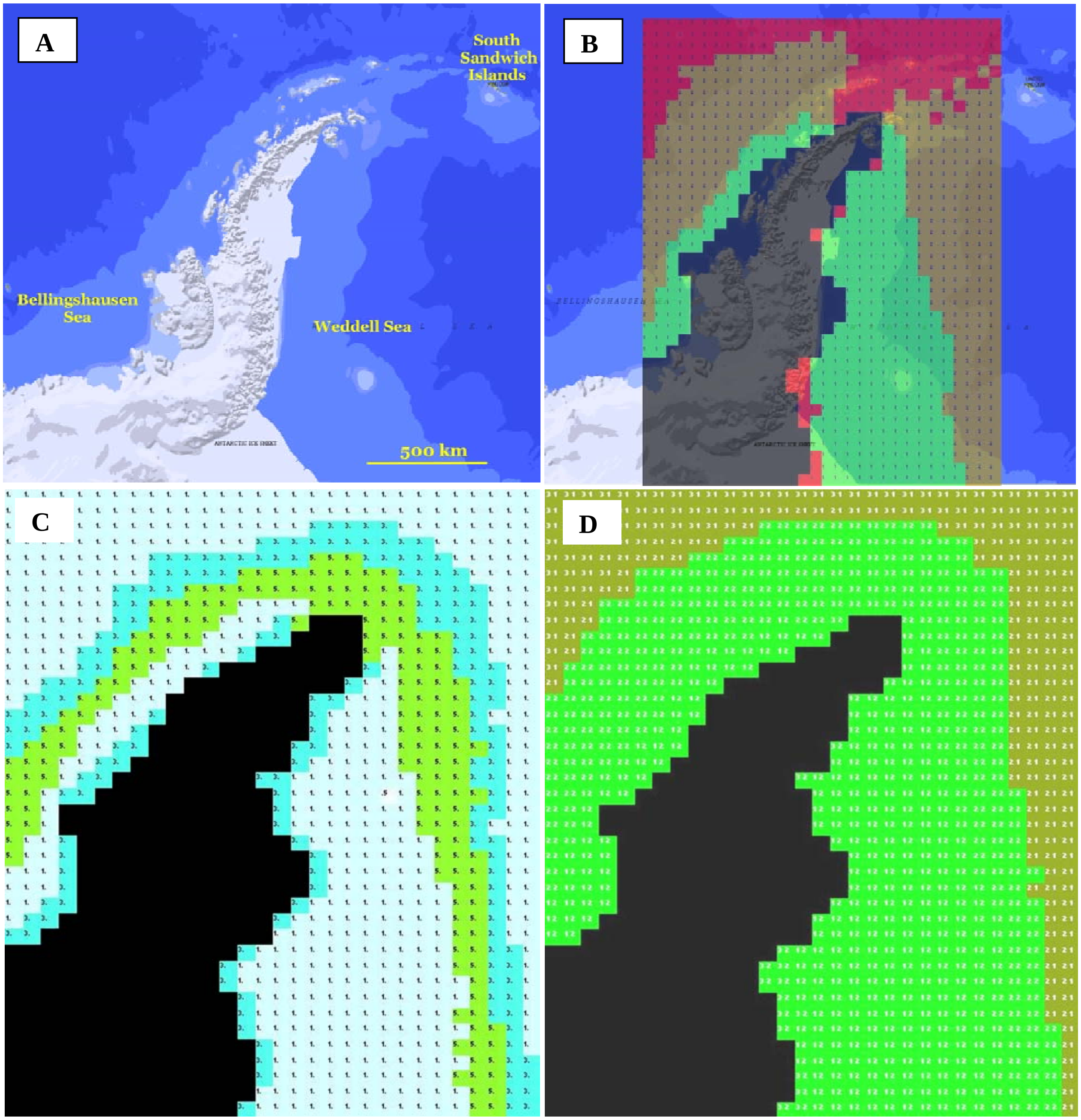

Figure 2. Maps of the Antarctic Peninsula showing the zones used in the spatial ecosystem model. A. Antarctic peninsula, scale and nearby ocean areas. B. Overlay grid showing habitats distinguished in the model: black = coastline ; red = ice free zones; brown = seasonal pack ice zone; green = 'High Antarctic' ice zone. C. Relative primary production levels: green = high; blue = medium; turquoise = medium. D. Fishery management zones used in the spatial model scenarios brown = outer, offshore; green = inner, coastal zone. The modeled area is divided into 1200 (40° south to north by 30° east to west) cells each approx 4 km² (see online version for these colors).

Assigning habitats

Each of the functional groups within *Ecopath* were 'assigned,' i.e., based on occurrence within a given zone(s), to one of the 3 defined habitats based on available literature and speculations and/or assumptions were used in other cases.

Spatial distribution of marine mammals was based on Ribic *et al.* (1991) who suggested that crabeater and leopard seals were only seen on the ice during the summer, while fur seals were seen in the open water, and minke whales were seen along the ice edge. Based on this information, the crabeater and leopard seals were assigned to the high-Antarctic zone, fur seals to the seasonal pack-ice and the ice-free zones, and baleen whales to the seasonal pack-ice zone. Based on their similarity to fur seals, the Ross, Weddell and elephant seals were assigned to the seaonal pack-ice and the ice-free zone. Toothed whales were assigned to the seasonal pack-ice and the Ice-free zone.

Spatial distribution of birds was adapted from Ainley *et al.* (1994), a spring survey which examined the pack-ice, the near-to-ice and the far-from-ice zones. Ainley *et al.* found Adélie penguins and a number of flying birds in the pack-ice zone. A number of other penguins and more flying birds were found in the near-to-ice zone, and only flying birds in the far-from ice zone. Based on these observations, the Adelie penguins were assigned to the high-Antarctic zone, other penguins were assigned to the seasonal pack-ice zone, and flying seabirds were assigned to all 3 habitats.

The spatial distribution of krill was adapted from Lascara *et al.* (1999). This study used length frequency distributions of krill collected by nets to show an across-shelf pattern of krill during the spring-summer season, i.e., large-sized krill were found offshore and small krill more inshore. Following this, juvenile krill were assigned to the seasonal pack-ice zone and the adult krill to the seasonal pack-ice as well as the ice-free zones.

In absence of sufficient data at this point all other groups (i.e., fish, invertebrates, zooplankton, phytoplankton and detritus) were assigned to all 3 habitats. The spatial distribution of phytoplankton was mapped separately (see below) and it was found that though fish and invertebrates were assigned to all habitats they tend to concentrate in areas where primary production is high.

Table 5. Ecospace dispersal parameters, see text for description of changes to default values.

Model Group	Base Dispersal rate (km·yr^{-1})	Relative dispersal in bad habitat	Relative vulnerability in bad habitat	Relative feeding rate in bad habitat
Ross seal	1000.0	10.0	2.0	0.01
Weddell seal	1000.0	10.0	2.0	2.00
Crabeater seal	1000.0	10.0	2.0	2.00
Leopard seal	1000.0	10.0	2.0	1.00
Antarcitc fur seal	1000.0	10.0	2.0	0.01
S elephant seal	1000.0	10.0	2.0	0.01
Toothed whales	2000.0	5.0	2.0	0.01
Baleen whales	2000.0	5.0	2.0	0.01
Other penguins	2000.0	10.0	2.0	1.00
Adélie penguin	2000.0	10.0	2.0	2.00
Flying birds	1000.0	10.0	2.0	1.00
Cephalopods	30.0	5.0	2.0	0.01
Large pelagics	150.0	5.0	2.0	0.01
Small pelagics	150.0	5.0	2.0	0.01
Large demersals	150.0	5.0	2.0	0.01
Small demersals	150.0	5.0	2.0	0.01
Large Benthopel.	150.0	5.0	2.0	0.01
Small Benthopel.	150.0	5.0	2.0	0.01
Large bathypel.	150.0	5.0	2.0	0.01
Small bathypel.	150.0	5.0	2.0	0.01
Large bathydem.	150.0	5.0	2.0	0.01
Small bathydem.	150.0	5.0	2.0	0.01
Benthic mollusca	10.0	5.0	2.0	0.01
Tunicata	10.0	5.0	2.0	0.01
Porifera	10.0	5.0	2.0	0.01
Hemichordata	10.0	5.0	2.0	0.01
Loph'ph/Cnidaria	10.0	5.0	2.0	0.01
Ben. Crus/Chelic.	10.0	5.0	2.0	0.01
Polychaeta+	10.0	5.0	2.0	0.01
Echinoidea	10.0	5.0	2.0	0.01
Crinoidea	10.0	5.0	2.0	0.01
Ophiuroidea	10.0	5.0	2.0	0.01
Asteroidea	10.0	5.0	2.0	0.01
Holothuroidea	10.0	5.0	2.0	0.01
Krill larva	10.0	5.0	2.0	0.01
Krill adult	300.0	5.0	2.0	0.01
Zooplankton	10.0	5.0	2.0	0.01
Phytoplankton	10.0	5.0	2.0	0.01

Dispersal

Though each group is 'assigned' to specific habitats, dispersal parameters are provided (see Table 5) which allow the group to go outside of their assigned habitat. This is particularly important for seals and penguins that often live on or near the ice, but routinely go into the open water to feed. The current Antarctic Peninsula Ecospace model has high dispersal values for mammals and seabirds, relatively lower dispersal values for fish, and low dispersal values for invertebrates and plankton.

'Base dispersal rates' for mammals and birds were raised from the default value of 300 to numbers in the range of 1000-2000 km·year^{-1}. The 'relative dispersal in bad habitat' parameter was raised from the default of 5 to 10. The 'relative feeding rate in bad habitat' parameter was raised from the default value of

0.01 to values in the range of 1-2. 'Base dispersal rates' for fish groups were lowered from the default value of 300 to 150 km·year^{-1} while the 'relative dispersal in bad habitat' and 'relative feeding rate in bad habitat' parameters were left at default values. 'Base dispersal rates' for invertebrates and plankton were lowered from the default value of 300 to 10 km·year^{-1} while the 'relative dispersal in bad habitat' and 'relative feeding rate in bad habitat' parameters were left at default values. 'Base dispersal rate' for the adult krill group as well as all other parameters were set to default values. Finally, base dispersal of the detritus group was set to 1, signifying minimum dispersal abilities, while other factors were left at default values.

Spatial Aspects of the Fisheries

Assuming that fishing vessels do not enter the ice, fisheries in the Ecospace model were restricted to the seasonal pack-ice zone and the ice-free zone. In some scenarios they were not allowed to fish in the coastal zone, and these scenarios were contrasted with results with free access to fishing all areas (see Pitcher and Erfan, this volume).

Basemaps

The shape of the Ecospace basemap was defined as having 40 rows and 30 columns, which produced a total of 1200 cells, each representing a 20 km by 20 km grid. Note that Ecospace requires a rectangular grid, making an exact representation of the Antarctic Peninsula difficult. As a result, the current Ecospace model includes part of the Weddell Sea.

Four maps were generated. The first two maps are those of the straight forward land area map which outlines the land and water sections of the Antarctic Peninsula and the habitat type map which represents the spatial extent of the 3 habitat types defined above. The extreme variations in the ice extent throughout the year made mapping the habitats difficult, thus, the ice, i.e., the high-Antarctic zone, was drawn subjectively to represent an 'average summer ice-extent'. The seasonal pack-ice zone was drawn to represent the difference between this average summer ice-extent and the maximum ice-extent which would occur during the winter. The ice-free zone was drawn as the area outside of the maximum winter ice-extent.

The third map drawn was that of protected areas. Though no MPAs existed in the Antarctic Peninsula during the period being investigated, two management areas were defined in using *Ecospace*'s protected area function, for investigation purposes. The first management area was drawn next to the coast of the Peninsula and extending approximately 5 cells (i.e., 100 m) outward from the edge of the ice. The second management area was drawn outside the first management area, covering a strip of about the same width. The purpose of these management areas is discussed in more detail by Erfan and Pitcher (this volume).

The last map drawn was of that of relative primary production, showing areas of low and relatively high primary production. As Smith *et al.* (1998) suggested, the least productive areas are those under the ice and those far from ice in the open ocean. The areas right next to the edge of the ice have the highest primary production and were thus given a value of 5 (representing 5 times as much primary production as that in the non-productive areas just described), while a narrow strip next to the coastline and right outside the highly productive area was given an intermediate relative productivity of 3.

CONCLUSIONS

This *Ecopath* and Ecospace model tries to capture the shape and spatial characteristics of the Antarctic Peninsula marine food web and provide the basis for a series of simulation scenarios presented in Erfan and Pitcher (this volume). We recommend here that subsequent work on this model include time-series biomass data to be fitted and the effects of climate change on the marine food web. It is hoped that this model of the Antarctic Peninsula will contribute to the *Sea Around Us* Project's overall goal of providing an integrated analysis of the impacts of fisheries on marine ecosystems, and eventually to devise policies that can mitigate and reverse harmful trends whilst ensuring the social and economic benefits of sustainable fisheries.

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THE KRILL FISHERY IN THE ANTARCTIC PENINSULA: SPATIAL ECOSYSTEM-BASED SIMULATIONS ADDRESSING CONSERVATION CONCERNS FOR CHARISMATIC SPECIES[1]

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ABSTRACT

A spatial ecosystem trophodynamic simulation model is used to analyze the impacts on the food web of potential fisheries for krill at the Antarctic Peninsula. Results suggest that krill fisheries at the maximum level recommended by CCAMLR quotas would have few effects on krill predators, unless catches were concentrated near to the coast within the foraging range of charismatic species living close to the ice edge. Explorations of uncertainty in the model parameter values show simulations are highly sensitive to the production to biomass ratio of juvenile krill, somewhat less sensitive to predation factors for the species in Antarctic Peninsula ecosystem, and not very sensitive to the type of recruitment relationship assumed for krill. The sensitivities of the simulation, however, do not alter the general conclusion of the need for spatial management of the location of permitted fisheries for Antarctic krill.

INTRODUCTION

Human activities, such as harvesting, have impacts on the different components of an Antarctic marine ecosystem. A common concern is that the increased fishery on the Antarctic krill (*Euphausia superba*) could negatively impact a wide range of organisms such as birds, seals and whales that prey predominantly on krill (Croll and Tershy, 1998; Tinan, 1998). Antarctic krill, called a 'keystone' zooplankton by some (Laws, 1985; Reid, 2001), seems to play a pivotal role in these ecosystems. Although the specifics of this role are to some extent uncertain, information on the trophic ecology of many species suggests that krill is a very important part of many diets and can affect the size and length of Antarctic food chains. Krill have been a target of commercial fisheries since the late 1970s (CCAMLR, 2001) and up to 100,000 t has been taken in some years (Figure 1). Any increase in krill fisheries is a potential threat to sustainabilty and conservation of charismatic organisms such as penguins, seals, whales and others (Everson *et al.* 2000). CCAMLR has established precautionary quota for krill fisheries using a simple adaptation of the Gulland single species model whose parameters are natural mortality and biomass.

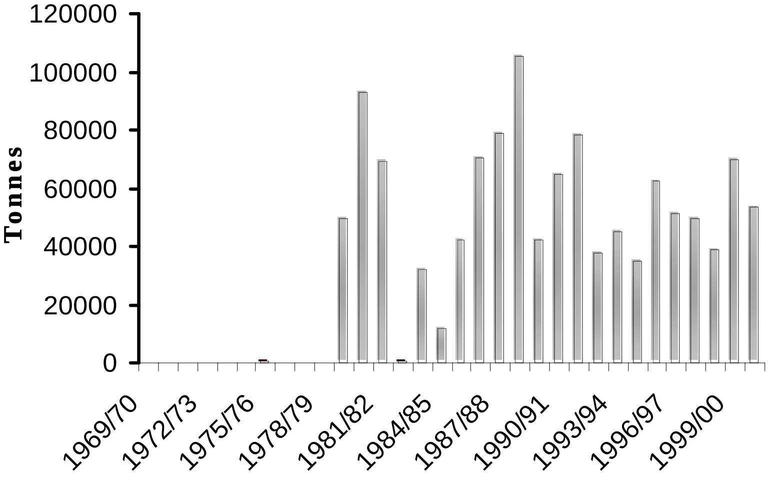

Figure 1. Annual catch history of the krill fishery in CCAMLR sub-area 48.1 (1970-2000) based on data from CCAMLR Statistical Bulletins.

In this paper, a tool commonly used to model marine ecosystems, *Ecopath*-with-*Ecosim* (EwE,

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[1] Cite as: Pitcher, T.J., Erfan, A., 2005. The krill fishery in the Antarctic Peninsula: spatial ecosystem-based simulations addressing conservation concerns for charismatic species. *In*: Palomares, M.L.D., Pruvost, P., Pitcher, T.J., Pauly, D. (eds.) Modeling Antarctic marine ecosystems. Fisheries Centre Research Reports 13 (7). Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 21-27.

Christensen and Walters, 2004), is applied to the Antarctic Peninsula region in CCAMLR sub-area 48.1. While a complex whole-ecosystem model contains many uncertainties, we show how it may be used to explore management scenarios for the krill fishery and determine the relative importance of the principal sets of uncertainties in the model.

At present krill fisheries are significantly less than the levels recommended by CCAMLR, but concerns have been raised about the fact that they are localized into relatively small areas close to the shelf, which also happen to be those areas in which many land based predators forage at the height of the breeding season (Everson and de la Mare, 1996). Fisheries may compete with krill predators in these locales. Our paper addresses this question by simulating situations where krill fisheries are close to the ice edge.

METHODS

Full details of the parameters and construction of the whole-ecosystem EwE model used in this paper, including the spatial components, are described by Erfan and Pitcher (2005, this volume).

Our general approach of this study was to carry out 'thought experiments' by generating simulation scenarios in EwE that were identical in all aspects except for the value of the parameter being examined First we used *Ecosim* to explore the potential impact of the CCAMLR krill quota using non-spatial analysis. The optimal policy search facility in EwE (Walters *et al.*, 2002) was employed to find the maximum size of fishery that reduced the biomass of charismatic species by no more than 20 % while maximising profit (using approximate price and costs values from the literature).

Next, we used *Ecospace* to explore spatial aspects of the problem. To investigate the difference in krill predator response to the location of krill fishery, two scenarios were generated in *Ecospace*. One restricted the krill fishery to a band around the ice edge (resembling the current fishing grounds in the area) using the 'MPA' utility of *Ecospace*, while the second scenario restricted the krill fishery to the area outside of this band. This meant that in the first scenario the spatial grounds of fisheries and predator foraging overlapped, while in the second scenario the two grounds were mutually exclusive.

We have also addressed some of the uncertainties by investigating the sensitivity to values of model parameters that we are not confident about. Uncertainties arise in particular with respect to the life history of krill. Published studies for the Antarctic Peninsula focus discussion on krill inter-annual variability (Siegel *et al.*, 1998), recruitment successes (Siege, 1992), diel feeding behavior (Hamandez-Leon *et al.*, 2001), seasonal variability and distributions (Siegel, 1989 and Lascara *et al.*, 1999) and the development of krill fisheries (Nicol and Endo, 1999). We have examined 3 aspects of uncertainty about krill ecology; the productivity of juvenile krill, expressed as the P/B ration used in the mass-balance *Ecopath* model; the type of recruitment relationship for krill populations; and the predator-prey vulnerability parameters that determine the trophodynamic responses in *Ecosim* and Ecospace.

The first uncertainty addressed in this study concerns the value of the production to biomass (P/B) ratio for juvenile krill. In the absence of data, the original *Ecopath* model was balanced using a 'guesstimate' of 4.0 year^{-1} for the P/B ratio of juvenile krill. Yet, it is possible that P/B for juveniles is actually much closer to the P/B ratio of adult krill of 1.0 year^{-1}. To investigate the sensitivity of the model to uncertainty in juvenile krill P/B ratios, two scenarios were created. In the first scenario, the *Ecopath* model was balanced for krill P/B=4.0 year^{-1}, while in the second scenario the *Ecopath* model was balanced for P/B=1 year^{-1}.

The second uncertainty addressed here concerns the recruitment power parameter used in the krill stock/recruit relationship. Originally a default recruitment power parameter of 1 was used for the stock-recruit relationship. Under high fishing pressure, this resulted in a strongly density-dependent Ricker-type recruitment curve (Figure 2). On the other hand, a power value of 0.1 produced a characteristic asymptotic Beverton and Holt recruitment curve. Since studies on recruitment of krill are rare, we have virtually no way of deciding if the power parameter should be set to 1, 0.1 or an intermediate value. Hence, to investigate the sensitivity of the model to recruitment power parameter, we set up two scenarios in which the first set the recruitment power parameter in *Ecosim* to 1, emulating a strongly density-dependent Ricker type of recruitment curve, while the second set the recruitment power parameter in *Ecosim* to 0.1, emulating an asymptotic Beverton-Holt type of recruitment curve (Figure 2).

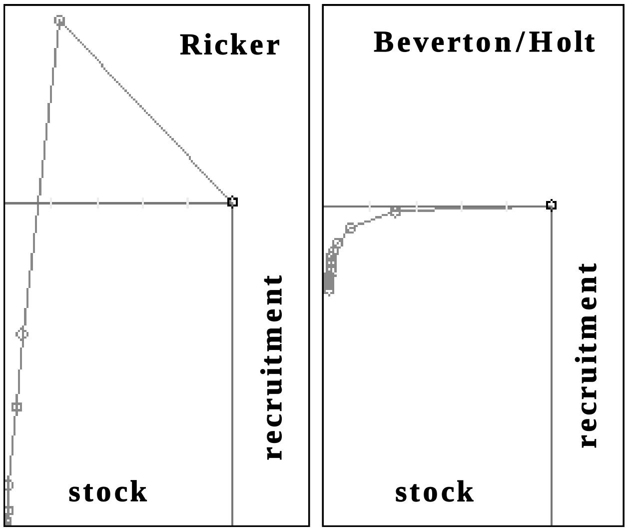

Figure 2. Recruitment curves resulting from different values of the recruitment power parameter in *Ecosim* models. Ricker-type peaked curve (left) is generated with the default power value of 1, and the Beverton-and-Holt-type asymptotic curve (right) with power value = 0.1.

A third uncertainty addressed in this paper concerns the value of predator-prey vulnerability. In *Ecosim*, vulnerabilities are used to simulate top-down or bottom-up control mechanisms between the modeled components of marine ecosystems. Because vulnerability values are practically impossible to measure in the field, we are often quite uncertain about them unless the *Ecosim* vulnerabilities are individually adjusted when fitting the model to time series biomass and survey data. A short-cut convention, that has proven helpful and was used in the original runs of this model, is to set the vulnerability to a number in a given range (usually 0.2 to 0.7) which is proportional to the trophic level of the functional group (Cheung *et al.* 2002; Ainsworth, 2004). This implies that organisms of high trophic level tend to exert a top-down effect while those of low trophic level exert a bottom-up effect. This is obviously an over-simplification, and alternative approximations are worth exploring. To investigate the sensitivity of the model to the vulnerability value of test parameters, 3 scenarios were created. The first scenario set the vulnerability of groups proportional to their trophic levels, varying between a minimum of 0.3 and a maximum of 0.6. A second scenario set all vulnerabilities to 0.3 representing a 'bottom-up' system while a third scenario set all vulnerabilities to 0.6, representing a 'top-down' system.

We note that the spatial modeling results achieved by *Ecospace* are mainly qualitative and based on comparisons with baseline or *status quo* simulation runs. When scenarios were run for increasing fishing pressure, the results were graphed so that sets of scenarios could be compared visually. Note that in each set of *Ecospace* scenarios, the first scenario is the 'default' or the original model constructed which (a) restricted the fisheries to a band around the ice edge, (b) set the juvenile krill P/B ratio to 4 year^{-1}, (c) set the recruitment power parameter of krill to 1 as in a Ricker curve, and (d) set all vulnerabilities proportional to trophic level as discussed above. Four other sets of scenarios were constructed to compare with this default: (1) fisheries allowed to the ice edge or kept away from the ice edge; (2) juvenile krill P/B ratio set to 1 year^{-1}; (3) recruitment parameter 0.1 as in aysmptotic Beverton-Holt recruitment; (4) vulnerabilities adjusted fromthe default 'mixed-control' model to 'top down' or 'bottom up' according to the rules outlined above.

For each scenario, we ran the *Ecospace* model at 8 levels of fishing mortalities (F): namely the current fishery and 25, 50, 75, 100, 250, 500 and 1000 times larger than the current fishery. These not only allowed us to check if krill and their predators responded differently at low and high fishing pressures, but also determined the ecosystem responses to fisheries at and above the CCAMLR allowable catch limits.

RESULTS AND DISCUSSION

Non-spatial results

First, we used the non-spatial version of *Ecosim* to investigate the effects of different levels of krill fisheries. Initial runs suggested that the recommended CCAMLR level for the fishery had a very small effect on krill biomass and an even smaller effect on other organisms in the ecosystem.

Next, using 20-year *Ecosim* simulations with random fishing mortalities for the krill fisheries as starting values, we seached for an 'optimal' krill fishery that maximised the value of an objective function including (a) ecosystem structure (vector of P/B ratios for all modeled components), and (b) Net Present Value (NPV) calculated as discounted revenue less operating costs. Components (a) and (b) were set to equal weighting (and results iterated until their influence on the objective function value was equalised at the maximum).

Results suggested that the krill fishery was optimised according to these criteria at 78 times its present level, reducing the krill population to 68 % of its unfished biomass, and inceasing the fishery from a yield of 0.23 t·km² to 9.2 t·km². This is remarkably close to the CCAMLR precautionary level for the krill fishery, although Adélie penguins were reduced by 28 % in this scenario. The weighting on the ecological component of the objective function had to be increased four-fold in order to restrain this penguin biomass reduction to 20 %. Note that a more recent version of the optimal search algorithm can use target biomass as a goal.

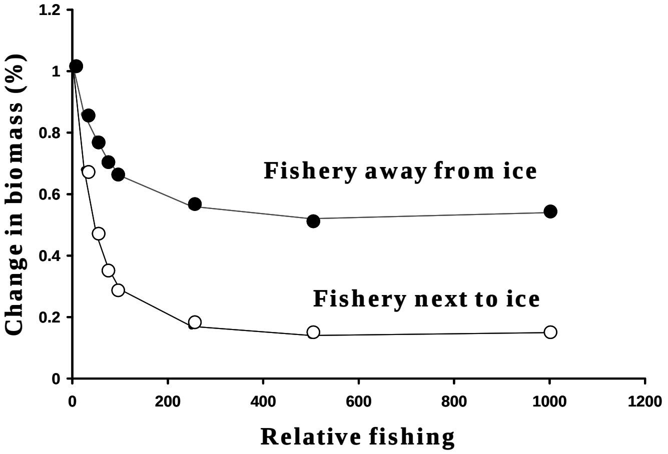

Figure 3. Krill biomass response to simulation scenarios based on proximity of krill fisheries to the ice edge. Fishing rate axis refers to size of simulated fishery in relation to present fishery.

Spatial scenarios: fishery zonation

Figure 3 compares changes in krill biomass where krill fishing was allowed close to the ice edge and penguin colonies, with the situation where krill fishing was allowed only in areas away from the ice. Results show that a fishery next to the ice edge, similar to the present fishery, has a higher impact on krill populations than one kept away for the ice. This result from the model is as expected, considering that the ice edge is likely the major spawning ground of krill and where juveniles are usually found.

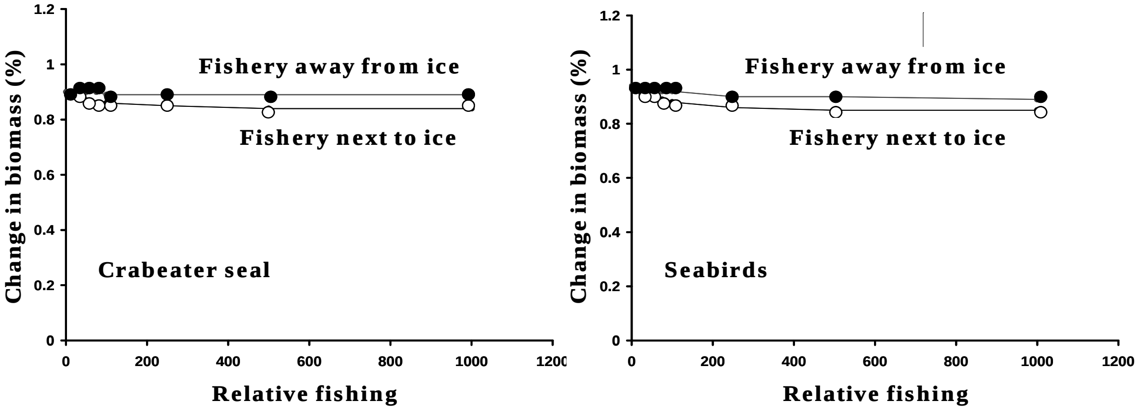

Figure 4. Crabeater seal and seabird biomass response to scenarios based on proximity to the ice edge.

Figure 4 illustrates the simulated change of biomass in krill predators for the same set of scenarios. The Crabeater seal and seabird groups have been chosen as examples as they are typical of many results of charismatic groups in the model. The results suggest that fishing away from the ice edge reduces the impacts on the biomasses of these krill predators, although the magnitude of the difference in not as large as that demonstrated for the krill biomass itself. Note also that while populations of krill fall sharply as fishing increases while the populations of seals and seabirds fall only slightly, by less than 10 %.

Spatial Scenarios: P/B ratio

Figure 5 shows that adult krill biomass, as expected, is sensitive to the changes in the turnover rates of juvenile krill, and decreases to lower levels if the juvenile P/B ratio is set to 1.

However, this is not true for seals and birds, which, in the model, showed almost no sensitivity to changes in the P/B ratio of juvenile krill (Figure 6).

Spatial scenarios: krill recruitment pattern and vulnerability parameters

Figure 7 (left hand column) shows that that different assumptions about the recruitment dynamics of krill have little effect. Similarly, adjustments in the vulnerability parameters for all marine ecosystem components have little effect on the modeled biomass of krill, seal and birds over this wide range of fishery sizes (Figure 7: right hand column).

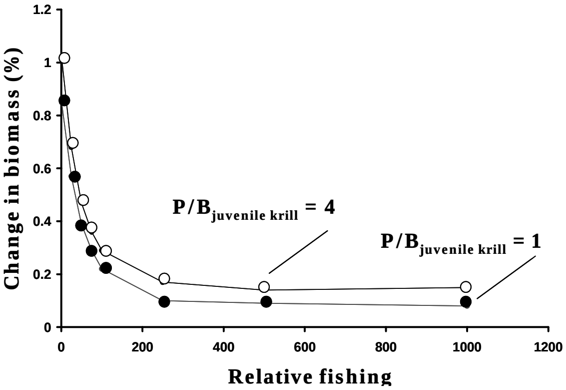

Figure 5. Adult krill biomass response to scenario based on changes to juvenile krill P/B ratios.

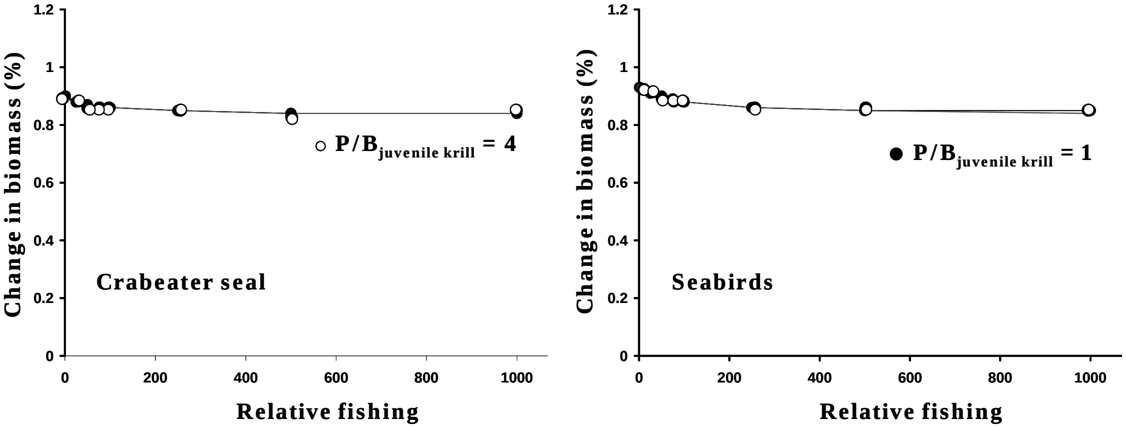

Figure 6. Crabeater seal and seabird biomass response to scenarios based on different assumptions about juvenile krill P/B ratios. Almost no differences were seen in the model.

Discussion and Conclusions

Since the establishment of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) in the early 1980s, there have been many efforts to better understand and to model different ecological aspects and places in Antarctica. An ecosystem modeling approach, such as that employed here, is especially appropriate in this context because CCAMLR, as well as understanding the physical processes dominating the marine ecosystem, has an explicit mandate to follow an 'ecosystem' approach in its management, *viz*:

> "*An ecosystem approach does not concentrate solely on the species fished but also seeks to minimise the risk of fisheries adversely effecting 'dependent and related species', that is, the species with which humans compete for food. However, regulating large and complex marine ecosystems is a task for which we currently have neither sufficient knowledge nor adequate tools. Instead, CCAMLR's approach is to regulate human activities (e.g. fishing) so that deleterious changes in the Antarctic ecosystems are avoided*" (de la Mare, 2000).

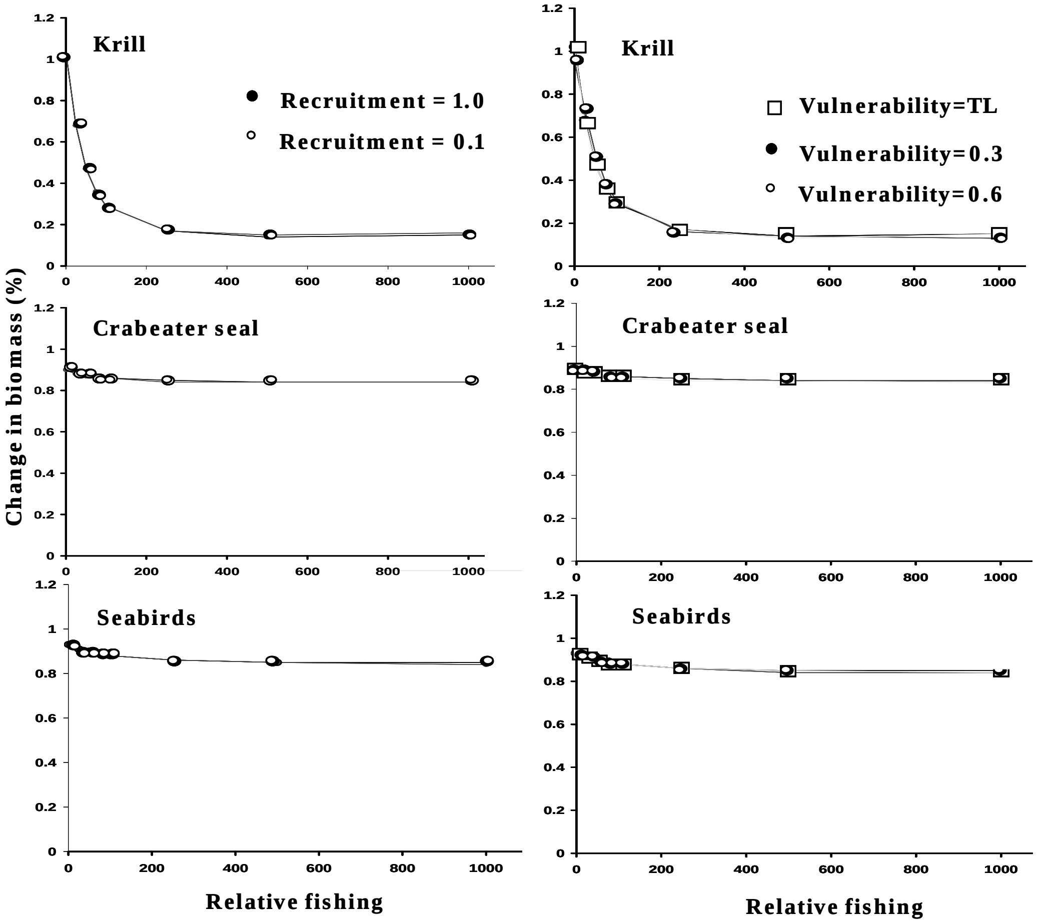

Figure 7. Adult krill, Crabeater seal and seabird biomass response to scenarios based on recruitment dynamics (left) and vulnerability parameters for all marine ecosystem predator-prey interactions (right).

Our approach in this paper represents a preliminary attempt to follow these recommendations, and help to develop new tools to enhance the ecosystem-based precautionary management which CCAMLR has pioneered. The whole-ecosystem simulation approach of *Ecosim* and *Ecospace* has not been used before on Antarctic ecosystems. Our basic mass-balance model (reported in full in Erfan and Pitcher, this volume) is only at the pilot stage; it certainly needs a lot of improvement, especially with more specific and local data about key parameters for Antarctic organisms. The functional groups in the model need to be expanded to capture more explicitly more species of conservation and commercial concern. In the dynamic *Ecosim* and *Ecospace* versions, the food web dynamics and spatial dynamics components of the simulation model can also surely be further refined. Parameters in the existing *Ecosim* model need to be tuned so that the models fit time series of local biomass survey and stock assessment data. The resulting tuned model has then to be challenged with parameter uncertainties and likely inter-annual climate fluctuations using Monte Carlo techniques before the full validity of results, and the likely risks associated with alternative management options, can be assessed (see Pitcher *et al.*, 2005).

Nevertheless, most of our general conclusions seem to be robust to alternative formulations of the key factors in our basic assumptions. The current ecosystem model is only slightly sensitive to uncertainties in juvenile krill P/B ratios, and not at all sensitive to uncertainties in the assumed krill recruitment dynamics, or the predator-prey vulnerability parameters that simulate ‘top-down’ or ‘bottom-up’ control in the ecosystem.

A non-spatial *Ecosim* optimization procedure confirms the CCAMLR precautionary harvest level for krill, which was estimated using a very different and much simpler algorithm. Spatial simulations suggest that, at the current level of krill fisheries, no significant impacts on charismatic animals such as seals and seabirds are likely to ensue. However, a large increase in fisheries can cause sharp drops in the population of krill, affecting populations that eat krill. However, at most realistic fishery levels, the effects on seal and seabird biomasses are not large, suggested by the fact that seals and seabirds show less steep decreases in biomasses as fishing pressure increases.

However, our spatial simulations comparing alternative configurations of krill fishery management zones suggest that the effects on both krill and its predators can be reduced if fisheries are kept away from the edge of the ice. The ice-edge zone appears to be the main spawning ground of krill, and a major part of the foraging grounds of colony-living breeding seals and sea birds.

In light of the drastic seasonal changes in sea ice cover and species habitat in and around the Antarctic Peninsula, it would be of interest to incorporate seasonality in the current model and examine the effects of different fishing scenarios on krill and its predators. As Nicol and Endo (1999) point out, fisheries in the Antarctic are limited by the ice extent. If in the future, and under CCAMLR guidelines, the krill fishery requires a year-round operation to maintain its viability then it may be that the sustainable limit of winter catches in small areas would be a factor constraining the size of the fishery. Winter models need to capture more precisely the ecological dynamics occurring at the ice-edge, including the mechanisms that maintain populations of krill and their predators through to the next austral spring. It appears that the spatial features of *Ecospace* would be useful for continuing these investigations.

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SUMMARY OF A PRELIMINARY MODEL OF THE MINKE WHALE – BLUE WHALE – KRILL INTERACTION IN THE ANTARCTIC[1]

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EXECUTIVE SUMMARY

As a first step in investigating the major predator-prey interactions in the Antarctic, a model describing blue whales, minke whales and krill is developed. Blue whales and minke whales both feed mainly on krill, and they share a similar feeding range in the Antarctic. In the early 20th century, the large baleen whales in the Antarctic were heavily harvested, some to near extinction (Figure 1). Blue whales were taken for almost 60 years, before being officially protected in 1964. Harvesting of the smaller minke whales commenced only in the 1970s, and the population probably increased during the mid 20th century, likely in response to increased krill abundance following the depletion of the large baleen whales. Figure 2 shows the estimated change in consumption of krill by baleen whales in the Antarctic before and after exploitation (Laws, 1977). From this comparison the suggestion followed that because of the intensive harvesting of the large baleen whales that feed mainly on krill, some 150 million tonnes of 'surplus' krill were available for other krill-feeding predators, such as minke whales and crabeater seals. Recent studies show recoveries of some of these large baleen whale species in response to protection, and also a possible recent decrease in the minke whales as the larger whales recover (Butterworth *et al.*, 1999). A recent analysis of blue whale abundance estimates from surveys yields a 8 % year^{-1} increase (Branch *et al.*, 2003), West Australian humpback whale surveys show a 11 % year^{-1} increase (Bannister, 1994), and the East

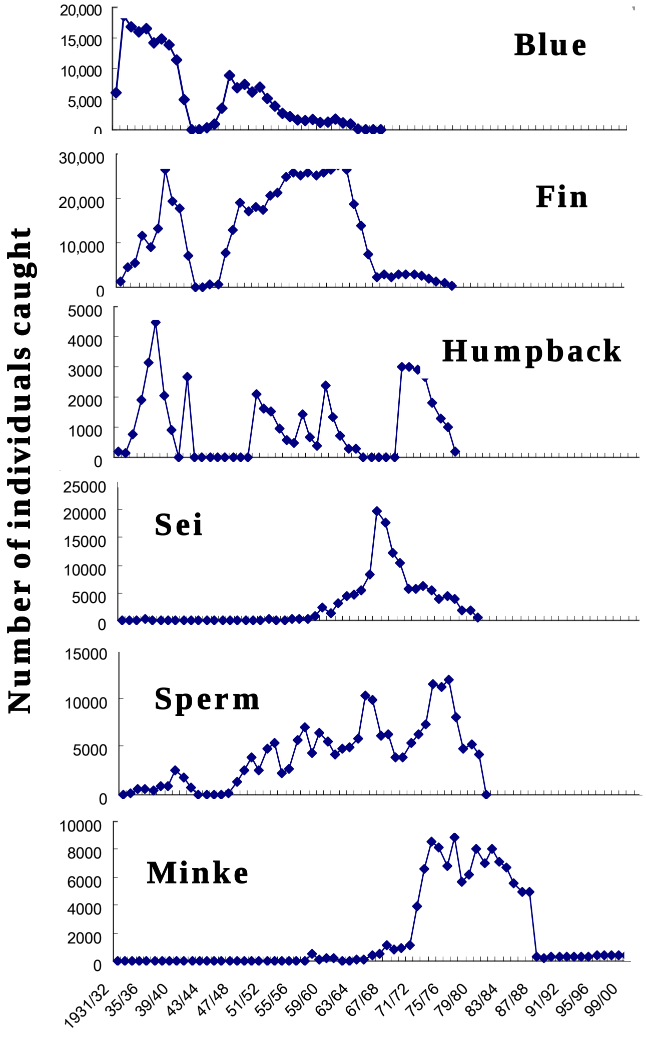

Figure 1. Catch history for whales in the Antarctic (data obtained from http://luna.pos.to/whale/sta.html).

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[1] Cite as: Mori, M., Butterworth, D.S., 2005. Summary of a preliminary model of the minke whale–blue whale–krill interaction in the Antarctic. *In*: Palomares, M.L.D., Pruvost, P., Pitcher, T.J., Pauly, D. (eds.) Modeling Antarctic marine ecosystems. Fisheries Centre Research Reports 13(7). Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 28-30.

Australian humpback whale surveys a 12 % year^{-1} increase (IWC, 2000).

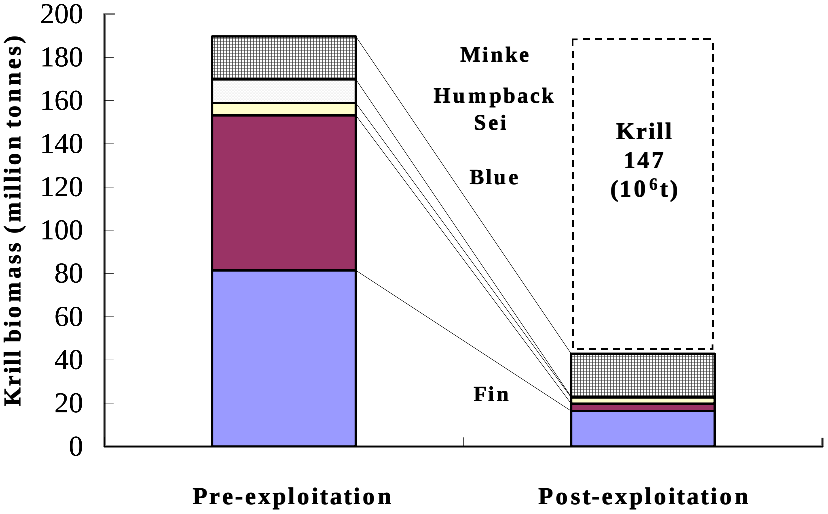

Figure 2. Estimated consumption of krill by baleen whales in the Antarctic. The plot shows the situation for 'pre-exploitation' and 'after exploitation' of the whales (from Laws, 1977).

We investigated whether the abundance trends indicated by survey and other information for these species can be explained by considering only harvesting and the predator-prey interactions between these species. Using the historical catch data for blue whales and minke whales, a simple age-aggregated model including species interactions is fitted to the observed abundance estimates for these species. Uncertainties in the abundance estimates and the biological parameters are taken into account in this process by considering plausible ranges for their values. Figure 3 shows some of the results of the trajectories for minke whales, blue whales and krill that did reflect these trends reasonably, provided these parameter values show certain features. These include: (i) blue whales are able to maintain their birth and krill consumption rate until krill abundance drops to relatively low levels, and (ii) both minke and blue whales show relatively high growth rates if krill is abundant, but the minke growth rate falls more rapidly as krill abundance drops. The model suggests two interesting features of the dynamics of these species:

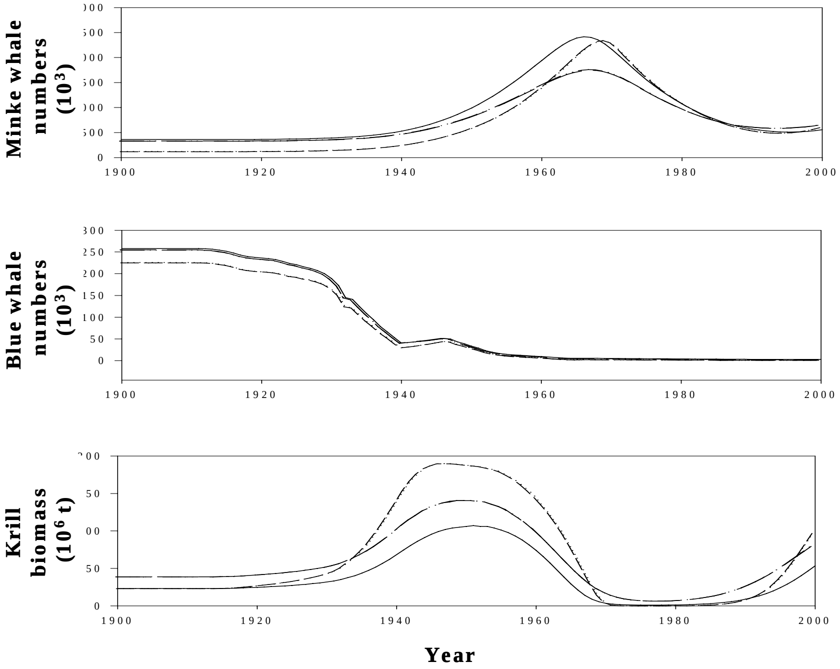

Figure 3. Trajectories of minke whales, blue whales and krill that reflect trends suggested by surveys and related analyses. Whale numbers are shown in thousands and krill abundance in million tons. A minke whale abundance in 1985 of 750,000 is fit in all these cases

- A substantial decrease in krill biomass from the 1970s to the 1990s due to the rapid increase in minke whale abundance, and hence krill consumption, following the depletion of the larger baleen whales.

- A recent recovery of blue whales in spite of the minke whale increase and impact on krill abundance, because blue whales are better able to tolerate decreased krill abundance.

Future projections for these species show a gradual increasing trend in blue whale abundance, with a gradual decrease in minke whale abundance, with large amplitude oscillations superimposed. The size of these oscillations is likely a reflection of the simplistic nature of the model, and is likely to be reduced by further planned model refinements. Long-term monitoring of biological parameters and abundance are essential to provide a basis for verification or otherwise of such predictions. For future work, we are considering refining the model structure, incorporating age-structure, some other major predator species that feed on krill, and some spatial structure.

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KERGUELEN ISLANDS

FEEDING HABITS OF SEABIRDS AND MARINE MAMMALS OF THE KERGUELEN ARCHIPELAGO[1]

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ABSTRACT

Birds and mammals in the Kerguelen Archipelago represent an essential component of the wild life that we can observe both at sea and on land. The strong impact of the seabird community on the ecosystem of the Kerguelen Archipelago merits emphasis on a special study to improve our knowledge of their behavior. The numerous studies on birds and mammals supported by the Institut Polaire Paul-Emile Victor to estimate their populations and to understand the inter-group and within-group interactions in the ecosystem are summarized in this article. This synthesis aims to complement information for the construction of an *Ecopath* model of the exclusive economic zone of the Kerguelen Islands.

BIRDS

Species, population sizes and breeding cycle

Thirty-five species of birds are known to breed in the area around the Kerguelen Islands. The only available census was made between 1984 and 1987, during which most of the archipelago was surveyed (Weimerskirch *et al.*, 1989). The avifauna includes 4 penguin species, 24 procellariiforms, 1 shag, 1 duck and 5 charadriiforms. The last 6 species plus the northern and southern giant petrels are excluded from the present work along with others which are totally (duck) or partially terrestrial (Lesser sheathbill and Kerguelen tern). Others are either coastal foragers, e.g., the Kelp gull which forages all year long (Stahl and Mougin, 1986) and the Antarctic tern which forages during summer (Stahl and Weimerskirch, 1982); or apex predators that feed mainly on seabirds and marine mammals during the breeding season, e.g., the Subantarctic skua (Moncorps *et al.*, 1998) and Giant petrels (Ridoux, 1994).

The remaining 27 avian species can be divided into several groups according to the length and period of their breeding seasons, foraging areas and feeding strategies (Table 1). The two largest species, the King penguin and the Wandering albatross, have very long breeding cycles, about one year and 13-14 months, respectively. Breeding adults foray from and to the colonies all year long. Three species are winter breeders, i.e., the Gentoo penguin, the Great-winged petrel and the Grey petrel. The other 22 species are summer breeders (see Table 1). Most of the species are migratory, being present in the colony during the reproductive cycle only. However, two species, the Kerguelen shag and the Gentoo penguin remain within the archipelago all year long (Bost and Jouventin, 1990), along with a part of the population of the Common diving petrel (Bocher *et al.*, 2000b).

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Table 1. Population sizes and foraging parameters of seabirds and marine mammals at Kerguelen Islands. Population size is given in breeding pairs, H. forage and V. forage are the horizontal and vertical forage area, respectively. Occur is the presence of the species in the area and For. time is the forage time in the area in percent.

Species	Common name	Pop. size	H. forage	V. forage	Occur	For. time (%)
Seabirds						
Aptenodytes patagonicus	King penguin	173000	slope, oceanic	epi-mesopelagic	all year round	75
Pygoscelis papua	Gentoo penguin	35000	coastal, neritic	benthic	all year round	100
Eudyptes chrysolophus	Macaroni penguin	1800000	neritic, slope, oceanic	epipelagic	summer	82
Eudyptes chrysocome	Rockhopper penguin	85500	coastal, neritic	epipelagic	summer	100
Diomedea exulans	Wandering albatross	1095	slope, oceanic	surface	all year round	35
Diomedea melanophris	Black-browed albatross	3165	neritic, slope	surface	summer	100
Diomedea chrysostoma	Grey-headed albatross	7900	slope, oceanic	surface	summer	35
Diomedea chlororhynchos	Yellow-nosed albatross	50	slope, oceanic	surface	summer	35
Phoebetria fusca	Sooty albatross	4	oceanic	surface	summer	35
Phoebetria palpebrata	Light-mantled sooty albatross	4000	slope, oceanic	surface	summer	35
Daption capense	Cape petrel	4000	neritic, slope	surface	summer	100
Pterodroma macroptera	Great-winged petrel	150000	oceanic	surface	winter	35
Pterodroma lessoni	White-headed petrel	35000	oceanic	surface	summer	35
Pterodroma brevirostris	Kerguelen petrel	40000	oceanic	surface	summer	35
Pterodroma mollis	Soft-plumaged petrel	5500	oceanic	surface	summer	35
Halobaena caerulea	Blue petrel	150000	slope, oceanic	surface	summer	35
Pachyptila desolata	Antarctic prion	2500000	neritic, slope, oceanic	surface	summer	35
Pachyptila belcheri	Thin-billed prion	850000	neritic, slope, oceanic	surface	summer	35
Pachyptila turtur	Fairy prion	5500	neritic, slope	surface	summer	100
Procellaria aequinoctialis	White-chinned petrel	200000	neritic, slope, oceanic	surface	summer	35
Procellaria cinerea	Grey petrel	7500	neritic, slope, oceanic	surface	winter	90
Oceanites oceanicus	Wilson's storm petrel	350000	neritic, slope	surface	summer	100
Fregetta tropica	Black-bellied storm petrel	7500	neritic, slope, oceanic	surface	summer	90
Garrodia nereis	Grey-backed storm petrel	4000	neritic, slope	surface	summer	100
Pelecanoides urinatrix	Common diving petrel	750000	coastal, neritic, slope	epipelagic	summer	100
Pelecanoides georgicus	South georgian diving petrel	1500000	neritic, slope	epipelagic	summer	100
Phalacrocorax verrucosus	Kerguelen shag	6500	coastal	benthic	all year round	100
Marine Mammals						
Arctocephalus gazelle	Antarctic fur seal (cows)	10000	slope	epipelagic	summer	100
	Antarctic fur seal (bulls)	*1000*				
Mirounga leonina	Elephant seal (cows)	41000	slope, oceanic	meso-bathypelagic	all year round	20
	Elephant seal (bulls)	2660				
Cephalorhynchus commersonii	Commerson's dolphin	600	coastal, neritic	epipelagic	all year round	100
Orcinus orca	Killer whale	50	neritic, slope	epipelagic	all year round	100
Physeter macrocephalus	Sperm whale (males)	800	slope, oceanic	meso-bathypelagic	all year round	70
Eubalaena australis	Southern right whale	30	neritic, slope	epipelagic	summer	100
Balaenoptera acutorostrata	Minke whale	2500	slope, oceanic	epipelagic	all year round	100
Balaenoptera musculus brevicauda	Pygmy blue whale	50	slope, oceanic	epipelagic	summer	50
Balaenoptera physalus	Fin whale	700	slope, oceanic	epipelagic	all year round	70
Megaptera novaeangliae	Humpback whale	100	neritic, slope	epipelagic	summer	100

Foraging time and areas

Foraging time spent in the archipelago is the period during which species are known to occur in Kerguelen waters, e.g., equivalent to the breeding season for migratory species and all year long for resident birds. Given the foraging areas and dietary habits of seabirds (see below), foraging time was estimated to be 35 % of a given year for procellariiform species feeding mainly outside the study area, in offshore oceanic waters, during the breeding season. These species are known or suspected to have a dual foraging strategy during the chick-rearing period (Weimerskirch *et al*., 1994), performing alternate long trips outside the study area and short trips within the study area when feeding their chicks (Cherel *et al*., 2002a, b).

Determination of foraging areas was mainly based on observations at sea, i.e., quantitative surveys undertaken on board the R/V *Marion Dufresne* between 1978 and 1988 (Stahl *et al*., in press). Additional information was obtained from satellite tracking of large seabirds, i.e., Black-browed albatrosses (Cherel *et al*., 2000) and King penguins (Bost *et al*., 2002), and from the biogeography of prey of smaller seabird species, i.e., planktivorous procellariiforms (Bocher *et al*., 2000a; Cherel *et al*., 2002a, b). The area was divided into 4 distinct foraging zones according to distance to the shore and bathymetry, i.e., coastal, neritic (< 200 m), slope (200-1000 m) and oceanic (> 1000 m) zones.

The main feeding strategies of seabirds are surface feeding (procellariiforms) and diving (penguins, Diving petrels and Kerguelen shag). Consequently, water column was divided into 5 zones, the surface (subsurface), epipelagic (0-200 m), mesopelagic (200-800 m), bathypelagic (> 800 m) and benthic zones. Studies on the food and feeding ecology of seabirds indicate that two guilds dominate the Kerguelen community, i.e., surface feeders on pelagic prey (procellariiforms), and pelagic divers (penguins and Diving petrels). A third guild, benthic divers, includes two species only, the Kerguelen shag and, to a lesser extent, the Gentoo penguin.

Food habits

Guinet *et al*. (1996) reviewed the dietary habits of many species of the Kerguelen Archipelago (see Table 2) and pointed out the general lack of information for some procellariiform species, e.g., for the White-headed petrel. Thus, food habits of seabirds not available for the Kerguelen region were assumed similar to the closely related Crozet Archipelago populations (Ridoux, 1994).

Prey items were divided into 8 categories (Table 2). Pelagic crustaceans were split into copepods (mesozooplankton), euphausids (mainly *Thysanoessa* spp. and the Subantarctic krill, *Euphausia vallentini*) and amphipods (mainly the hyperiid *Themisto gaudichaudii*). Note that Antarctic krill *Euphausia superba* does not occur in latitudes of the southern Indian Ocean (Miquel, 1991) and that *Themisto gaudichaudii* is the dominant component of the trophic web in both coastal and offshore waters of the Kerguelen Archipelago (Bocher, 2001). Larvae and small juveniles of notothenioid fishes are pelagic, while larger individuals are benthic over the shelf; they were consequently included in the benthic (neritic) fish section (Table 2). Others refer to broad taxonomic groups pooled together, e.g., salps, annelids and carrion.

Overall, pelagic swarming crustaceans are the major component of Crested penguins' diet as well as that of the bulk of medium-sized and small procellariiforms. Mesopelagic fish (mainly myctophids) dominate the diet of King penguins and are an important component of the diet of Crested penguins and some petrels. Finally, one species, the Kerguelen shag, specializes on benthic fish. Albatrosses feed mainly on cephalopods and, to a lesser extent, on carrion.

MAMMALS

Population sizes of pinnipeds, i.e., fur and elephant seals, were obtained from Guinet *et al*. (1996). Those of larger whales were estimated according first to the whale catch database of the International Whaling Commission (considering that sperm whale and baleen whale populations were reduced to 30 % and 10 % of their pre-whaling numbers, respectively), and second to abundance indexes for the Kerguelen area obtained from ship surveys (unpublished data).

Table 2. Diet composition (% weight) of seabirds at Kerguelen Islands.

Species	Copeps.	Euphaus.	Amphip.	Other crust.	Cephalopods	Pelagic fish	Benthic fish	Others	References
King penguin					3.0	96.9	0.1		Bost and Cherel unpublished data
Gentoo penguin		12.7	0.2	0.2	9.7	12.0	59.0	6.1	Lescroël *et al.* (in press)
Macaroni penguin		22.3	1.4		0.1	76.2			Bost unpublished data
Rockhopper penguin		58.6	2.4		18.9		20.1		Cherel unpublished data
Wandering albatross				0.1	76.7		14.9	8.4	Ridoux (1994)
Black-browed albatross					37.4		47.6	15.0	Cherel *et al.* (2002c)
Grey-headed albatross		1.0	0.2	0.2	55.4	1.8	27.6	13.9	Cherel *et al.* (2002c)
Yellow-nosed albatross				2.8	12.8	54.4	30.0		Cherel *et al.* (2002c)
Sooty albatross		0.4	0.9	1.4	40.5	1.7	3.8	51.2	Ridoux (1994)
Light-mantled sooty albatross		14.8	0.3	0.9	56.3	10.9		16.7	Ridoux (1994)
Cape petrel	5.5	33.7	11.5	0.3	2.0	2.0		45.0	Ridoux (1994)
Great-winged petrel			3.0	26.0	63.7	7.4			Ridoux (1994)
White-headed petrel				15	48	37			Zotier (1990)
Kerguelen petrel		1.3	17.6	53.6	6.0	0.3		21.2	Ridoux (1994)
Soft-plumaged petrel		0.1	6.3	0.1	21.2	63.9	7.9	0.4	Cherel unpublished data
Blue petrel	0.1	16.0	15.4	5.9	2.1	54.1	2.7	3.7	Cherel *et al.* (2002b)
Antarctic prion	0.4	19.5	60.2	2.1	2.9	12.8	0.1	2.0	Cherel *et al.* (2002a)
Thin-billed prion	0.1	20.0	59.2	2.6	6.0	11.5	0.1	0.6	Cherel *et al.* (2002a)
Fairy prion		1.5	63.2	30.7	4.6			0.1	Ridoux (1994)
White-chinned petrel		13.3	1.0	2.0	24.7	44.0	10.7	4.3	Ridoux (1994)
Grey petrel		3.3		0.1	34.7	24.6	24.6	12.7	Cherel unpublished data
Wilson's storm petrel	4.9	55.7	14.9	12.0		11.9		0.6	Ridoux (1994)
Black-bellied storm petrel		15.5	14.3	3.5	6.1	21.2		39.4	Ridoux (1994)
Grey-backed storm petrel		1.6	1.7	96.7					Ridoux (1994)
Common diving petrel	78.7	0.1	20.1	0.1			0.4	0.6	Bocher (2001)
South georgian diving petrel	10.9	81.2	5.8	0.1		0.8	1.2		Bocher *et al.* (2000a)
Kerguelen shag				0.1			97.0	2.9	Cherel unpublished data

Since dietary information by wet weight is very limited for elephant seals and sperm whales, we followed the estimated diet composition of 55 % cephalopods and 45 % fish, and 90 % cephalopods and 10 % fish reported by Hindell *et al.* (2003) and Mikhalev *et al.* (1981), respectively. It was assumed that the diets of fin and pygmy blue whales are identical to those of the Crozet Island populations (Pervushin, 1968). Finally, the diets of minke, humpback whales, and the poorly known southern right whales were estimated from Bushuev (1986), Kawamura (1980) and (1978), respectively (Table 3).

Table 3. Diet composition (% weight) of marine mammals at Kerguelen Island.

Species	Copeps.	Euphaus.	Amphip.	Other crust.	Cephalopods	Pelagic fish	Benthic fish	Others	References
Antarctic fur seal					9.2	81.7	9.1		Calculated from Lea *et al.* (2002)
Elephant seal					55.0	22.5	22.5		Hindell *et al.* (2003)
Commerson's dolphin		1.5	1.5	1.0			95.0	1.0	Estimated from Robineau and Duhamel (1984)
Killer whale							50.0	50.0	Guinet, unpublished estimation
Sperm whale					90.0		10.0		Estimated from Mikhalev *et al.* (1981)
Southern right whale	main prey	alter. prey[a]	alter. prey[a]						Kawamura (1978)
Minke whale		main prey	alter. prey[a]			alter. prey[a]			Estimated from Bushuev (1986)
Pygmy blue whale		98.0			1.0	1.0			Estimated from Pervushin 1968
Fin whale		100.0							Estimated from Pervushin (1968)
Humpback whale		main prey	alter. prey[a]						Estimated from Kawamura (1980)

[a] alternative, or secondary prey

CONCLUSIONS

The synthesis of the different studies conduct around the Kerguelen Archipelago gives a good estimation of the population size for the principal taxa of birds and top predators. Though there are not enough data on the marine mammal population sizes, our estimation can be considered as representative of the overall status of these groups. Thus, we are confident that the information we presented in this short contribution can be used in an ecosystem model of Kerguelen's EEZ through the *Ecopath* with *Ecosim* software.

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ESTIMATIONS DE LA BIOMASSE DES ZOOPLANCTONS DANS L'ARCHIPEL DE KERGUELEN[1]

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ABSTRACT

The importance of zooplankton in the Kerguelen Archipelago's ecosystem is reiterated. Biomass estimates were obtained from (1) scientific surveys of the R/V *Marion-Dufresnes* and (2) a study on bird-zooplankton interactions on the Morbihan Gulf and the eastern part of the Kerguelen plateau from scientific surveys on the R/V *La Curieuse*. Experiments performed at the Institut Polaire Paul-Emile Victor provide estimates of production-biomass ratios as well as ingestion rates of some important zooplankton species.

RESUME

L'importance du zooplancton dans l'ecosystème de l'archipel des Kerguelens a été réévaluée. La biomasse estimée a été obtenue à partir des campagnes océanographiques (1) du *Marion-Dufresne* et (2) d'une étude sur les interactions oiseaux-zooplancton dans le golfe du Morbihan et la partie Est du plateau de Kerguelen à partir de *La Curieuse*. Ces campagnes supportées par l'Institut Polaire Paul-Emile Victor ont permis d'estimer un rapport production-biomasse ainsi qu'un calcul du taux d'ingestion de quelques espèces importantes du zooplancton.

INTRODUCTION

Le zooplancton joue un rôle essentiel dans la chaîne alimentaire et représente la principale source d'alimentation des stocks de poissons. La composition globale du zooplancton est représentée à 60 % par les copépodes. L'estimation de la biomasse des copépodes et de leur croissance permet de disposer d'élément d'information important pour la création d'un modèle *Ecopath*.

Une étude sur les transferts de matières et d'énergie entre les premiers échelons de la chaîne trophique a été menée au large dans la zone de Kerguelen au cours des campagnes Antarès 3 et 4 en octobre-novembre 1995 et en janvier-février 1999 à partir du navire océanographique *Marion-Dufresnes*. Des stations de prélèvements ont été faites depuis l'ouest de Kerguelen de 49°S à 68°S permettant d'échantillonner trois zones hydrologiques différentes du nord au sud. Nous ne retenons pour cette analyse que les stations les plus au nord. Une autre étude sur les Interactions Oiseaux-Zooplancton (IOZ) a été faite en zone côtière dans le golfe du Morbihan et plus au large dans l'est sur le plateau a partir du navire océanographique *La Curieuse*.

Les données recueillies, au cours de ces différents programmes scientifiques nous permettent de faire des calculs de la biomasse et de P/B du zooplancton de la zone de Kerguelen. Nous avons ensuite comparé les résultats obtenus avec les estimations faites pour le modèle de Prince William Sound (Okey et Pauly, 1999) et vérifié ainsi la cohérence de nos calculs.

La synthèse de ces données a été faite à la suite du groupe de travail d'expert français de la zone de Kerguelen qui a eu lieu au Muséum national d'histoire naturelle à Paris en septembre 2003.

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MATERIELS ET METHODES

Au cours des campagnes Antarès 3 et 4 des séries d'échantillonnage ont été réalisées du nord au sud à partir de la zone ouest de Kerguelen et jusqu'au continent antarctique. A chaque station des prélèvements de zooplancton étaient faites avec un filet WP2 triple (0,25 m-^{2} et 200 µm de maille) par des traits verticaux de 200 m à la surface durant la nuit. Le matériel collecté dans le premier filet a été conservé congelé puis déshydraté avant d'être pesé au laboratoire. Nous n'avons retenu pour nos calculs de biomasse que la station numéro 3 de la campagne Antarès 4. Ces stations situées environ à 46° S et 63° O se trouvent dans le nord-ouest au large du plateau de Kerguelen. Les autres stations de ces campagnes situées trop au sud pour notre zone d'étude n'ont pas été retenues dans notre analyse. Nous avons également utilisé pour le calcul de la biomasse les données collectées dans les stations 4 et 5 du programme IOZ qui se trouvaient au large dans le secteur est du golfe du Morbihan sur le plateau par environ 45°45' S et 71°00 E. Le zooplancton a été prélevé à l'aide d'un filet WP2 simple par des traits verticaux de 200 m à la surface. Le matériel échantillonné a été analysé ensuite au laboratoire ce qui a permis de calculer le poids humide par groupe de tailles en g·m^{-2} a partir du poids sec en utilisant un ratio de poids sec/poids humide de 0.2 (données non publiées, J.-P. Labat).

Le calcul du P/B pour les copépodes a été réalisé à partir de l'étude de la composition, de la structure d'âge et des activités physiologiques dans le secteur de l'océan indien sud faites par Mayzaud *et al.* (2002) à partir des données des campagnes *Antarès 3*. La contribution des différentes espèces à la biomasse totale est issue de la littérature. Des expériences faites à bord du *Marion-Dufresne* ont permis de calculer : le taux d'alimentation par la méthode de la fluorescence intestinale ; le taux de respiration et le taux de production d'œuf pour les principales espèces représentées. L'analyse de ces données nous a permis de calculer le P/B.

RESULTATS

La biomasse

La biomasse du zooplancton total à partir de 0.25 mm, à la station 3, intégré sur 200 m est de 3.5371 g·m-^{2} de poids sec soit un poids frais de 17.556 g·m^{-2} pour un ratio P_{sec}/P_{humide} de 0,2 et un nombre de 126800 ind·m^{-2} intégré sur 70 m (Labat *et al.*, 2002).

Les échantillonnages de zooplancton pour les stations 4 et 5 de IOZ permettent de calculer des biomasses pour trois groupes de tailles différentes : le zooplancton de tailles inferieures à 1 mm ; celle de 1 à 3 mm et supérieures à 3 mm. Pour chaque groupe, le poids secs a pu être calculé et transformé en poids humides en considérant toujours un ratio P_{sec}/P_{humide} de 0,2 (J.-P. Labat, comm. pers.). Nous avons pu ainsi calculer le poids de chaque groupe en pourcentage dans la composition globale du zooplancton (Tableau 1).

Tableau 1. Valeur du poids sec et du poids humide calculé du zooplancton collecté pendant les campagnes Antarès (en g·m^{-2}) par groupe de taille et calcul du pourcentage de la fraction totale

Groupe de tailles (mm)	Poids sec (g·m^{-2})	Poids humide (g·m^{-2})	Fraction (%)
< 1	2.52	12.60	56.9
1-3	0.61	3.04	13.7
> 3	1.30	6.50	29.4
Total	4.43	22.13	

Le P/B

Tableau 2. Estimation des valeurs de P/B pour trois espèces des zooplancton dan l'archipel de Kerguelen adapté de Mayzaud *et al.* (2002).

Espèces	Poids sec (µg·ind·m^{-1})	Ingestion journalière (µgC·ind^{-1}·jr^{-1})	P/B an^{-1}	Régime alimentaire
Calanus simillimus	284	4,2	10,79	omnivore
Rhincalanus gigas	1287	15,3	4,34	herbivore
Calanus propinquus	1343	30,3	16,47	herbivore

Les abondances estimées en nombre·m^{-3} pour les principaux taxon zooplancton au cours de campagnes *Antarès* montre une très forte dominance des copépodes pendant l'automne austral dans le secteur indien de l'océan antarctique. Pour 299 ind·m^{-3} de copépodes nous avons 1,6 ind·m^{-3} de larves d'euphausiacés, 5,7 ind·m^{-3} d'ostracodes, 5,2 ind·m^{-3} de chaetognathes, 0,6 ind·m^{-3} de ptéropodes et 0,7 ind·m^{-3} de polychètes (Mayzaud, 2002). La contribution des différentes espèces à la biomasse totale est largement dominée par *Calanus simillimus* qui représente plus de 57 % de la biomasse, puis par *Metridia lucens* (22 %) et *Ctenocalanus citer* (15 %). La biomasse trouvée dans la littérature pour *Calanus simillimus* est de 284 µg·ind·m^{-1} (Atkinson, 1996). Nous retenons les biomasses de deux autres espèces représentatives du zooplancton herbivore, *Rhincalanus gigas* et *Calanus propinquus* (Conover et Huntley, 1991). La production de carbone a pu être calculée pour les principales espèces en prenant en compte la respiration et la production d'œuf. L'ingestion journalière pour différentes espèces de zooplancton nous est donnée dans la Table 9 de Mayzaud *et al.* (2002). Les valeurs de l'ingestion journalière en (µgC·ind^{-1}·jour^{-1}) et la biomasse trouvée dans la littérature sont reprises ici dans la Table 2 pour trois espèces représentatives du zooplancton herbivore et omnivore. En considérant que le ratio P_{sec}/P_{humide} =0,2, le P/B est calculé à partir de la formule P/B=Ing·a·2/B (Ing: Ingestion journalière en µgC·ind^{-1}·jr^{-1} ; a: nombre de jour annuel en jour (jr); B : Biomasse sèche en µg·ind^{-1} et C=0.2 poids sec).

CONCLUSIONS

La biomasse calculée pour le zooplancton est relativement faible. Elle est dominée essentiellement par quelques espèces identique à celle que l'on trouve dans les autres zone antarctique : *C. simillimus*, *C. propinquus*, *C. acutus*, *R. gigas (*Mayzaud *et al.*, 2002). Nous constatons ainsi l'importance en biomasse de la fraction petite < 1 mm, qui représente presque 57 % de la population de zooplancton dans cette zone. Ces biomasses semblent être cohérentes avec les synthèses faite par Mayzaud *et al.* (2002).

Le P/B calculé à partir des données de terrain sont tout à fait comparable avec les données de P/B du zooplancton de Prince William Sound (Okey et Pauly, 1999). Ces calculs de biomasses et de P/B que nous avons obtenus peuvent être intégré au modèle d'écosystème de Kerguelen (voir Pruvost *et al.*, ce volume).

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AN ECOSYSTEM MODEL OF THE KERGUELEN ISLANDS' EEZ[1]

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ABSTRACT

A preliminary ecosystem model of the Exclusive Economic Zone of the Kerguelen Islands is presented here. It emphasizes the Sub-Antarctic Patagonian toothfish (*Dissostichus eleginoides*) fishery zone, monitored since the 1980s by the *Muséum National d'Histoire Naturelle* (Paris, France). The model covers the periinsular shelf of the Kerguelen Islands and their surrounding slopes up to the EEZ limit, which totals a surface area of 575,000 km². The period treated is between 1987-1988, for which data from a series of oceanographic surveys are available, used as the basis for the estimation of biomasses of the different components of this ecosystem. Data from other sources were used in cases where no survey data is available, notably results of *Ecopath* models from similar systems, e.g., that of the Weddell Sea.

RESUME

Nous avons élaboré un modèle préliminaire des rapports trophiques entre les différents groupes d'organismes marins de l'écosystème des îles de Kerguelen. La zone choisie pour notre étude concerne une pêcherie sub-antarctique de légine (*Dissostichus eleginoides*) suivie depuis les années 1980s par le Muséum national d'histoire naturelle (Paris). Nous avons considéré la totalité du plateau de Kerguelen et les pentes environnantes dans la limite de la ZEE de Kerguelen. La superficie de cette zone est de 575 000 km². Pour construire ce modèle nous avons choisi de nous limiter à la période de 1987 et 1988, durant laquelle une série de campagnes océanographiques a été réalisée et a servi de base à l'estimation des biomasses de différents composants de l'écosystème. Les données utilisées dans notre modèle proviennent de nombreuses publications. En absence de certaines informations, nous avons utilisé des données concernant des systèmes écologiques proches ou des informations spécifiques à certaines espèces. Nous avons également eu recours dans certains cas à des données extraites d'autres modèles *Ecopath* (essentiellement celui de la mer de Weddell en Antarctique).

INTRODUCTION

The combined periinsular shelf of Kerguelen and Heard islands, known as the Kerguelen Plateau, is one of the largest in the Southern Ocean (Figure 1). It extends from the southern Indian Ocean to the edge of the Antarctic continent along the drift of the westerly Antarctic currents. The system's hydrology is particularly complex as the northern edge is bounded by the sub-tropical front while the polar front bounds the south. These two fronts meet northeast of Kerguelen where the zone classified as sub-Antarctic waters becomes narrow (Park *et al.*, 1998), thus providing Kerguelen with a special and relatively rich ecosystem compared to other sub-Antarctic ecosystems, e.g., the Kerguelen Plateau presents a strong Patagonian toothfish (*Dissostichus eleginoides*) fisheries potential.

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The Kerguelen EEZ, as claimed by France, includes the entirety of Kerguelen's periinsular shelf area, as well as all of the island's fisheries activities, which are considerable throughout the zone. The regular monitoring of the island's fishing industry by the MNHN since the creation of the EEZ (data available through the KERPECHE database from 1978 to present), and the numerous oceanographic surveys, notably by the French Polar Institute - Paul Emile Victor (IPEV, formerly IFRTP) and the French Antarctic and Sub-Antarctic Territory (TAAF), provided us the necessary data to include all of the island's EEZ in this study. We were able to define 7 bathymetrically characterized habitats around the archipelago, *viz.*: (1) shallow littoral zone with depths <10 m; (2) shallow coastal zone at 10-50 m; (3) inshore shelf at 50-100 m; (4) deepwater shelf at 100-200 m; (5) continental slope at 200-1,000 m; (6) high seas at >1000 m; and (7) Skiff Bank, a submerged volcano (see Reusch, 2002) on the northwest extremity of the Kerguelen Plateau (50°11'S, 63°56'E; top at about 250 m below sea level). Table 1 gives detailed information on the differences between these 7 habitat zones in terms of their surface area and coverage in relation to the total surface area of the Kerguelen EEZ.

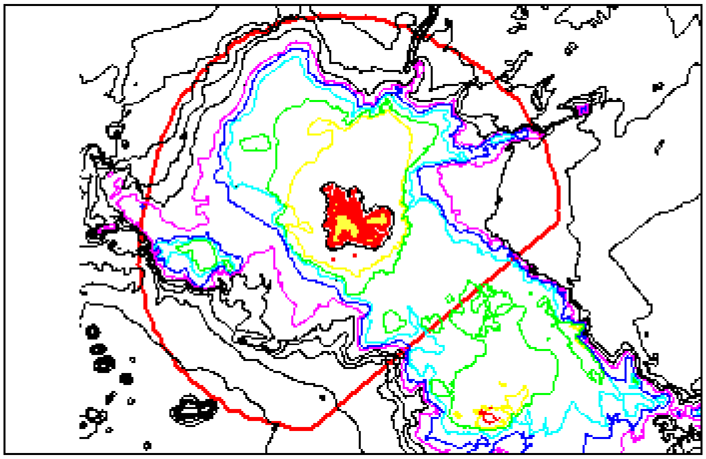

Figure 1. The Kerguelen Peninsula showing its depth contour and the EEZ claimed by the French government.

PERIOD OF STUDY

In 1987 and 1988, various oceanographic surveys, e.g., SKALP survey (see Duhamel, 1993) and fishing explorations using bottom trawls were conducted in order to better understand the Kerguelen ecosystem and to evaluate the potential of fisheries resources in the area. During the SKALP survey, plankton samples from WP2 and other nets and Bongo ichthyoplankton tows were obtained from 10 radials, each covering 5-7 stations, around the archipelago and repeated at different times of the year. Simultaneous bottom trawl sampling was performed in the same area. The sampling data obtained from this survey were used in the estimation of biomasses for plankton, ichthyoplankton and fish groups. In addition, data from more recent surveys, mainly in the pelagic domain, were used.

Table 1. Surface area of the different habitats identified for the Kerguelen Archipelago model in proportion to the total surface area of the archipelago's EEZ.

Habitat	Description	Surface area (km^2)	Surface area total EEZ (%)
1	Littoral zone (<10 m)	1,150	0.2
2	Shallow coastal zone (10-50 m)	2,875	0.5
3	Inshore shelf (50-100 m)	10,350	1.8
4	Offshore shelf (100-200 m)	29,900	5.2
5	Continental slope (200-1000 m)	152,375	26.5
6	High seas (>1000 m)	373,750	65.0
7	Skiff Bank (450 m)	4,600	0.8
–	Total surface of Kerguelen EEZ	575,000	100.0

DEFINITION OF SPECIES GROUPS

Species groups were defined first as a function of (i) their taxonomic and trophic levels and (ii) their maximum sizes. We thus came up with 23 species groups having either similar diets or size. Primary productivity is represented here by two groups, i.e., phytoplankton and benthic algae (predominantly of the genus *Macrocystis*). Zooplankton is represented by 3 groups, *viz.*: herbivores, usually of small size and feeding almost exclusively on phytoplankton; omnivores, usually bigger than herbivorous zooplankton and mostly feeding on small zooplankton; and zooplankton carnivores (copepods and euphausiids), representing a large proportion of the zooplankton biomass and an important prey item of pelagic fish species. Benthic epifauna are also represented by 3 groups: herbivores in shallow waters, omnivores in shallow waters and omnivores in deep waters. Cephalopods are separated into two size groups, e.g., small and large. Fish species are represented by 7 groups. The first 5 are easily defined according to their size and habitat, *viz.*: large benthic fishes, other benthic fishes, small pelagics, large pelagics, sharks and rays. The two other groups pertain to shallow water juvenile and deep water adults of the Patagonian toothfish (*Dissostichus eleginoides*), which are the target of a commercially valuable fishery. The 35 species of birds were separated into 2 groups, surface seabirds essentially procellariiforms and diving seabirds made up of 4 penguin species. Mammals are represented by 3 groups, i.e., hunting and filtering mammals and top predators essentially orca and sperm whales.

PARAMETER ESTIMATIONS

Biomass estimates in t·km^{-2} were prorated by the fraction of habitat area to the total EEZ surface area. Most mortality estimates were expressed as annual natural mortality because the Kerguelen ecosystem during this period was practically an unfished environment. Annual food consumption per unit biomass values, for fish groups, were obtained using the predictive equation of Palomares and Pauly (1998). Diets were mostly estimated as 'informed guesses' from sources inferring on the feeding habits and food items of the different species groups. In cases where there is no available information for a group referring to particular studies from the Kerguelen area, data from other similar ecosystems or similar groups in the same habitat or area were used, e.g., the Weddell Sea in Antarctica and Prince William Sound in Alaska (Jarre *et al.*, 1991; Okey and Pauly, 1998).

Primary production

The Kerguelen Archipelago is situated at the boundary of two important fronts, both contributing to the high phytoplanktonic production of the area. Primary productivity is also enhanced by an important biomass of giant seaweeds abounding in rocky shores, notably in the Morbihan Gulf (Belsher and Mouchot, 1992) and northeastern shallow waters, with *Durvillea antarctica* dominating inshore waters and kelp belts, mainly *Macrocystis pyrifera*, dominating deeper waters (Clark and Dingwall, 1985). These two groups were thus considered in this study.

Phytoplankton

The structure of the phytoplankton population in the Kerguelen Archipelago was established from the results of a four-year survey (1992-1994) conducted by IPEV (ex-IFRTP) for the Joint Global Ocean Flux Studies (JGOFS) on the French research vessel (trawler) '*La Curieuse*'. The phytoplankton population density estimated from water samples taken at the KERFIX sampling station at 50°40' S 68°25' E was low and mostly composed of picoflagellates and nanoflagellates (2–20 mm), *Coccolithus*, diatoms and dinoflagellates (Kopczynska *et al.*, 1998; see Table 2). These results did not provide an estimate of the phytoplankton biomass in the area and we opted to use the value of 7 t·km^{-2} estimated through satellite observations (SeaWifs; see Hoepffner *et al.*, 2001) for a primary production estimate of 118 gC·m^{-2}·an^{-1} or 1,064 gWW·m^{-2}·year^{-1} and an estimate of P/B at 150 year^{-1}.

Benthic algae

Biomass estimates of the dominant giant kelp species, *Durvillea antarctica* and *Macrocystis pyrifera* were not available. However, since the Kerguelen ecosystem is similar in structure to the Prince William Sound *Ecopath* model (see Dean, 1998a), we opted to apply the P/B ratio of 4 year^{-1} (originally reported by Luning, 1990) to obtain an estimate of 5.9 t·km^{-2} for the Kerguelen EEZ.

Zooplankton

Table 3 presents the species composition of the 3 zooplankton groups considered in this model, *viz.*: small sized pelagic zooplankton feeding exclusively on phytoplankton; bigger-sized zooplankton mostly feeding on small zooplankton but also ingesting phytoplankton and other plant material; and a group for carnivores including copepods and euphausids, which represents a large proportion of the zooplankton biomass and an important prey item of pelagic fish species.

Table 2. Dominant phytoplankton species observed in Kerguelen during the KERFIX survey from 1992 to 1995 (adapted from Table 3 in Kopczynaska *et al.*, 1998).

Group	Order	Family	Species
Nanoplankters	Coccosphaerales	Coccolithaceae	*Coccolithus huxleyi (Emiliania huxleyi)*
Diatoms	Bacillariales	Bacillariaceae	*Fragilariopsis curta*
			Fragilariopsis cylindrus
			Fragilariopsis kerguelensis
			Fragilariopsis oceanica
			Fragilariopsis pseudonana
			Nitzschia closterium
			Nitzschia longissima
			Pseudonitzschia heimii
			Pseudonitzschia lineola
			Pseudonitzschia spp.
	Biddulphiales	Biddulphiaceae	*Eucampia balaustium*
	Chaetocerotales	Chaetocerotaceae	*Chaetoceros atlanticus*
			Chaetoceros bulbosus
			Chaetoceros dichaeta
			Chaetoceros spp.
	Corethrales	Corethraceae	*Corethron criophilum*
	Thalassiosirales	Thalassiosiraceae	*Thalassiosira gracilis*
			Thalassiosira lentiginosa
			Thalassiosira (Coscinodiscus) spp.
	Thalassionematales	Thalassionemataceae	*Thalassionema nitzschioides*
			Thalassiothrix antarctica
Dinoflagellates	Gonyaulacales	Ceratiaceae	*Ceratium pentagonum*
		Gonyaulacaceae	*Gonyaulax* spp. *(kofoidii)*
		Oxytoxaceae	*Oxytoxum criophilum*
	Gymnodiniales	Gymnodiniaceae	*Amphidinium hadai*
		Gymnodiniaceae	*Gymnodinium flavum*
			Gymnodinium guttula
			Gymnodinium minor
			Gymnodinium spp.
			Gyrodinium spp.
	Peridiniales	Protoperidinaceae	*Protoperidinium antarcticum*
			Protoperidinium cruciferum
	Prorocentrales	Prorocentraceae	*Prorocentrum antarcticum*
			Prorocentrum micans
			Prorocentrum minimum
			Prorocentrum spp.

Table 3. Zooplankton composition of Kerguelen waters inferred from the 1987-1988 SKALP survey (Duhamel 1993).

Plankton group	Herbivores or detritivores	Omnivores	Carnivores
Copepods	*Oithona similis*	*Ctenocalanus parvus*	*Metridia lucens*
	Calanus propinquus	*Drepanopus pectinatus*	*Pareucheata antarctica*
	Rhincalanus gigas	*Calanus simillimus*	
		Calanoides acutus	
Hyperid amphipods	5-7 species		*Themisto* gaudichaudii (≈18 %)
Polychaetes		5-7 species	
Chaetognathes	5-7 species		*Eukrohnia hamata* (+5-7 species)
Pteropods	*Limacina* spp.		
Euphausiacea		*Thysanoessa* spp.	*Euphausia triacantha*
		Euphausia vallentini	*Euphausia frigida*
Tunicea		*Salpa thompsoni*	
Mysidacea			unidentified mysid species
Annelids			unidentified annelid species

A first estimate of zooplankton biomass was calculated from data obtained during the 1987 SKALP survey (Pakhomov, 1993a; Semelkina, 1993) where two different gears were used for sampling two different sizes of plankton. Small pelagic organisms were sampled using a net with 68 holes·cm^{-2} while bigger organisms were caught with an MRC net with 32 holes·cm^{-2}. Each net had a diameter of 80 cm and was sampled at different depths with weight messengers.

Thirty eight species of large zooplankton were reported by the SKALP survey which consisted of: tunicates, *Salpa* spp. (20 %); crustacean hyperid amphipods, *Themisto* spp. (18 %); chaetognaths (12 %), *Eukronia hamata, Sagitta gazellae* and *S. maxima*. Table 4 presents the species composition of zooplankton and their corresponding summer densities (number of individuals·m^{-2}) and biomasses (g·m^{-2}) as reported in Pakhomov (1993a). An average individual zooplankton (summer 1988) dry weight was estimated as 1.92 g·m^{-2}/105 individuals·m^{-2}=0.018 g. In order to estimate the zooplankton biomass for 1987, data presented in Table 5 were converted to g·m^{-2} by multiplication with the average individual dry weight. Using a dry to wet weight ratio of 20 % (Labat and Mayzaud, this volume), we estimated a total annual biomass for 1987 of 22.2 t·km^{-2} (Table 5).

Table 4. Species composition of zooplankton (number of individuals per m^2) and dry biomass (g·m^{-2}) in the Kerguelen Archipelago in summer (February) 1988 (adapted from Table 2 of Pakhomov, 1993a).

Order	Taxon	Number of ind. per m^2	Biomass (g·m^{-2})
Medusa		0.01	0.001
Syphonophora			0.013
Ctenophora		1.08	0.001
Polychaeta		0.03	0.009
Crustacea	Mysidacea	0.08	0.002
	Cumacea	0.01	
	Amphipoda, Hyperiidae		
	Themisto gaudichaudii	14.47	0.624
	Euphausiacea		
	Thysanoessa spp.	45.29	0.216
	Decapoda	0.02	
	Gammaridae	0.44	0.005
Pteropoda		0.20	0.005
Chaetognatha		40.72	0.402
Tunicea	*Salpa thompsoni*	2.40	0.639
		104.75	1.917

The biomasses obtained in Table 5 are similar to those observed by Labat and Mayzaud (this volume) in the east and northwest regions of the Kerguelen Archipelago. The percentage composition by 3 zooplankton particulate size groups reported in Table 1 of Labat and Mayzaud (this volume) provided us with a basis to calculate biomasses separately for our 3 diet-based zooplankton groups. We took the average of the total zooplankton biomass (19.8 t·km^{-2}) from that obtained for the northwest (22.1 t·km^{-2}) and the eastern regions (17.6 t·km^{-2}). We then assumed that small organic particulates (< 1 mm) represented herbivorous zooplankton, those 1-3 mm are omnivorous zooplankton and those > 3 mm are carnivorous zooplankton. Table 6 summarizes the results of these calculations.

Table 5. Average number for omnivorous zooplankton per m^{-2} in the Kerguelen Archipelago in 1987 during the SKALP survey (Duhamel, 1993) and dry biomass calculated from the average weight of individuals from survey data in summer (February) 1988(see Table 4 and text).

Species group	Summer 1987 (February)	Autumn 1987 (March-April)	Winter 1987 (July-August)	Theoretical (September)
Amphipoda	7.060	49.210	2.54	49.210
Hyperidae				
Themisto gaudichaudii	–	1.740	0.41	1.740
Chaetognatha	158.800	244.60	143.4	244.600
Tunicea				
Salpa thompsoni	12.700	25.160	0.31	25.160
Total (number·m^{-2})	178.56	320.710	146.66	320.710
Average weight in 1988 (g)	0.0183	–	–	–
Omnivorous Zooplankton (g·m^{-2})	3.276	5.884	2.691	5.884
Average biomass in 1987 (g·m^{-2})				4.433

General knowledge on the feeding biology of these groups permitted us to assign 'informed' estimates of their diet compositions (see also Pakhomov, 1993b). We assumed that herbivores could consume about 90 % of phytoplankton and about 10 % of detritus, while omnivores would consume about 70 % of herbivorous zooplankton and about 30 % of phytoplankton. We assumed that the carnivores ingest about 60 % of herbivorous zooplankton, 10 % of omnivorous zooplankton, 5 % of carnivorous zooplankton, 10 % phytoplankton, and about 15 % of detritus.

Herbivorous Zooplankton

Semelkina (1993) reported more than 70 species of crustacean copepods which are by far the most important and the most representative of this group while Semelkina (1993) reported 5-7 species each of crustacean amphipods, hyperids, chaetognaths and polychaet annelids. The estimated biomass for this group (see Table 6) is 11.3 t·km^{-2}. The estimate of P/B ratio (24 year^{-1}) from the Prince William Sound model (Okey, 1998b) was used in lieu of a better estimate for the Kerguelen EEZ.

Table 6. Distribution of the total biomass (g·m^{-2}) among the different particule sizes calculated from an average biomass of 19.843 (g·m^{-2}). Fractions were adapted from Table 1 of Labat and Mayzaud (this volume).

Particule size (mm)	Assumed zooplankton group	Dry weight (g·m-2)	Wet weight (g·m^{-2})	Fraction (%)	Wet weight (g·m^{-2})
< 1	herbivores	2.52	12.60	56.9	11.298
1-3	omnivores	0.61	3.05	13.7	2.726
> 3	carnivores	1.30	6.50	29.4	5.828
Total	–	4.43	22.15	–	19.84

Omnivorous Zooplankton

The estimated biomass for this group (see Table 6) is 2.7 t·km^{-2}. The P/B ratio of 11 year^{-1} was adapted from the Prince William Sound model (Okey, 1998b).

Carnivorous Zooplankton

In Kerguelen, *Euphausia vallentini* (1.3 g·m^{-2}), *E. triacantha* (0.034 g·m^{-2}), *Thysanoessa macrura* and *T. vicina* (0.22 g·m^{-2}) are the most common euphausiids sampled (Pakhomov, 1993a). To obtain the biomass of this group we used the data provided by Labat and Mayzaud (this volume) for large particles and retained the value of 5.828 t·km^{-2}.

We opted to adapt the P/B value from the Weddell Sea model (Jarre *et al.* 1991), even though this ecosystem is in colder climes, a semi-enclosed area, as there is a considerable similarity in the groups from these two different ecosystems; P/B for the Euphausiacae from the Weddell Sea was estimated to be 0.95 year^{-1}, averaged from the observed range of 0.8 to 1.1 year^{-1} (Siegel 1986).

Benthic fauna

As diet compositions of organisms in this functional group depend on body size and the habitat extent, we categorized them in 3 groups, *viz.*: 1) benthic shallow herbivorous epifauna; 2) benthic shallow omnivorous epifauna; and 3) benthic deep omnivorous epifauna (see Table 7). The first two groups are found in depths below 200 m, i.e., the photic zone where algae occur, with the first group consuming 96 % detritus and the second consuming 66 % of detritus and 30 % of small epifauna. The third group are mostly deepwater species (>200 m) whose diet is composed mainly of detritus.

Shallow benthic herbivores

The group of shallow benthic herbivores contains small, mostly sessile invertebrates living at the bottom of middle range depths that are rich in algae. One of the polychaet species, *Thelepus extensus*, occurs all around Kerguelen. Large areas of mussel beds also occur in the intertidal zone, e.g., *Mytilus desolationis* and *Aulacomyna ater*, which generate ‘reefs’ close to the Fjords (Féral, 1999). In the absence of detailed results, the biomass value for this group was adapted from the Prince William Sound model, i.e., 8.7 t·km^{-2} along with a P/B ratio of 2 year^{-1} and Q/B of 10 year^{-1} (Dean, 1998b).

Shallow benthic omnivores

This group includes large invertebrates living at the bottom of shallow waters. As with the previous group, values of biomass (3.1 t·km^{-2}), P/B (2.1 year^{-1}) and Q/B (10 year^{-1}) were adapted from the Prince William Sound model (Dean, 1998c) in lieu of detailed results for the Kerguelen ecosystem.

Deep benthic omnivores

This group includes large epibenthic fauna living at deeper depths of the sea bottom. Again, values of biomass (30 t·km^{-2}), P/B (3 year^{-1}) and Q/B (10 year^{-1}) were adapted from the Prince William Sound model (Okey, 1998a).

Table 7. List of dominant epibenthic species occurring in the Kerguelen ecosystem assembled from different sources.

Group	Shallow benthic herbivorous epifauna	Shallow benthic omnivorous epifauna	Deep benthic omnivorous epifauna	Reference
Mollusks	*Mytilus desolationis*			Féral (1999)
	Aulacomya ater			Féral (1999)
	Gaidmardia trapenisa	*Provocator pulcher*		Duhamel and Gasco (in press.)
	Nacella kerguelenensis			Duhamel and Gasco (in press.)
	Laevilittorina caliginosa			Duhamel and Gasco (in press.)
Crustaceans		*Halicarcinus planatus*	*Paralomis aculeata*	Duhamel and Gasco (in press.)
		Exosphaeroma gigas	*Neolithodes* sp.	Duhamel and Gasco (in press.)
		Gnathia sp.	*Thymopides grobovi*	Duhamel and Gasco (in press.)
		Serolis spp.	*Munida spica*	Duhamel and Gasco (in press.)
			Pasiphea balsii	Duhamel and Gasco (in press.)
			Nematocarcinus romenskyi	Duhamel and Gasco (in press.)
Annelids	*Thelepus extensus*			Féral (1999)
	Boccardia polybranchia			Féral (1999)
	Platynereis magalhaensis			Féral (1999)
	Aglaophamus trissophyllus			Féral (1999)
Echinoderms		Ophiuroids and Asteroids	Ophiuroids and Asteroids	
	Abatus cordatus			Féral (1999), Poulain and Féral (1995)
	Sterechinus diadema			Féral (1999)
	Plexechinus spp.			David and Mooi (2000)

Cephalopods

Cephalopods occurring around the Kerguelen Archipelago are not well known because they are undersampled by conventional nets. The important role of cephalopods in this ecosystem is however reiterated by results of recent studies on the feeding ecology of large marine predators (seabirds, sharks, marine mammals and fish) as well as from reports of fishing observers and oceanographic surveys, e.g., IPEKER (1995), ICHTYOKER (1998-2000) and KERAMS (1999). Thirty-eight cephalopod species from 15 families are reported in this area (Cherel *et al.*, 2004), from which we identified two functional groups, *viz.*: 1) large and 2) small cephalopods (see Table 8). Due to the lack of specific estimates for these groups in Kerguelen waters, we employed the P/B ratio of 1.0 and 0.6 year^{-1}, respectively, as used in Jarre *et al.* (1991) for the Weddell Sea ecosystem.

Ichthyofauna

We categorized the fish species occurring in the Kerguelen EEZ into 7 groups based on their habitat, e.g., shallow vs. offshore waters and benthic vs. pelagic, the surface of the said habitat and their diet compositions. The first 5 categories include: 1) large benthic fishes; 2) other benthic species; 3) small pelagic fishes; 4) large pelagics; 5) sharks and rays. The next two categories involve the Patagonian toothfish (*Dissostichus eleginoides*) which, due to its commercial value and importance in the fisheries was assigned to two distinct groups, i.e., 6) adults in deep seas; and 7) juveniles in shallow waters.

Most of the data on pelagic fishes were provided by the IPEKER (1995) and ICHTYOKER (1998-2000) mesopelagic surveys conducted in the EEZ, i.e., over 800 offshore trawls covering 4 survey years. Table 9 presents the catch distribution of samples obtained from these surveys. On the other hand, data on large commercial benthic fishes were obtained from observations documented in the fisheries database known as KERPECHE developed and maintained since 1980 by the Muséum National d'Histoire Naturelle in Paris. The data from these studies will soon be available as an atlas on Kerguelen fishes (see Duhamel and Gasco, in press).

Values of P/B were often generated using the equation proposed by Froese *et al.* (2000; http://www.fishbase.org/manual/key%20facts.htm): $M=10^\wedge(0.566-0.718\cdot\log_{10}L_\infty+0.02\cdot T$; where L_{max} is 95 % of L_∞ given the assumption that no growth parameters are available. In cases where growth parameter values are available, either from the Kerguelen Islands or for a similar habitat/locality, the empirical equation of Pauly (1980) was used: $\log_{10}M=0.0066-0.279\cdot\log_{10}L_\infty+0.65431\cdot\log_{10}K+0.4631\cdot\log_{10}T$; where L_∞ is in cm TL, K in year^{-1} and T in °C.

Table 8. List of cephalopod species occurring in Kerguelen waters obtained from oceanographic surveys, e.g., IPEKER (1995), ICHTYOKER (1998-2000) and KERAMS (1999) and from Cherel *et al.* (2004) and Cherel and Duhame (2004).

Group	Family	Species
Large cephalopods	Architeuthidae	*Architeuthis dux*
	Ommastrephidae	*Martialia hyadesi* *Todarodes* sp.
	Onychoteuthidae	*Moroteuthis ingens* *Moroteuthis knipovitchi* *Moroteuthis robsoni* *Moroteuthis* sp. B *Kondakovia longimana* *Onychoteuthis* sp. C
	Pholidoteuthidae	*Pholidoteuthis boschmai*
	Psychroteuthidae	*Psychroteuthis glacialis*
	Gonatidae	*Gonatus antarcticus*
	Octopoteuthidae	*Taningia danae*
	Histioteuthidae	*Histioteuthis atlantica* *Histioteuthis eltaninae*
	Neoteuthidae	*Alluroteuthis antarcticus* *Nototeuthis dimegacotyle*
	Mastigoteuthidae	*Mastigoteuthis psychrophila* ?*Mastigoteuthis* A ?*Mastigoteuthis* B
	Chiroteuthidae	*Chiroteuthis veranyi* *Chiroteuthis* sp. F
	Batoteuthidae	*Batoteuthis skolops*
	Cranchidae	*Galiteuthis glacialis* *Galiteuthis* St sp.C *Mesonychoteuthis hamiltoni* *Taonius* sp. B *Teuthowenia pellucida* *Oegopsida* sp. B *Oegopsida* sp. C
	Stauroteuthidae	*Stauroteuthis gilchristi*
	Opistoteuthidae	*Opistoteuthis* sp. *Cirrata* sp. A
	Octopodidae	*Graneledone gonzalezi* *Benthoctopus thielei*
Small cephalopods	Brachioteuthidae	*Brachioteuthis linkovskyi* *Slosarczykovia circumantarctica*
	Cycloteuthidae	*Cycloteuthis akimushkini*
	Sepiolodae	*Stoloteuthis cf leucoptera*

Values of Q/B were obtained from the empirical equation proposed by Palomares and Pauly (1998), i.e., $\log_{10}Q/B=7.964-0.204\cdot\log_{10}W_\infty-1.96\cdot T'+0.083\cdot A+0.532\cdot h+0.398\cdot d$; where W_∞ (or asymptotic weight in grams) is the weight converted from L_∞ as $W=a\cdot L^b$; T' is the mean environmental temperature (=1000 / (°C+ 273)); A is the aspect ratio of the caudal fin indicative of metabolic activity and expressed as the ratio of the square of the height of the caudal fin and its surface area, 'h' and 'd' are dummy variables indicating herbivores (h=1, d=0), detritivores (h=0, d=1), omnivores (h=0.5, d=0.5), and carnivores (h=0, d=0). In cases where no length-weight relationships were available, estimates of W_∞ were obtained using assumed values of a=1 and b=3. In cases where L_{max} and L_∞ are available only as standard length and no conversion relationships are given, SL:TL ratios were measured from the morphologically correct drawings provided in the FishBase pictures gallery for the species.

Large benthic fishes

This group represents fish species living on the continental shelf at depths less than 1,000 m and includes all bottom trawl fishing targets from 1970 to the middle of 1990. Mackerel icefish, *Champsocephalus gunnari*, is added to this group because it has a feeding behavior similar to large benthic fishes even though it could also be considered as a semi-pelagic fish. It may be wise to separate this one species as a single group in future models, but for the meantime we consider mackerel icefish a large benthic fish.

Most of the large benthic fishes belong to the family Nototheniidae, whose members have an average life expectancy of around twenty years. Adult nototheniids live in the deep waters around Kerguelen but juveniles stay in shallow water. For example, juveniles of the marbled rockcod, *Notothenia rossii*, live in kelp belts (*Macrocystis*) feeding mostly on crustaceans and small fish associated with algae while adults migrate over shelf areas and become more zooplanktivorous consuming ctenophores, salps and euphausiids.

Table 9. Total weight (grams) and number of pelagic fish specimens caught by family during the ICHTYOKER cruises conducted in 1998-2000 off the Kerguelen Islands (unpublished data, ICHTYOKER database, P. Pruvost).

Family	Total weight (g)	Total number	Weight (%)	Number (%)
Myctophidae	482766	168408	70.46	94.30
Centrolophidae	110617	195	16.15	0.11
Gempylidae	39758	854	5.80	0.48
Stomiidae	17437	2033	2.55	1.14
Bathylagidae	14218	844	2.08	0.47
Others	20281	6216	2.96	3.48

In 1988, the yield of all commercially important large benthic fishes was estimated at 279,000 t at the 100-500 m depth range (Duhamel, 1988). We assumed an average biomass of 0.49 $t \cdot km^{-2}$ for the whole area (Table 10). Note that in Table 10, the large difference of catches between the two years considered is affected by an influx of new *Chamsocephalus gunnari* recruits (length at first catch, L_c, at about 25 cm) to the fishery in early 1988.

Since mackerel icefish represented the bulk of the large benthic fish biomass (almost 80 %), this justified the use of the P/B ratio of 0.19 $year^{-1}$, i.e., from the natural mortality (M) value of mackerel icefish females from Elephant Island, Eastern Antarctic Ocean, estimated by Erzini (1991) from data in Tomo and Oro (1985). The Q/B value of 1.98 $year^{-1}$ was obtained as the average of values presented in Table 11 weighted by the dominance of the species (% biomass) presented in Table 10.

The diet composition for this group is based on 75 % of mackerel icefish diet and 25 % of the diet of grey rockcod, *Lepidonotothen squamifrons*. Data on the diet composition of mackerel icefish was adapted from Kozlov *et al.* (1988) for samples obtained from South Georgia Island, Southern Atlantic Ocean, and which consumes 73 % of euphausiids (66 % *Euphausia superba* and 7 % *Thysanoessa* sp.), 16 % hyperid amphipods (*Themisto gaudichaudii*), 10 % mysids, 1 % bony fishes. Data on the diet of *L. squamifrons* adapted from Pakhomov (1993b) for samples obtained from Lena Tablemount on the Indian Ocean sector of the Antarctic for the period 1970-1989 indicates that it consumes 60 % mostly salps, 36 % planktonic crustaceans, 2.2 % bony fish, 1.8 % jellyfishes and 0.7 % of other planktonic invertebrates.

Table 10. Total biomass estimation (279,140 t) for the major commercial benthic fish species, except Patagonian toothfish, *Dissostichus eligenoides*, caught in the Kerguelen EEZ in 1988 for the 100-500 m depth range (total surface area of 575,100 km^{-2}; see Duhamel, 1988).

Species	Common name	1987 (t)	1988 (t)	Mean biomass (t)	Biomass (%)
Champsocephalus gunnari	Mackerel icefish	15,024	429,052	222,038	79.5
Notothenia rossi	Marbled rockcod	28,290	17,940	23,115	8.3
Channichthys rhinoceratus	Unicorn icefish	20,330	23,247	21,789	7.8
Lepidonotothen squamifrons	Gray rockcod	9,189	5,407	7,298	2.6
Others		6,335	3,467	4,901	1.8
Total		79,168	479,113	279,140	

Other benthic fishes

Fishes considered in this group are smaller than 50 cm and live on the shelf close to the coast. Table 12 lists the species categorized under this group with the estimates of their L_{max} used to estimate P/B and Q/B ratios according to the equations described above. Average values of P/B = 0.502 $year^{-1}$ and Q/B = 7.33 $year^{-1}$ were obtained from species dominating the system.

Small pelagic fishes

This group contains specimens smaller than 45 cm inhabiting the upper parts of the water column on all depths. Catch distributions obtained from the ICHTYOKER and IPEKER surveys show that most of the fishes caught under this category belong to the lanternfish family, Myctophidae, i.e., 94 % of the numbers and 70 % of the weight caught (see Tables 9 and 13). Lanternfishes effect nighttime daily migrations to the surface from depths of more than 1000 m, mostly following the migration patterns of their planktonic prey. Average lanternfish longevity is 3-4 years. The biomass estimation is based on the estimate of

Gjøsaeter and Kawaguchi (1980) at 4.5 t·km^{-2}. As in the previous fish groups, average estimates of P/B = 0.5 year^{-1} and Q/B = 6.1 year^{-1} were obtained from L_{max} (see Table 14) and the empirical equations of Froese and Binohlan (2000) and Palomares and Pauly (1998) for Q/B.

Table 11. Values of L_{max}, P/B and Q/B ratios of large benthic fishes considered in the Kerguelen EEZ ecosystem model obtained mostly from the FishBase database (Froese and Pauly, 2000; see www.fishbase.org). Calculated values of P/B and Q/B were estimated from empirical equations (see text) and values of L_{max} (cm; TL) and the mean environmental temperature of 4°C.

Species	L_{max} (LT; cm)	Source	P/B (year^{-1})	Parameters used	Q/B (year^{-1})	Parameters used (W in g)
Bathyraja irrasa	120	McEachran and Dunn (1998)	0.14	L_∞=123	1.1	W_∞=18,654, A=0.5, carnivore
Bathyraja eatonii	100	McEachran and Dunn (1998)	0.16	L_∞=102	1.2	W_∞=10,864, A=0.5, carnivore
Macrourus carinatus	100	Cohen *et al.* (1990)	0.18	L_∞=103	1.2	W_∞=10,864, A=0.5, carnivore
Notothenia rossii	92	Tankevich (1990)	0.19	L_∞=89.2, K=0.152, θ′=3.08, a=0.213, b=2.88 (Tankevich, 1990)	1.5	W_∞=8819, A=1.32, carnivore
Antimora rostrata	75*	Chiu *et al.* (1990)	0.34	L_∞=66.0, K=0.3, θ′=3.12 (Fitch and Lavenberg, 1968), a=0.0005, b=3.73 (Vázquez, 1991)	1.9	W_∞=3061, A=1.32, carnivore
Notothenia coriiceps	62	Dewitt et al. (1990)	0.30	L_∞=48.0, K=0.22, θ′=2.70 (Hureau, 1970), a=0.0011, b=3.513 (Kock, 1981)	6.2	W_∞=3207, A=1.32, herbivore
Channichthys rhinoceratus	60	Hureau (1985a)	0.23	L_∞=62.2	2.0	W_∞=2,406, A=1.32, carnivore
Bathyraja murrayi	60	McEachran and Dunn (1998)	0.23	L_∞=62.2	4.1	W_∞=2,406, A=0.50, carnivore
Etmopterus cf. granulosus	60	Compagno *et al.* (1989)	–	–	–	–
Lamna nasus						
Coryphaenoides armatus	60	Iwamoto (1990)	–	–	–	–
Lepidonotothen squamifrons	55	Dewitt *et al.* (1990)	0.13	L_∞=67.0, K=0.078, θ′=2.54 (Duhamel and Ozouf-Costaz, 1985), a=1, b=3 (assumed values)	2.5	W_∞=795, A=1.32, carnivore
Champsocephalus gunnari	45	Iwami and Kock (1990)	0.25	L_∞=62.7, K=0.19, θ′=2.87 (Erzini, 1991), a=0.029, b=3.00 (Everson 1970)	2.0	W_∞=2,266, A=1.32, carnivore

* SL, cm

Large pelagic fishes

Fishes in this group are bigger than 50 cm and inhabit the mesopelagic part of the water column, and sometimes the slopes of the periinsular shelf, and may undertake diel vertical migrations (see Table 14). The diet of this group consists mainly of smaller fishes, notably lanternfishes, and cephalopods of all sizes. The average estimated values of P/B = 0.22 year^{-1} and Q/B = 2.56 year^{-1} were obtained using the methodology described for fish groups above.

Sharks and rays

Five species of sharks and 4 species of rays occur in the Kerguelen area and regularly appear in the catch. We assumed that the biomass of this group is low compared to other fish groups, and made a 'guesstimate' of 0.001 t·km^{-2} which is equivalent to 1 % of the total fish biomass. The average estimated values of P/B = 0.17 year^{-1} and Q/B = 1 year^{-1} were obtained using the methodology described for fish groups above and the data from Aasen (1963) for *Lamna nasus*.

Patagonian toothfish (*Dissostichus eleginoides*)

This neritic and oceanodromous nototheniid occurs in sub-Antarctic waters between 28-55°S at depths of 5-3,850 m, growing slowly, i.e., females may reach more than 2 m (Dewitt *et al.*, 1990). The largest reported size is 215 cm (TL; see Hureau, 1985b). Toothfish mature at 6-8 years, i.e., 60-90 cm, TL (Duhamel, 1988). Spawning occurs in May-June near the bottom of the ocean with a planktonic larval stage and a juvenile pelagic zooplanktivorous stage with individuals staying on the upper shelf close to the coast at depths of 100-200 m (Duhamel, 1988; Christiansen *et al.*, 1997). Adults inhabit depths of 200-3,500 m, hunting macrofauna mainly fishes, but also euphausids, cephalopods, amphipods, shrimps and prawns and other invertebrates (McKenna, 1991). They are the natural prey of sperm whales (Yukhov, 1971), and large sharks, e.g., *Somniosus* spp. (unpublished data, P. Cherel and G. Duhamel). Tagging-recapture studies in Heard Island by Williams *et al.* (2002) show that tagged Patagonian toothfish may reach as far as the Crozet archipelago, indicating oceanodromous behavior, e.g., moving across oceans up to depths of 5,000 m. However, the majority of the toothfish population stay more or less in the same area.

Table 12. Values of L_{max}, P/B and Q/B ratios of other benthic fishes considered in the Kerguelen EEZ ecosystem model obtained mostly from the FishBase database (see Froese and Pauly 2000). Calculated values of P/B and Q/B were estimated from empirical equations (see text) and values of L_{max} (in cm TL, unless otherwise stated) and the mean environmental temperature of 4°C.

Species	L_{max} (TL; cm)	Source	P/B (year^{-1})	Parameters used	Q/B (year^{-1})	Parameters used (W in g)
Echiodon cryomargarites	41.0	Markle and Olney (1990)	–	–	–	–
Zanclorhynchus spinifer	40.0	Heemstra and Duhamel (1990)	0.30	L_∞=41.7	2.5	W_∞=725, A=1.32, carnivore
Achiropsetta tricholepis	39.0	Heemstra (1990)	–	–	–	–
Mancopsetta maculata maculata	35.0	Heemstra (1990)	–	–	–	–
Gobionotothen acuta	35.0	SL from Dewitt *et al.* (1990)	0.32	Assumed SL:TL ratio=90 % from photo in FishBase, L_∞=39.0	6.0	W_∞=725, A=1.32, omnivore
Notothenia cyanobrancha	30.0	Hureau (1985b)	0.47	L_∞=31.5	6.6	W_∞=313, A=1.32, omnivore
Lycenchelys hureaui	26.0	Anderson (1994)	–	–	–	–
Bathydraco antarcticus	24.0	Gon (1990a)	–	–	–	–
Paraliparis spp.	13.0	Stein and Andriashev (1990)	–	–	–	–
Harpagifer kerguelensis	8.2	Miller (1993)	0.93	L_∞=8.8	14.3	W_∞=7, A=1.32, omnivore
Melanostigma gelatinosum	–	–	–	–	–	–
Lepidonotothen mizops	–	–	–	–	–	–

Duhamel's (1988) preliminary biomass evaluation of 0.129 $t \cdot km^{-2}$ is used here along with the estimated value of P/B=0.105 year^{-1} (value applying specifically for adults) obtained from the L_{max}=215 cm (L_∞=218.5 cm) and a temperature of 4°C computed from the empirical equation of Froese and Binohlan (2000), as explained above. The value of Q/B for this carnivore is estimated at 0.9 year^{-1} from the empirical equation of Palomares and Pauly (1998) and values of W_∞=104,317 g (with a=1 and b=3) and A=1.32.

We estimate the values of P/B and Q/B of 1.4 year^{-1} and 0.2 year^{-1} of the juvenile toothfish population from the length at first maturity and assuming that the juvenile stage L_{max} is equivalent to 1/3 of the adult population L_{max}.

Birds

Two groups of birds, surface seabirds and divers, were considered here. Surface seabirds stay mostly surface and stalk the first 3 m of the water column for prey both in inshore and offshore areas of the Kerguelen EEZ. Divers are seabirds which are able to dive deeper, e.g., penguins, diving petrels and the Kerguelen shag which are ichthyovores and able to dive to 50 m (Ridoux, 1994). Data from Cherel *et al.* (this volume), based on results of surveys conducted in 1962 and 1985 in the Crozet and Kerguelen Islands were used to estimate biomass and Q/B values for these two seabird groups. This study estimated annual consumption rates of seabirds with 1985 as the reference year, i.e., the period when an inventory of the seabird fauna was completed (see Jouventin and Stonehouse, 1985; Weimerskirch *et al.*, 1989).

Table 13. Values of L_{max}, P/B and Q/B ratios of small pelagic fishes considered in the Kerguelen EEZ ecosystem model obtained from the ICHTYOKER database (P. Pruvost, MNHN, pers. comm.) for the major myctophid species and the FishBase database (Froese and Pauly, 2000; see also www.fishbase.org). Calculated values of P/B and Q/B were estimated from empirical equations (see text) and values of L_{max} (here given in cm SL, unless otherwise stated) and the mean environmental temperature of 4°C.

Species	ICHTYOKER catch biomass (%)	L_{max} (TL; cm)	Source	P/B (year^{-1})	Parameters used	Q/B (year^{-1})	Parameters used (W in g)
Electrona antarctica	14.8	10.3	–	0.21	L_∞=16.5 (SL_∞=12.9 in Linkowski (1987); assumed SL:TL ration=78 % from photo), K=0.1	5.8	W_∞=22, A=1.90, carnivore
Electrona carlsbergi	8.9	9.6	Hulley (1990)	0.59	L_∞=12.1 (SL_∞=9.7 in Linkowski (1987); assumed SL:TL ration=80 % from photo), K=0.35	6.9	W_∞=9, A=1.90, carnivore
Gymnoscopelus braueri	6.6	13.2	Hulley (1990)	0.6	Assumed SL:TL ratio=82 % from photo in FishBase, L_∞=16.1	5.5	W_∞=27, A=1.90, carnivore
Gymnoscopelus bolini	5.9	28.0	Hulley (1990)	–	–	–	–
Krefftichthys anderssoni	5.9	7.1	Hulley (1990)	–	–	–	–
Paradiplospinus gracilis	5.7						
Gymnoscopelus fraseri	5.5	8.8	Hulley (1990)	–	–	–	–
Protomyctophum bolini	4.9	6.7	Hulley (1990)	–	–	–	–
Gymnoscopelus piabilis	4.8	14.6	Hulley (1990)	–	–	–	–
Protomyctophum tenisoni	4.6	5.4	Hulley (1990)	–	–	–	–
Gymnoscopelus nicholsi	3.7	16.1	Hulley (1990)	–	–	–	–
Bathylagus tenuis	2.0	16.0	Gon (1990b)	–	–	–	–
Electrona subaspera	2.0	–	–	–	–	–	–
Stomias boa boa	2.0	33.2	Gibbs (1990)	–	–	–	–
Protomyctophum andriashevi	1.3	6.0	Hulley (1990)	–	–	–	–
Arctozenus risso	–	30.0	Muus and Nielsen (1999)	–	–	–	–
Astronestes psychrolutes	–	–	–	–	–	–	–
Benthalbella elongate	–	35.0	Post (1990a)	–	–	–	–
Benthalbella macropinna	–	24.0					
Borostomias antarcticus	–	30.0	Gon (1990d)	–	–	–	–

Surface seabirds

Four surface seabird species appear to dominate the Kerguelen system representing almost 70 % of the biomass of the surface seabird population, i.e., *Pelecanoides georgicus*, *Pachyptila desolata*, *Pelecanoides urinatrix* and *Procellaria aequinoctialis*, covering 24 species (see Table 15). No direct estimates of turnover rates for seabirds are known. Okey (2002) used a P/B ratio of 0.2 year^{-1} for surface seabirds of the Prince William Sound model. Note that this P/B value does not take into account seabird mortality due to the increase of longline legal and illegal fishing efforts in the Kerguelen Islands since 1997 affecting the populations of white-chinned petrel, giant petrel and albatrosses. The total seabird biomass of 0.00285 $t \cdot km^{-2}$ based on the data presented in Table 15 adapted from Table 1 of Cherel *et al.* (this volume). An estimate of Q/B=236 $year^{-1}$ was obtained from the total prey biomass of 0.674 $t \cdot km^{-2}$ reported by Guinet *et al.* (1996). This value is however, too high for this group. Thus, we decided to use a P/B = 0,30 $year^{-1}$ and a Q/B = 36.5 $year^{-1}$ adapted from the Southern Plateau (New-Zealand) model of Bradford-Grieve *et al.* (2003).

Table 13. Continued.

Species	ICHTYOKER survey catch biomass (%)	L_{max} (TL; cm)	Source	P/B ($year^{-1}$)	Parameters used	Q/B ($year^{-1}$)	Parameters used
Chiasmodon niger	–						
Cyclothone microdon	–	7.6	TL from Clemens and Wilby (1961)	–	–	–	–
Diplophos rebainsi	–	25.0	TL from Schaefer *et al.* (1986)	–	–	–	–
Electrona paucirastra	–	7.0	Hulley (1990)	–	–	–	–
Electrona subaspera	–						
Gymnoscopelus hintonoides	–						
Gymnoscopelus microlampas	–	11.7	Hulley (1990)	–	–	–	–
Lampadena speculigera	–						
Lampichthys procerus	–						
Luciosudis normani	–	20.7	Krefft (1990)	–	–	–	–
Melanonus gracilis	–	18.7	Chiu and Markle (1990)	–	–	–	–
Melanostigma vitiazi	–	17.0	TL from Anderson (1990)	–	–	–	–
Metelectrona ventralis	–	10.7	Hulley (1990)	–	–	–	–
Nannobrachium achirus	–	16.2	Hulley (1990)	–	–	–	–
Nansenia antarctica	–	22.0	Gon (1990c)	–	–	–	–
Notolepis coatsi	–	38.0	Post (1990b)	–	–	–	–
Poromitra crassiceps	–						
Protomyctophum choriodon	–	9.5	Hulley (1990)	–	–	–	–
Protomyctophum gemmatum	–	8.6	Hulley (1990)	–	–	–	–
Protomyctophum luciferum	–	6.1	Hulley (1990)	–	–	–	–
Protomyctophum normani	–	5.6	Hulley (1990)	–	–	–	–
Protomyctophum parallelum	–	5.0	Hulley (1990)	–	–	–	–
Pseudoscopelus scriptus	–	13.4	Uyeno *et al.* (1983)	–	–	–	–
Sio nordenskjoldii	–						
Stomias gracilis	–	29.0	Gon (1990d)	–	–	–	–
Trigonolampa miriceps	–	32.0	Gibbs and Barnett (1990)	–	–	–	–

Diving seabirds

This group contains all seabirds which swim far from their colonies and which dive deeper than 3 m, e.g., King penguins travel for 4-5 days and can dive to 100-150 m after their prey (Bost *et al.*, 2002). Crustaceans and lanternfishes are their most important prey, making up almost 90 % of their diet (see

Table 15b). We considered that the Q/B estimate of 67.9 year^{-1} obtained from the total prey biomass of 1.99 t·km^{-2} was too high given that Q/B estimates for similar ecosystems range from 12 year^{-1} (Weddell Sea; Jarre-Teichmann et al., 1991) to 18 year^{-1} (Southern Plateau, New Zealand; Bradford-Grieve et al., 2003). We opted to use the value from the Weddell Sea model as it applies to the same region and diving seabirds from the Kerguelen Islands probably share the same diet composition and feeding behaviour as those of the Weddell Sea. The total diving seabird biomass of 0.0292 t·km^{-2} was estimated using data presented in Table 15a. The P/B value of 0.06 year^{-1} reported by Ostrand and Irons (1999) for the Prince William Sound model was used here.

Table 14. Values of L$_{max}$, P/B and Q/B ratios of large pelagic fishes considered in the Kerguelen EEZ ecosystem model obtained mostly from the FishBase database (Froese and Pauly, 2000; www.fishbase.org). Calculated values of P/B and Q/B were estimated from empirical equations (see text) and values of L$_{max}$ (in cm; TL unless otherwise stated) and the mean environmental temperature of 4°C.

Species	L$_{max}$ (TL; cm)	Source	P/B (year^{-1})	Parameters used (L in TL; cm)	Q/B (year^{-1})	Parameters used (W in g)
Lampris immaculatus	110	Heemstra (1986)	–	–	–	–
Alepisaurus brevirostris	96	Heemstra and Smith (1986)	–	L_∞=98.8	1.7	W_∞=9644, A=1.90, carnivore
Icichthys australis	81	Haedrich (1986)	0.18	L_∞=83.6	3.6	W_∞=5843, A=1.32, omnivore
Magnisudis prionosa	55	Post (1986)	0.24	L_∞=57.1	2.3	W_∞=1862, A=1.9, carnivore
Idiacanthus atlanticus	53	SL from Krueger (1990)	–	–	–	–
Paradiplospinus gracilis	52	SL from Bianchi *et al.* (1993)	0.25	L_∞=55.9 (assumed SL:TL ratio of 93 % from photo)	2.4	W_∞=1575, A=1.9, carnivore
Scopelosaurus hamiltoni	50	Krefft (1986)	0.26	L_∞=52.0	2.5	W_∞=1406, A=1.9, carnivore
Ceratias tentaculatus	–	–	–	–	–	–

Mammals

Three groups are identified here according to their diet and trophic level: 1) filtering marine mammals; 2) hunting marine mammals; and 3) top predators. The large number of cetaceans occurring around the Kerguelen Archipelago fueled the development of an important fishery targeting marine mammals in the early 20th century and the consequent building of a Norwegian processing factory in Morbihan Gulf. This fishery specifically targeted baleen and sperm whales, elephant and fur seals and was flourishing until the late 1960s, when hunting of the marine mammals, some nearly depleted, was banned (IWC, 1994). The fishery ban permitted the local sperm whale and seal populations to slowly recover. Thus, fur seal colonies have recently begun to reappear in the Courbet Peninsula, though still in very small numbers.

The biomass of marine mammals, were obtained from population estimates adapted from Table 1 of Cherel *et al.* (this volume), using the mean wet weight from Table 2 of Trites and Pauly (1998). Thus, we obtained 0.0151 t·km^{-2}, 0.0837 t·km^{-2} and 0.0363t·km^{-2} for hunting and filtering mammals and top predator, respectivey (see Table 16).

Table 17 lists the biomass of prey items of marine mammals consumed in the Antarctic sector of the Pacific Ocean adapted from Table 4 of Trites *et al.* (1997). This data provided the total biomass of prey consumed as 9,286,000 t (or 0.89 t·km^{-2}) in FAO Area 88. Thus, at 5.5 %, the prey consumed by marine mammals in the Kerguelen Islands' EEZ is calculated at 510,730 t or 0.049 t·km^{-2}. Using this and the distribution of top predator and filtering mammals from Table 16, we obtained a Q/B value which seemed too low to be used in this model. We thus opted to use the Q/B of 10.9 year^{-1} for filtering mammals adapted from the Prince William Sound model (see Matkin and Hobbs, 1999). Hunting marine mammals' consumption was estimated at 188,240 t (adapted from Table 1 of Guinet *et al.*, 1996) or 0.33 t·km^{-2} resulting in Q/B estimate of 8.3 year^{-1}. We did not find Q/B values for the top predator group. Using the mass-balance theory of *Ecopath*, we modified Q/B until our ecotrophic efficiency values were not higher than 1 and came up with a Q/B of 2 year^{-1}.

Table 15a. Seabirds occurring in the Kerguelen EEZ. Population size, biomass and percentage prey consumption estimates were adapted from Table 1 of Cherel *et al.* (this volume; see also Cherel *et al.*, 2000, 2002a, b).

Scientific name	Common name	Population size (1000 pairs)	Body weight (kg)	Forage time in area	Biomass (t)	Biomass (t·km^{-2})	Prey biomass (t)	Prey biomass (t·km^{-2})
	Surface seabirds							
Pachyptila desolata	Antarctic prion	2500	0.14	35	245	0.0004	294960	0.5130
Pelecanoides georgicus	South Georgian diving petrel	1500	0.141	100	423	0.0007	125970	0.2191
Procellaria aequinoctialis	White-chinned petrel	200	0.154	35	169	0.0003	50983	0.0887
Pelecanoides urinatrix	Kerguelen diving petrel	750	0.154	100	231	0.0004	66360	0.1154
Pachyptila belcheri	Thin-billed prion	850	0.145	35	86	0.0001	79900	0.1390
Halobaena caerulea	Blue petrel	150	0.21	35	84	0.00004	18680	0.0325
Diomedea chrysostoma	Grey-headed albatross	15.8	3.8		55	0.0001	3425	0.0060
Pterodroma macroptera	Kerguelen petrel	150	0.587	35	62	0.0001	3860	0.0067
Phoebetria palpebrata	Light-mantled sooty albatross	4	3.15	35	25	0.00002	2021	0.0035
Pterodroma lessoni	White-headed petrel	35	0.708	35	25	0.00003	6230	0.0108
Diomedea melanophris	Black-browed albatross	3.165	3.66	100	23	0.00004	1388	0.0024
Diomedea exulans	Wandering albatross	1.095	9.15	35	21	0.00001	426	0.0007
Pterodroma cinerea	Grey petrel	7.5	1.131	90	15	0.00003	2543	0.0044
Macronectes halli	Northern giant petrel	3200	4.9		14	0.00002	320	0.0006
Oceanites oceanicus	Wilson's Storm Petrel	350	0.03	100	11	0.00004	4921	0.0086
Daption capense	Cape pigeon	4	0.45	100	4	0.00001	720	0.0013
Pterodroma mollis	Soft-plumaged Petrel	5.5	0.3	35	1	0.0000	547	0.0010
Fregatta tropica	Black-bellied storm petrel	7.5	0.05	35	1	0.0000	214	0.0004
Pterodroma turtur	Fairy prion	5.5	0.14	100	2	0.00002	436	0.0008
Diomedea chlororhynchos	Yellow-nosed albatross	0.05	2.06	35	0	0.0000	16	0.0000
Garodia nereis	Gray-backed storm petrel	4	0.04	100	0	0.0000	128	0.0002
Macronectes giganteus	Southern giant petrel	0.01	5.035		0	0.0000	1	0.0000
Phoebetria fusca	Sooty albatross	0.004	2.6	35	0	0.0000	2	0.0000
	Diving seabirds							
Phalacrocorax verrucosus	Kerguelen cormorant	6.5	2.63	100	29	0.00006	3330	0.0058
Eudyptes chrysolophus	Macaroni penguin	1800	4.3	82	15583	0.0271	712728	1.2395
Pygoscelis papua	Gentoo penguin	35	7.2	100	504	0.0009	26236	0.0456
Aptenodytes patagonicus	King penguin	173	12.1	75	4187	0.0073	158264	0.2752
Eudyptes chrysocome	Rockhopper penguin	85.5	2.9	100	496	0.0008	29756	0.0517

Table 15b. Seabirds occurring in the Kerguelen EEZ, their food consumption and diet composition.

Scientific name	Common name	Q/B (year^{-1})	Crustaceans	Myctophids	Other fishes	Cephalopods	Other prey items
	Surface seabirds						
Pachyptila desolata	Antarctic prion	351	79.10	20.90	0.00	0.00	0.00
Pelecanoides georgicus	South Georgian diving petrel	350	100.00	0.00	0.00	0.00	0.00
Procellaria aequinoctialis	White-chinned petrel	211	16.30	35.40	19.20	24.70	4.40
Pelecanoides urinatrix	Kerguelen diving petrel	316	100.00	0.00	0.00	0.00	0.00
Pachyptila belcheri	Thin-billed prion	650	65.10	25.60	0.00	9.30	0.00
Halobaena caerulea	Blue petrel	222	60.70	10.40	0.00	27.40	1.50
Diomedea chrysostoma	Grey-headed albatross	62	10.31	0.00	0.00	89.69	0.00
Pterodroma macroptera	Kerguelen petrel	148	72.28	0.00	0.31	5.91	21.50
Phoebetria palpebrata	Light-mantled sooty albatross	81	17.02	0.00	10.79	55.71	16.48
Pterodroma lessoni	White-headed petrel	249	50.00	0.00	0.00	50.00	0.00
Diomedea melanophris	Black-browed albatross	60	0.00	0.00	33.21	66.79	0.00
Diomedea exulans	Wandering albatross	20	0.00	0.00	15.26	76.06	8.69
Pterodroma cinerea	Grey petrel	159	0.39	0.00	27.80	70.39	1.42
Macronectes halli	Northern giant petrel	23	0.00	0.00	0.00	1.25	98.75
Oceanites oceanicus	Wilson's Storm Petrel	447	88.19	0.00	11.81	0.00	0.00
Daption capense	Cape pigeon	180	51.81	0.00	1.94	1.94	44.31
Pterodroma mollis	Soft-plumaged Petrel	182	77.88	0.00	0.00	15.72	6.40
Fregatta tropica	Black-bellied storm petrel	214	36.92	0.00	20.09	5.61	37.38
Pterodroma turtur	Fairy prion	436	95.41	0.00	0.00	4.59	0.00
Diomedea chlororhynchos	Yellow-nosed albatross	0	6.25	0.00	56.25	37.50	0.00
Garodia nereis	Gray-backed storm petrel	0	100.00	0.00	0.00	0.00	0.00
Macronectes giganteus	Southern giant petrel	0	0.00	0.00	0.00	0.00	100.00
Phoebetria fusca	Sooty albatross	0	0.00	0.00	0.00	50.00	50.00
	Diving seabirds						
Phalacrocorax verrucosus	Kerguelen cormorant	115	0.00	0.00	100.00	0.00	0.00
Eudyptes chrysolophus	Macaroni penguin	46	62.00	28.00	0.00	10.00	0.00
Pygoscelis papua	Gentoo penguin	5	49.30	26.40	22.50	1.70	0.10
Aptenodytes patagonicus	King penguin	38	0.00	92.40	0.00	7.60	0.00
Eudyptes chrysocome	Rockhopper penguin	60	73.00	10.90	0.00	16.10	0.00

Table 16a. Key statistics of marine mammals occurring in the Kerguelen EEZ: wet body weight data adapted from Table 2 of Trites and Pauly (1998); population data observed in Kerguelen Cherel *et al.* (this volume) and biomass (t·km^2) calculated from the wet body weight; population size of female *Physeter macrocephalus* was estimated from the male population size.

Functional group	Scientific name	Common name	Mean female wet weight (kg)	Mean male wet weight (kg)	Mean wet weight (kg)	Population size (numbers)	Biomass (t)
Top predators	*Orcinus orca*	Killer whale	1,974	2,587	2281	50	114
	Physeter macrocephalus (male)	Sperm whale		26,939		800	21,551
	Physeter macrocephalus (female)		10,098			800	8,078
Hunting mammals	*Mirounga leonina* (cows)	Southern elephant seal	327			41,000	13,407
	Mirounga leonina (bulls)			543		2,660	1,444
	Arctocephalus gazella (cows)	Antarctic fur seal	23			10,000	230
	Arctocephalus gazella (bulls)			31		1,000	31
	Cephalorhynchus commersonii	Commerson's dolphin	30	27	28	600	17
Filtering mammals	*Balaenoptera physalus*	Fin whale	59,819	51,361	55,590	700	38,913
	Eubalaena australis				19,576	30	587
	Balaenoptera acutorostrata				7,011	2,500	17,528
	Balaenoptera musculus brevicauda				95,347	50	4,767
	Megaptera novaeangliae				32,493	100	3,249

Table 16b. Key statistics of marine mammals occurring in the Kerguelen Island: computation of effective and group biomasses.

Functional group	Scientific name	Presence in the area (%)	Annual biomass (t)	Annual biomass (t·km^{-2})	Group biomass (t·km^{-2})
Top predators	*Orcinus orca*	100	114,05	0,0002	
	Physeter macrocephalus (male)	70	15,085,84	0,0262	
	Physeter macrocephalus (female)	70	5,654,88	0,0098	0.0363
Hunting mammals	*Mirounga leonina* (cows)	20	2,681,4	0,0047	
	Mirounga leonina (bulls)	20	288,876	0,0005	
	Arctocephalus gazella (cows)	25	57,5	0,0001	
	Arctocephalus gazella (bulls)	25	7,75	0,0000	
	Cephalorhynchus commersonii	100	16,8	0,0000	0.0151
Filtering mammals	*Balaenoptera physalus*	70	27,239,1	0,0474	
	Eubalaena australis	25	146,82	0,0003	
	Balaenoptera acutorostrata	100	1,7527,5	0,0305	
	Balaenoptera musculus brevicauda	50	2,383,675	0,0041	
	Megaptera novaeangliae	25	812,325	0,0014	0.0837

Filter feeding marine mammals consume a large proportion of zooplanktonic prey in the waters of the Kerguelen Islands. Based on the general diet composition of marine mammals presented in Table 17, we assumed the prey composition of filter feeding marine mammals to consist of 40 % euphausiids, 40 % omnivorous zooplankton; and 20 % herbivorous zooplankton. Feeding behavior of hunting mammals was based on a study on Kerguelen's fur seals conducted during 3 consecutive summers, i.e., 1998, 1999 and 2000 (Lea, 2002). The prey composition obtained during the summer of 1998 for Antarctic fur seals was used as a basis for the diet composition of hunting mammals (see Table 4.4 of Lea, 2002).

Table 17. Prey consumption of marine mammals occurring in the Kerguelen EEZ adapted from Table 4 of Trites *et al.* (1997) used in the calculation of Q/B given that the biomasses of marine mammals in the Kerguelen EEZ represent 5.5 % of the consumption in FAO Area 88 (Antarctic section of the Pacific Ocean).

Prey items	FAO Area 88 (10^3 t)	Kerguelen EEZ (10^3 t)	Diet composition (%)
Large zooplankton	2,548	140.14	27.4
Large squids	2,219	122.04	23.9
Small squids	1,332	73.26	14.3
Mesopelagic fishes	1,161	63.86	12.5
Small pelagic fishes	980	53.90	10.6
Misc. fishes	883	48.56	9.5
Higher vertebrates	108	5.94	1.2
Benthic invertebrates	55	3.02	0.6
Total	9,286	510.73	100.0

HUMAN IMPACTS ON THE ECOSYSTEM: THE FISHERY

After the development of the cetacean fishery in the beginning of the 20th century, no other 'new' fishery was developed until 1970. Modern exploitation started with bottom trawls targeting marbled rockcod, mackerel icefish and grey rockcod, from the top of the shelf to depths of 200-500 m, as a result of several fishery prospecting cruises in the 1960s, e.g., by the Soviet Union. More than 10 USSR trawlers circled around the islands 6 months per year without any management or control (G. Duhamel, pers. obs.). In 1978, the French EEZ was established and led to the creation and implementation of a fishery management scheme in 1980 (Duhamel, 1995). This management scheme strictly enforced the limit of 7 trawlers operating at the same time, the regular reporting of onboard fishing observers who go out with each fishing vessel and the encoding of all these observations to an electronic database, i.e., KERPECHE, hosted at the *Muséum national d'histoire naturelle* in Paris. In 1996, the USSR stopped trawling in Kerguelen waters, but 2 Ukrainian longliners and 2 French trawlers continued their Patagonian toothfish fishery in the area. The last ones stopped in 2001 and only French longliners continue to operate at the present time (unpublished data, G. Duhamel).

In 1996, a Franco-Japanese fish prospecting cruise aboard the M/V *Anyo-Maru* was conducted to estimate the deepwater populations of Patagonian toothfish (*D. eleginoides*) in Kerguelen waters. The stock was discovered during 1984-1985 on the slopes of the Kerguelen shelf (see Table 18). The Japanese took a liking to the white flaky flesh of this toothfish and this started the switch from bottom trawling for marbled rockcod and mackerel icefish to longlining for Patagonian toothfish. The highly profitable fishery of Patagonian toothfish led to the emergence of an illegal, unreported and unrecorded longline fishery in 1996-1997 was reduced after the 2003-2004 fishing season. The legal fishing effort in 2005 is limited to 7 licensed longliners. Catch statistics (see Table 18) from surrounding fish landing ports known as disembarking destinations of these illegal vessels coupled with local observations show disturbing signs of overexploitation of this deep-sea resource around the archipelago. Longlining also produces bycatch of other fish species, the most important of which are macrourid and skate bycatch (observed during the M/V *Anyo-Maru* cruise in 1997). This represents less than 10 % of the total weight of the catch (Duhamel *et al.*, 1997) but the total effect of this on these populations is still unknown. Moreover, another concern is the detrimental effect of this incidental fishery on seabird populations.

Table 18. Catch statistics (in tonnes) by major target species in the Kerguelen EEZ from 1979 to 2000 adapted from the KERPECHE database (unpublished data, P. Pruvost and G. Duhamel).

	Shelf and slope trawl fishery				Slope and deep-sea longline fishery		
Season	Mackerel icefish	Gray rockcod	Marbled rockcod	Sum	Demersal catch/effort	Toothfish catch	Toothfish catch/effort
1979-1980	1,347	4,451	1,175	6,974	2.86	159	0.07
1980-1981	1,095	6,287	7,927	15,309	2.69	43	0.01
1981-1982	16,048	4,051	9,792	29,890	3.44	124	0.01
1982-1983	25,852	1,815	1,823	29,489	4.54	144	0.02
1983-1984	7,127	3,794	744	11,664	1.42	147	0.02
1984-1985	8,265	7,408	1,704	17,377	2.43	6,673	0.93
1985-1986	17,055	2,464	801	20,319	4.58	459	0.10
1986-1987	2,625	1,641	483	4,748	1.15	3,161	0.77
1987-1988	213	41	23	277	0.18	1,053	0.69
1988-1989	23,047	1,825	260	25,132	3.43	1,581	0.22
1989-1990	259	1,112	164	1,535	0.86	1,161	0.65
1990-1991	12,692	89	296	13,077	3.07	1,854	0.44
1991-1992	45	0	0	45	0.01	6,712	1.77
1992-1993	0	0	0	0	0.00	2,630	3.63
1993-1994	12	0	0	12	0.00	4,195	1.46
1994-1995	3,882	0	1	3,883	0.61	4,198	0.65
1995-1996	12	19	0	31	0.01	3,648	1.38
1996-1997	0	0	0	0	0.00	3,676	1.41
1997-1998	0	0	0	0	0.00	3,610	1.72
1998-1999	0	0	1	1	0.00	3,507	1.16
1999-2000	0	0	0	0	0.00	2,394	0.67

CONSTRUCTING AND BALANCING THE KERGUELEN EEZ MODEL

This preliminary model of the Kerguelen EEZ resulted in a balanced model (see Tables 19 and 20) likely because the biomass estimations we used for the dominant components, e.g., omnivorous zooplankton, large benthic fishes, adult Patagonian toothfish, seabirds and hunting marine mammals, mostly came from reliable sources, based on studies conducted in the area. General studies on sub-Antarctic populations, most often including those in the Kerguelen area, e.g., small pelagic fishes and sea mammals, provided good base estimates. Studies on similar ecosystem, e.g., Prince Williams Sound and the Weddell Sea, permitted the estimation of diet compositions for low trophic level groups as well as P/B and Q/B estimates.

General knowledge of ecological and biological parameters helped us to make informed guesses and change some of the input data, when necessary, to obtain a balanced model. Because of some concerns about the bias induced by the sampling procedures employed during the SKALP survey (Ivanchenko, 1993), we used instead the primary production biomass estimate from data obtained through the satellite observation database hosted at the European Union Joint Research Center (Ispra, Italy).

Similarly, data from Semelkina (1993) and Pakhomov (1993a) gave zooplankton biomass estimates that seem to be rather low for this ecosystem, notably those for Euphausiacea. This might be due to the fact that sampling was mostly performed during daytime (undoubtedly for practical reasons), which would have introduced a bias in the estimation of biomasses especially if we take into account the diurnal vertical migration of zooplankton. Thus, we used values suggested by Labat and Mayzaud (this volume), which, seem more appropriate for the region and the time period being considered. We obtained a rather low ecotrophic efficiency value for this group given it is a primary food source for most of the higher trophic level groups, e.g., filtering mammals. However, this low value might justified by the overall low biomass estimates for marine mammals. Another source of bias might have been introduce in the use of the particulate size segregation to distribute zooplankton biomass to the 3 diet groups, i.e., herbivorous, omnivorous and carnivorous. The data obtained from particulate size distribution may not necessarily be representative of these feeding groups.

Table 19. Basic *Ecopath* estimates for the Kerguelen EEZ ecosystem for the period 1987-1988: unless otherwise marked, input data were adapted from other models (mostly from the Prince William Sound model; see Okey and Pauly, 1998). Those specific for Kerguelen area are in square brackets while those in italics and round brackets were calculated by *Ecopath* with *Ecosim*.

Group name	Trophic level	Biomass (t·km^{-2})	Prod./Biom. (year^{-1})	Cons/Biom. (year^{-1})	Ecotrophic efficiency	Prod./Cons.
Top predators	4.72	[0.0362]	0.050	(*2.000*)	(*0.000*)	(*0.025*)
Filtering marine mammals	3.36	[0.840]	0.060	10.900	(*0.000*)	(*0.006*)
Hunting marine mammals	4.52	[0.0151]	0.100	[8.460]	(*0.479*)	(*0.012*)
Surface seabirds	3.59	[0.0285]	0.300	36.500	(*0.009*)	(*0.008*)
Diving seabirds	4.05	[0.0292]	0.060	12.000	(*0.415*)	(*0.005*)
Sharks	4.63	0.0010	[0.170]	[1.000]	(*0.426*)	(*0.170*)
Patagonian toothfish, juvenils	4.29	(*0.0377*)	[0.200]	[1.400]	0.950	(*0.143*)
Patagonian toothfish, adults	4.39	[0.129]	[0.105]	[0.900]	(*0.751*)	(*0.117*)
Large pelagic fishes	4.23	(*0.0940*)	[0.220]	[2.560]	0.950	(*0.086*)
Small pelagic fishes	3.22	4.500	[0.500]	[6.100]	(*0.718*)	(*0.082*)
Large benthic fishes	3.76	[0.490]	[0.190]	[1.980]	(*0.775*)	(*0.096*)
Other benthic fishes	3.39	(*0.286*)	0.502	7.330	0.950	(*0.068*)
Cephalopods, large	3.64	(*0.355*)	0.600	(*2.000*)	0.950	0.300
Cephalopods, small	3.52	(*1.294*)	1.000	(*3.333*)	0.950	0.300
Deep benthic omnivores	2.11	30.000	3.000	10.000	(*0.344*)	0.300
Shallow benthic omnivores	2.33	3.100	2.100	10.000	(*0.241*)	(*0.210*)
Shallow benthic herbivores	2.02	8.700	2.000	10.000	(*0.687*)	(*0.200*)
Euphausiacea	2.86	[5.828]	0.950	(*3.800*)	(*0.805*)	0.250
Zooplankton, omnivores	2.70	[2.726]	10.795	(*43.180*)	(*0.571*)	0.250
Zooplankton, herbivores	2.00	[11.298]	24.000	(*96.000*)	(*0.386*)	0.250
Benthic algae	1.00	(*5.900*)	4.000	-	0.100	-
Phytoplankton	1.00	7.000	150.000	-	(*0.971*)	-
Detritus	1.00	100.000	-	-	(*0.660*)	-

The low EE values for deep epifauna, cephalopods, benthic algae and small benthic fish may be due to the fact that this is a model representing a pelagic ecosystem (given the breadth of area covered by deep waters around the archipelago). Though we considered the effect of demersal fish populations, their biomasses remain low and might have been misrepresented, e.g., by the lack of on-site specific biomass estimates. Although we obtained a balanced model by modifying the diet compositions (which were mostly based on informed guesses and through the automatic mass balancing of *Ecopath* and *Ecosim*), the mass balancing routine forced EE=0.95 for component groups for which we obtained EE values of more than 1.0 during the first run, *viz.*: diving seabirds, adult Patagonian toothfish, large benthic fishes, and deep benthic omnivores. It is best that future refinements of the model focus on correcting the biomass estimations of these groups rather than accepting EE values estimated by this routine. However, the low EE value for seabirds is probably a reasonable estimate for this model since there was little evidence of seabirds being impacted by the fisheries. This might, however, be different for another model, i.e., the last half of the 1990s, the period marking the begining of a new long line fishery known to have a great impact on seabird bycatch.

The categorization by habitats based on bathymetry as used in this model gave a good representation of this ecosystem. However, the area includes some 'special' habitats , e.g., the kelp beds of Morbihan Gulf, Baleiniers Gulf and the various coastal fjords, not considered in this model, but which merit further analyses as they no doubt contribute to the overall energy flow in this ecosystem. A necessary refinement of this model would include, compare and analyze the impact linked to their particular characteristics on the entire Kerguelen ecosystem.

Table 20. *Ecopath/Ecosim* estimated diet composition for each component group in the Kerguelen EEZ ecosystem for the period 1988-1987.

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10
1	Top predators										
2	Filtering marine mammals										
3	Hunting marine mammals	0.010									
4	Surface seabirds	0.001					0.005				
5	Diving seabirds	0.010					0.004				
6	Sharks	0.001									
7	Patagonian toothfish, juvenils	0.050		0.025			0.047				
8	Patagonian toothfish, adults	0.050		0.013			0.158				
9	Large pelagic fishes	0.050		0.044	0.010						
10	Small pelagic fishes	0.025		0.341	0.110	0.740	0.263	0.171	0.171	0.330	
11	Large benthic fishes	0.010		0.088			0.158		0.124		
12	Other benthic fishes	0.010		0.090	0.030		0.039	0.411	0.287		
13	Cephalopods, large	0.600		0.235	0.050	0.040	0.167		0.216	0.200	
14	Cephalopods, small	0.183		0.164	0.020	0.010	0.132	0.316	0.100	0.200	0.040
15	Deep benthic omnivores						0.017		0.102		
16	Shallow benthic omnivores						0.009	0.082			
17	Shallow benthic herbivores							0.020			
18	Euphausiacea		0.300		0.230	0.060				0.150	0.040
19	Zooplankton, omnivores		0.140		0.110	0.030				0.080	0.470
20	Zooplankton, herbivores		0.560		0.440	0.120				0.030	0.250
21	Benthic algae										
22	Phytoplankton										0.200
23	Detritus										
24	Import									0.010	

Table 20. Continued.

	Prey \ Predator	11	12	13	14	15	16	17	18	19	20
1	Top predators										
2	Filtering marine mammals										
3	Hunting marine mammals										
4	Surface seabirds										
5	Diving seabirds										
6	Sharks										
7	Patagonian toothfish, juvenils										
8	Patagonian toothfish, adults										
9	Large pelagic fishes										
10	Small pelagic fishes	0.012		0.300	0.200						
11	Large benthic fishes										
12	Other benthic fishes	0.024									
13	Cephalopods, large										
14	Cephalopods, small										
15	Deep benthic omnivores	0.119	0.155	0.100	0.100	0.100					
16	Shallow benthic omnivores		0.210	0.100	0.100		0.020				
17	Shallow benthic herbivores		0.200	0.100	0.100		0.300	0.020			
18	Euphausiacea	0.647	0.264	0.100	0.100				0.050		
19	Zooplankton, omnivores	0.195	0.100	0.200	0.200				0.100		
20	Zooplankton, herbivores		0.070	0.100	0.200				0.600	0.700	
21	Benthic algae						0.020	0.020			
22	Phytoplankton								0.100	0.300	0.900
23	Detritus					0.90	0.660	0.960	0.150		0.100
24	Import	0.004	0.001								

Another interesting characteristic of this ecosystem is the change from the bottom trawling for mackerel icefish and marbled rockcod to the longlining for Patagonian toothfish over a 20-year history of resource exploitation. Integration of a time series of fishing fleet data may help give indications of the impact of this change in target species on the different components of the ecosystem. Since we only considered 23 groups in this preliminary model, new groups of key species or additional and more precise biomass estimates are needed. For example, it would be useful to separate mackerel icefish into two groups of adults and juveniles as there is particular interest in its fishery, biology and diet behaviour. It might also be useful to separate copepods and euphausiids. In addition, new data on fur seals might be useful to isolate this species from the other 'hunter' mammals.

In the final mass balancing process, our model would not balance unless we increased the estimate of Q/B (0.5 year^{-1}) for top predators. We modified this parameter until we obtained a balanced model, but found that our model could not handle top predator Q/B values greater than 2 year^{-1}, a rather low value considering that models for similar ecosystems, e.g. Southern Plateau (New Zealand) used a Q/B range of 11.0-14.6 year^{-1} (Bradford-Grieve *et al.*, 2003). Note also that we did not introduce temporal data in this model. Though good fisheries statistics are available for the 1980s, there is a general lack of information on the population size and dynamics of these exploited species.

Overall, the Kerguelen ecosystem can be considered as 'poor' as the total biomass level is low compared to other sub-Antarctic ecosystems, e.g., the Southern Plateau in New Zealand (Bradford-Grieve *et al.*, 2003). However, the particular hydrography and topology of these islands provide a haven for isolated, slow-growing deepwater species which have high commercial values and which have become the target of new fisheries in recent years. The low biomasses indicated in this model may however indicate the inability of these populations to sustain high amounts of fishing effort, a concern that will soon need immediate attention given the growing number of illegal fishing fleets in the area.

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FALKLAND ISLANDS

A MASS-BALANCE MODEL OF THE FALKLAND ISLANDS FISHERIES AND ECOSYSTEMS[1]

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ABSTRACT

We present a preliminary mass-balance model of the Falkland Islands marine ecosystem, representing its state in the 1990s. The model consists of 44 functional groups, including phytoplankton, zooplankton, benthic invertebrates, fish and other vertebrate groups such as penguins and sea lions. Input parameters are based on local and regional data, global databases and meta-analyses. The relative quality of these data is compiled in a pedigree table. This *Ecosim* model is intended to initialize dynamic simulations of alternative policy scenarios using *Ecosim*. Using *Ecosim* itself, we find that an alternative model, with penguin abundance and diet composition of the 1980s, requires a higher biomass for most of the groups in the ecosystem, particularly commercially-targeted *Illex* squid. This may provide insight into the relationship between fishing, ecosystem dynamics and the abundance of charismatic top predators.

INTRODUCTION

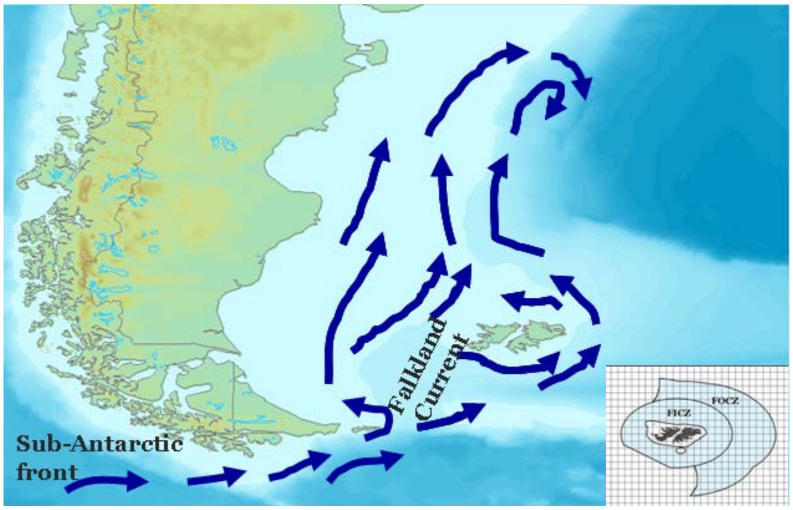

Figure 1. Map of the Falkland Islands showing approximate oceanography of the surrounding waters and the present jurisdictional boundaries. FOCZ = Falkland Islands Outer Conservation Zone; FICZ = Falkland Islands Interim Conservation and Management Zone.

The Falkland Islands are situated in the southwest Atlantic between 51 and 53°S 47-62°W (Figure 1). They are composed of two main islands, East and West Falklands, and hundreds of smaller islands, which lie on the edge of the Patagonian shelf. The Falkland Islands have a temperate oceanic climate, with air temperature ranging from around 9°C during the austral summer (January to June) to around 2°C during the austral winter (June to December; see Bingham, 2002a). The marine ecosystem around the Falkland Islands is heavily influenced by oceanographic features such as the Falkland Current (Figure 1), an extension of the Subantarctic Front of the southeast Pacific Ocean which is part of the flow of the Antarctic Circumpolar Current. The Subantarctic Front forms the Falkland Current as it is entrained into the lower latitudes on rounding Cape Horn (Longhurst, 1998); it splits around the Falkland Islands, and then rejoins to meet the warm southward Brazil Current at about 36°S. Thus the meeting of the Brazil and Falkland currents generates a strong upwelling of Antarctic waters along the Falkland Islands shelf. This results in areas of high productivity (e.g., of macrozooplankton, an important food source for larvae

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and adults), making the region an important feeding ground for many commercially important fish (e.g., the Argentine hake, *Merluccius hubbsi*), and squid species (e.g., *Illex argentinus;* see Longhurst, 1998). In addition, cold-water species, such as the southern blue whiting (*Micromesistius australis*), southern hake (*Merluccius australis*), tadpole codling (*Salilota australis*) and Patagonian toothfish (*Dissostichus eleginoides*) migrate to the Falkland Islands for feeding and eventual spawning (Agnew *et al.*, 2000).

The rich marine resources support large assemblages of marine mammals, penguins and seabirds. Elephant seal, sea lion and fur seal breed on the islands, while leopard seal is an occasional visitor (Bingham, 2002a). Five species of penguins breed here: King penguin (*Aptenodytes patagonicus*), Gentoo penguin (*Pygoscelis papua*), Rockhopper penguin (*Eudyptes chrysocome*), Macaroni penguin (*Eudyptes chrysolophus*) and Magellanic penguin (*Spheniscus magellanicus*; see Bingham, 2002b). Breeding populations of other seabirds and shorebirds such as the black-browed albatross (*Thalassarche melanophris*), southern giant petrel (*Macronectes giganteus*) and imperial shag (*Phalacrocorax atriceps*) can also be found (Bingham, 2002a).

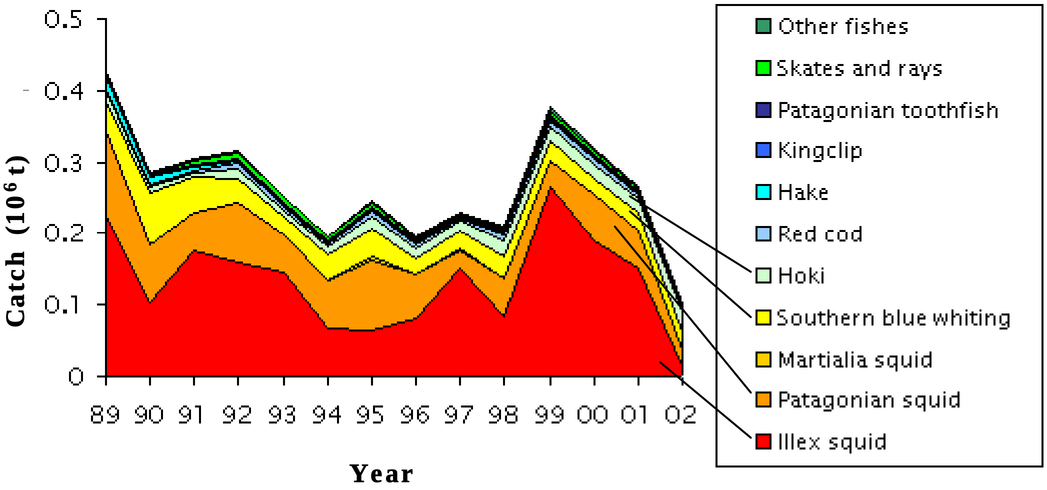

Figure 2. Total reported annual fishery catches from the Falkland Islands Interim Conservation and Management Zone (FICZ) and Falkland Islands Outer Conservation Zone (FOCZ), 1989-2002 (Falkland Islands Government, 1999).

This ecosystem is exploited commercially with an average annual catch of about 280,000 t in 1989-2002. The majority of the fishing fleets are either foreign-flagged or in joint ventures with Falkland companies (Falkland Islands Government, 2002a). *Illex* squid jigging and Patagonian squid (*Loligo gahi*) trawl fisheries are among the biggest in terms of both volume and value (Figure 2). Southern blue whiting and Patagonian grenadier (*Macruronus magellanicus),* exploited mainly by the surimi vessels and bottom trawlers, have taken the biggest finfish catches in recent years. Other finfish catches include pink cusk-eel (*Genypterus blacodes,* = kingclip, pink ling), tadpole codling, skate (Rajidae) and Patagonian toothfish taken by mixed trawlers and longliners (Barton, 2002).

With the introduction of the Falkland Conservation Zone, the fisheries within this area started to be managed by the Falkland Island Government (FIG). The conservation zone is composed of the Falkland Island Interim Conservation and Management Zone (FICZ) and the Falkland Islands Outer Conservation Zone (FOCZ), which were designated in 1986 and 1987, respectively. The FICZ and FOCZ extend to 200 miles from the coastline and consist of a total sea area of about 527,000 km^2 (Figure 1). Fishing is managed by a licensing scheme. *Illex* squid fishing is only allowed in one season (February to June), while Patagonian squid fishing is allowed in two seasons. Finfish fisheries are allowed throughout the year. The issuing of licenses is reviewed annually based on the status of the resources (Barton, 2002). At the same time, there is rigorous in-season effort management of these two squid fisheries based on real-time estimates of changes of the species' local population densities (Basson *et al.*, 1996; Agnew *et al.*, 1998).

Strong linkages exist between different groups of organisms in the Falklands marine ecosystem and the fisheries. It has been proposed that the high volatility in annual catches of some major commercial species results from fluctuations in oceanographic conditions which change the patterns of primary production and thus affect the spatial distribution, recruitment and productivity of the species directly or indirectly through the food chain (Agnew *et al.*, 2000, 2002; Agnew, 2002; Falkland Islands Government, 2003). Competition between species such as the *Illex* and Patagonian squid has been suggested (Arkhipkin and Middleton, 2002). There are also concerns about possible trophic competition between fisheries and resident charismatic species such as penguins and pinnipeds (Pütz *et al.*, 2001; Bingham, 2002a, 2002b). Developing an understanding of the tropho-dynamics of the Falklands marine ecosystem is an important step to investigate these issues.

General aspects of the Falkland Islands marine ecosystem have been described (e.g., Agnew, 2002), but a comprehensive, quantitative description of the ecosystem is lacking. Quantitative modeling is useful to understand the dynamics of the ecosystem. Therefore, the objective of this study is to describe and investigate the Falklands ecosystem quantitatively using a mass-balance model – *Ecosim* (Christensen *et al.*, 2000).

Ecosim is a steady-state, mass-balance model which can be used to describe a snap-shot of the ecosystem at a particular time period. The basic equation for each component (functional group) in the model is:

$$(P/B)_i \cdot B_i \cdot (1\text{-}EE_i) - B_j \cdot (Q/B)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0 \qquad \ldots 1)$$

where $(P/B)_i$ is the production to biomass ratio; B_i the total biomass; EE_i the ecotrophic efficiency (mortality other than predation and fishing); Y_i the total catch; E_i the net migration; BA_i the biomass accumulation of functional group i; B_j and $(Q/B)_j$ are the biomass and consumption to biomass ratio for predator groups j; and DC_{ji} is the proportion of group i in the diet of predator groups j. Three of the 4 input parameters – B, P/B, Q/B, EE - together with the diet composition matrix, total catch, net migration, biomass accumulation of each living functional groups are required in this modeling approach (see detailed descriptions of the *Ecopath* with *Ecosim* concept in Christensen *et al.*, 2000).

Here, the Falkland Islands marine ecosystem (FIME) is defined as the area within the FICZ and FOCZ. We develop a model of the ecosystem in the late 1990s because our parameters were estimated using data sources from this period. The abundance and occurrence of species in FIME fluctuate dramatically within a year. However, only an average snapshot of the ecosystem can be described by *Ecosim*. Therefore, for simplification in modeling the ecosystem, it was assumed that the FIME was in its summer state (January to June), when commercially important taxa such as *Illex* squids were more abundant in the region. This paper describes the sources and methods used to estimate model parameters, and discusses preliminary results obtained from model outputs. Major model assumptions and uncertainties are noted and areas for further investigation are suggested.

METHOD

The FIME were categorized into 44 functional groups; 43 living and 1 non-living (detritus). The living groups were generally categorized according to their functional roles, taxonomy, sizes and depth range. These include 1 group of planktonic primary producers, 6 groups of planktonic invertebrates, 3 groups of benthic invertebrates, 4 groups of cephalopods, 22 groups of fish, 3 groups of marine mammals and 3 groups of birds (Table 1). The commercially important species, such as *Illex* and Patagonian squids, southern blue whiting and pink cusk-eel, were categorized as individual groups in order to better represent interactions between the fisheries and organisms. Moreover, for southern blue whiting, pink cusk-eel and Patagonian toothfish, juveniles and adults were modeled as separate but linked ‘split pool’ groups.

Input parameters were estimated using published literature and survey reports. When information specifically for the FIME was not available, values from nearby areas or similar ecosystems were adopted. Guesstimates were used when information from other sources was lacking. Detailed descriptions of the input parameters for each functional group are presented below.

Phytoplankton

Phytoplankton is represented, as in most published *Ecosim* models, by a single functional group. Total phytoplankton biomass was converted from the average chlorophyll *a* concentration of waters northeast of the FIME in 1997. The annual average euphotic layer-integrated chlorophyll *a* concentration in the area around 50°W and 56°S was estimated at 31.3 t·km^{-2} (Maranon *et al.*, 2001). By assuming a carbon to chlorophyll *a* ratio of 43.9 % and a carbon dry to wet weight ratio of 1 to 9 (Bundy *et al.*, 2000), the annual phytoplankton biomass in FIME was estimated to be 124 t·km^{-2}. The P/B ratio was estimated from the average primary productivity of the FIME area from the *Sea Around Us* Project database (www.seaaroundus.org) to be 244 year^{-1}.

Table 1. Functional groups and their member taxa/species in the Falkland Island marine ecosystem model.

Group #	Functional group	Member groups/Species
1	Phytoplankton	Diatoms and other planktonic primary producers
2	Herbivorous zooplankton	Hyperiid amphipods, mysids, tunicates and icthyoplankton
3	Carnivorous zooplanktons	Chaetognaths, hyperiid amphipods, mysids, tunicates and icthyoplankton
4	Krill	Euphausiacea
5	Jellyfish	Scyphozoa
6	Large zoobenthos	Polychaetes, bivalves and others
7	Small zoobenthos	Polychaetes, echinoderms, bivalves and others
8	Benthic crustaceans	Decapods and other crustaceans
9	*Illex* Squid	*Illex argentinus*
10	Patagonian squid	*Loligo gahi*
11	Small cephalopods	*Batoteuthis skolops*, ornate arm squid (*Brachioteuthis picta*), *Benthoctopus magellanicus*, *Graneledone macrotyla*, Tehuelche octopus (*Octopus tehuelchus*), sevenstar flying squid (*Martialia hyadesi*)
12	Large cephalopods	Anatarctic cranch squid (*Mesonychoteuthis hamiltoni*), red flying squid (*Ommastrephes bartramii*), antarctic flying squid (*Todarodes filippovae*), greater hooked squid (*Moroteuthis ingens*)
13	Pelagic fish	Falkland sprat (*Sprattus fuegensis*), southern driftfish (*Icichthys australis*), *Odontesthes nigricans*
14	Small demersal fish	*Agonopsis chiloensis*, *Harpagifer bispinis*, *H. palliolatus*, *Phucocoetes latitans*, *Maynea puncta*, *M. patagonica*, *Galaxias platei*, Patagonian redfish (*Sebastes oculatus*), fatheads (*Psychrolutes marmoratus*), *Cottoperca gobio*, elephantfish (*Callorhinchus callorynchus*), *Crossostomus fasciatus*
15	Large demersal fish	Pouched lamprey (*Geotria australis*), *Austrolycus depressiceps*, Brazilian flounder (*Paralichthys brasiliensis*)
16	Bathypelagic fish	Half-naked hatchetfish (*Argyropelecus hemigymnus*), *Bathylutichthys taranetzi*, common fangtooth (*Anoplogaster cornuta*), ribbon barracudina (*Arctozenus risso*), *Stromateus brasiliensis*, slender escolar (*Paradiplospinus gracilis*), Patagonian blennie (*Eleginops maclovinus*), Patagonian moray cod (*Muraenolepis orangiensis*), smooth oreo (*Pseudocyttus maculatus*)
17	Small bathydemersal fish	Marginate snailfish (*Careproctus aureomarginatus*), *Letholycus microphthalmus*, *Oidiphorus brevis*, *Iluocoetes fimbriatus*, Eelpouts (*Lycodonus malvinensis*), *Cottunculus granulosus*, *Cataetyx messieri*, messmate (*Echodon cryomagarites*), small-spine snailfish (*Careproctus aculeolatus*), *C. armatus*
18	Large bathydemesal fish	Antarctic escolar (*Paradiplospinus antarcticus*), *Ceratias tentaculatus*, Pink cusk-eel (*Genypterus blacodes*)
19	Grenadier	Longrayed whiptail (*Coryphaenoides subserrulatus*), marini's grenadier (*Caelorinchus marinii*), Campbell whiptail (*C. kaiyomaru*), banded whiptail (*C. fasciatus*), Whitson's grenadier (*Macrourus whitsoni*), bigeye grenadier (*M. holotrachys*), ridge scaled rattail (*M. carinatus*)
20	Myctophidae	*Krefftichthys anderssoni*, *Gymnoscopelus fraseri*, rakery beaconlamp (*Lampanyctus macdonaldi*), *G. nicholsi*, *G. opisthopterus*
21	Codling	Dwarf codling (*Austrophycis marginata*), Patagonian codling (*Lepidion ensiferus*), tadpole codling (*Salilota australis*), slender codling (*Halargyreus johnsonii*), Blue antimora (*Antimora rostrata*)
22	Dogfish	Granular dogfish (*Centroscyllium granulatum*), piked dogfish (*Squalus acanthias*)
23	Rock cod	*Patagonotothen cornucola*, *P. wiltoni*, Patagonian rock cod (*P. brevicauda brevicauda*), yellowfin notothen (*P. guntheri*), *P. sima*, black southern cod (*P. tessellata*), maori cod (*P. magellanica*)
24	Flounder	Southern flounder (*Mancopsetta maculata maculata*), armless flounder (*M. milfordi*), *Thysanopsetta naresi*, finless flounder (*Achiropsetta tricholepis*), *Xystreurys rasile*,
25	Hagfish	*Myxine knappi* and *M. fernholmi*
26	M. australis	Southern hake (*Merluccius australis*)

Table 1. Continued.

Group #	Functional group	Member groups/Species
27	M. hubbsi	Common hake (*M. australis*)
28	Snoek Juvenile	Immature snoek (*Thrsites atun*)
29	Snoek Adult	Mature snoek (*Thrsites atun*)
30	Southern blue whiting Juvenile	Immature southern blue whiting (*Micromesistius australis*)
31	Southern blue whiting Adult	Mature southern blue whiting (*Micromesistius australis*)
32	Toothfish Juvenile	immature patagonian toothfish (*Dissostichus eleginoides*)
33	Toothfish Adult	Mature patagonian toothfish (*Dissostichus eleginoides*)
34	Hoki Juvenile	Immature hoki (*Macruronus magellanicus*)
35	Hoki Adult	Mature hoki (*Macruronus magellanicus*)
36	Rays and sharks	*Bathyraja* spp., *Dipturus* spp., *Etmopterus* spp.
37	Basking shark	Basking shark (*Cetorhinus maximus*)
38	Baleen whales	Southern right whale (*Eubalaena australis*), Pygmy right whale (*Caperea marginata*), Blue whale (*Balaenoptera musculus*), Fin whale (*Balaenoptera physalus*), Sei whale (*Balaenoptera borealis*), Minke whale (*Balaebiotera acutorostrata*), Humpback whale (*Megaptera novaeangliae*)
39	Toothed whales, dolphins & porpoises	Sperm whale (*Physeter catodon*), Arnoux's beaked whale (*Berardius arnuxii*), Cuvier's beaked whale (*Ziphius cavirostris*), Southern bottlenose whale (*Hyperoodon planifrons*), Gray's beaked whale (*Mesoplodon grayi*), Hector's beaked whale (*Mesoplodon hectori*), Strap-toothed whale (*Mesoplodon layardii*), Killer whale (*Orcinus orca*), Long-finned pilot whale (*Globicephala melas*), Peale's dolphin (*Lagenorphynchus australis*), Dusky dolphin (*Lagenorhynchus obscurus*), Hourglass dolphin (*Lagenorhynchus cruciger*), Risso's dolphin (*Grampus griseus*), Bottlenose dolphin (*Tursiops layardii*), Southern right whale dolphin (*Lissodelphis peronii*), Commerson's dolphin (*Cephalorphynchus commersonii*), Spectacled porpoise (*Australophocaena dioptrica*)
40	Seals and sea lion	South American sea lion (*Otaria byronia*), South American fur seal (*Arctocephalus australis*), Southern elephant seal (*Mirounga leonine*), crabeater seal (*Lobodon carcinophagus*), Leopard seal (*Hydrurga leptonyx*)
41	Penguins	King Penguin (*Aptenodytese patagonicus*), Gentoo Penguin (*Pygoscelis papua*), Southern Rockhopper Penguin (*Eudyptes chrysocome chrysocome*), Macaroni Penguin (*Eudyptes chrysolophus*), Magellanic Penguin (*Spheniscus magellanicus*)
42	Seabirds	Black-browed albatross (*Diomedea melanophris*), Southern Giant Petrel (*Macronectes gianteus*)
43	Shorebirds	Cormorant (*Phalacrocorax* spp.), Black-crowned Night Heron (*Nycticorax nycticorax falklandicus*), Kelp Goose (*Chloephaga hybrida malvinarum*), Patagonian Crested Duck (*Lophonetta specularioides specularioides*), Flightless Steamer Duck (*Tachyeres brachypterus*), Oystercatcher (*Haematopus* spp.), White-rumped Sandpiper (*Calidris fuscicollis*), Gull (*Larus* spp.), Tern (*Sterna* spp.)
44	Detritus	--

Zooplankton

Zooplankton is divided into herbivorous zooplankton, feeding primarily on phytoplankton, carnivorous zooplankton and krill. Krill includes all species belonging to the order Euphausiacea.

Local data on herbivorous zooplankton were lacking; therefore, estimates of P/B (8.4 year^{-1}) and Q/B (20.7 year^{-1}) ratios were taken from the 1995-1997 'Newfoundland ' model by Heymans and Pitcher (2002). Ecotrophic efficiency was assumed to be 0.95 and diet was assumed to be 100 % phytoplankton.

Since local biomass estimates for carnivorous zooplankton were not available, biomass was assumed to be the average carnivorous zooplankton biomass (28.9 t·km^{-2}) between longitude 0° and latitude 57°28' S and 47°23' S as suggested in Pakhomov *et al.* (1999). Pakhomov *et al.* (1999) also estimated this group's diet and gave an average daily ration estimate of 4.7 % of the standing stock, i.e., equivalent to an annual Q/B ratio of 17 year^{-1}. The P/B ratio was estimated from an assumed P/Q ratio of 0.3 (upper limit of the range of general P/Q ratio for marine organisms; Christensen *et al.*, 2000).

As local krill biomass estimate was lacking, the median of biomass estimates of *Euphausia superba* from South Georgia in 1990-1998 (50 t·km^{-2}) was taken from Brierley *et al.* (1999) and Siegel (2000). The P/B ratio of krill was assumed to be the mean annual P/B ratio for all developmental stages of Antarctic krill

(5 year^{-1}; see Siegel, 1986 in Siegel, 2000). The mid-point of the upper and lower bounds of the daily ration of Euphausiacea noted in Pakhomov *et al.* (1999) is 9.4 %, resulting in an annual Q/B ratio of 34 year^{-1}. The diet of krill was adopted from Perissinotto *et al.* (2000).

Jellyfish

This group includes all species belonging to the class Scyphozoa. Since local data on the group were lacking, we used the P/B and Q/B ratio for large zooplankton from Heymans and Pitcher's (2002) 'Newfoundland' model for 1995-1997 (3.43 year^{-1}; 19.5 year^{-1}). Diet composition was adapted from the jellyfish group in the 1990s 'Hong Kong' model of Buchary *et al.* (2002). Ecotrophic efficiency was assumed to be 0.95.

Zoobenthos

This group was divided into small and large zoobenthos, defined as burrowing invertebrates <1 mm and >1 mm in size, respectively. P/B (2.0 year^{-1}) and Q/B (6.3 year^{-1}) ratios of small zoobenthos were adapted from the polychaete group of the 1995-97 'Newfoundland' model (Heymans and Pitcher, 2002). Biomass of large zoobenthos (12 t·km^{-2}) was estimated as the average of estimates in the Falkland Islands area between the abyssal and coastal zones (Vinogradova *et al.*, 1974). The P/B ratio (0.261 year^{-1}) for the Strait of Magellan macrozoobenthos estimated by Thatje and Mutschke (1999) was used, while the Q/B ratio was estimated from an assumed P/Q ratio of 0.25 year^{-1} (see Christensen *et al.*, 2000). Diet composition for both of the zoobenthos groups was adapted from the 1990s 'Hong Kong' model of Buchary *et al.* (2002).

Benthic crustaceans

This group includes all benthic decapods and other crustaceans. The average values of P/B (0.82 year^{-1}) and Q/B (4.42 year^{-1}) were estimated from values for large crabs (0.38 year^{-1} and 4 42 year^{-1}), small crabs (0.63 year^{-1} and 4.42 year^{-1}) and shrimp (1.45 year^{-1} and 4.42 year^{-1}) of the 1995-97 'Newfoundland' model (Heymans and Pitcher, 2002). The diet compositions of these 3 groups were also used to obtain the average diet composition used in this model.

Illex squid (Illex argentinus)

Illex squid performs an annual migration cycle from their northern breeding grounds to the Falkland Islands in January-February and back in July-August to spawn and eventually expire (Basson *et al.*, 1996). As noted previously, the migratory nature of the system was methodologically simplified with the assumption that the modeled FIME is in the January-June state.

Biomass of *Illex* squid in the FIME at the end of the fishing season of 1999 was estimated to be 43,000 t while the total catch for the season was 266,169 t (Falkland Islands Government, 1999). Assuming the weekly natural mortality (M) rate of *Illex* at FIME is 0.06 (Basson *et al.*, 1996) and the time between the peak *Illex* abundance in the FIME and the end of the fishing season is 10 weeks (Basson *et al.*, 1996), then the estimated peak biomass is 344,520 t, i.e., the mid-point between the season's peak and end biomass, and thus an annual *Illex* squid biomass average of 0.372 t·km^{-2}.

Fishing mortality (F) of *Illex* was approximated as the ratio between catch and biomass. Given an estimated natural and fishing mortality rate in the modeled period of 0.96 year^{-1} (assuming 16 weeks of occurrence in the modeled system) and 1.38 respectively, the effective P/B (assumed to be equal to total mortality; Allen, 1971) of *Illex* in our model becomes 2.34 year^{-1}. Q/B ratio was estimated from an assumed P/Q ratio of 0.25 (see Christensen *et al.*, 2000). Diet composition was estimated from information available in the CephBase database (www.cephbase.utmb.edu) and Haimovic *et al.* (1998). Because of the migratory behavior of the group, we assumed that *Illex* squid spent half of the year feeding outside the FIME, therefore, its diet was scaled to a sum of 0.5, while the remaining half was allocated to 'import'[1].

Patagonian squid (Loligo gahi)

Similar to the *Illex* squid, Patagonian squid also undergoes an annual migratory cycle. Agnew *et al.* (1998) observed at least two stocks alternately present in each half of the year. The biomass of this group (0.239 t·km^{-2}) is adapted from the average annual biomass estimated by Agnew *et al.* (1998) from stock

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[1] In *Ecosim*, 'import' to a system is the consumption of prey not part of the system as it is defined (Christensen *et al.*, 2000).

assessment data for 1992 to 1996. The P/B ratio was assumed to be the same as that of *Illex* squid, while Q/B ratio was estimated from an assumed P/Q ratio of 0.25 (see Christensen *et al.*, 2000). Diet composition was estimated from information available in the CephBase database (www.cephbase.utmb.edu).

Small and large cephalopods

These two groups consist of cephalopods other than *Illex* and Patagonian squids with mantle length of less than and greater than 50 cm, respectively. The P/B ratio of small cephalopods was assumed to be the same as those of *Illex* and Patagonian squids because of their similar life histories. The P/B ratio for large cephalopods was assumed to be half that of the small cephalopods. The Q/B ratio was estimated from an assumed P/Q ratio of 0.25. Diet compositions were estimated from information available in the CephBase database (www.cephbase.utmb.edu).

Fish groups

Biomasses of the fish groups were extrapolated from fishing surveys conducted in the FIME in 2000-2001. The average species composition matrix was estimated from catch compositions of the pelagic, deepwater pelagic and bottom trawl surveys in 2001 (Falkland Islands Government, 2002b, c, d). Poisson sampling was assumed, i.e., catches of fish species that were absent in a particular survey were assumed to be the average of all surveys. As biomass estimates are only available for southern blue whiting (Falkland Islands Government, 1999), the only way of approximating other species' biomasses was to extrapolate from the blue whiting survey values and the average species composition matrix. Biomass estimates for fish species using this method have a large margin of error as differences in catchability are not accounted for. Thus, functional groups with biomasses assessed as inappropriate according to the rule of mass-balance were left to have their biomass estimated by the *Ecosim* model. Unless stated specifically, natural mortalities of the fish species were estimated using Pauly's (1984) empirical equation based on asymptotic length, growth rate and average water temperature (assumed in FIME to be 5°C). The Q/B ratio was estimated using the empirical equations of Palomares and Pauly (1989, 1998) based on a species' asymptotic weight, shape of the caudal fin, the average water temperature and its principal food item.

Pelagic fish

This group includes all clupeids, centrolophids and atherinids in the FIME. The biomass estimate extrapolated from the trawl survey was too low to maintain the mass-balance criteria of the system. Thus, it was left to be estimated by the model with an assumed ecotrophic efficiency value of 0.95, a shortcut that may be adopted in preliminary *Ecopath* models (Christensen *et al.*, 2000). Assuming that the pelagic fish are between under-exploited and fully-exploited, the fishing mortality rate was guessed to be a quarter of the natural mortality (Patterson, 1992). Diet composition was estimated from qualitative information available for the species in this group through FishBase (Froese and Pauly, 2003).

Small and large demersal fish

This group includes demersal fish occurring at depths of less than 500 m. Species categorized as small demersal have maximum lengths of less than 50 cm, while large demersal fishes are those with maximum lengths of more than 50 cm. The biomass of small demersal fishes was extrapolated from fishing surveys (Falkland Islands Government, 2002b, c, d), while biomass of the large demersal fishes was estimated by the model for lack of reliable estimates. Diet composition was estimated from qualitative information available for the species in this group through FishBase (Froese and Pauly, 2003).

Bathypelagic and bathydemersal fish

Pelagic fish species inhabiting the bathypelagic layer (median occurrence depth over 500 m) were placed in the bathypelagic fish category, while demersal fishes living at depths greater than 500 m were categorized as bathydemersal fish. Bathydemersal fishes with maximum lengths of less than 50 cm were categorized as small, and those greater than this size as large bathydemersal fish. Here again, biomasses of these 3 groups extrapolated from the trawl surveys (Falkland Islands Government, 2002b, c, d) were found to be too low to maintain the mass-balance required of the system. Thus, these biomasses were left to be estimated by the model with an assumed ecotrophic efficiency of 0.95. Assuming that the group was between under-exploited to fully-exploited, fishing mortality rate was assumed to be a quarter of their natural mortality (Patterson, 1992). Diet composition was estimated from qualitative information available for the member species in FishBase (Froese and Pauly, 2003).

Grenadier, myctophids, codling, dogfish, rock cod, flounder and hagfish

These groups were defined as macrourids (grenadiers, except Patagonian grenadier or hoki, see below), all myctophids (myctophids), all morids (codlings), dalatiids and squalids (dogfishes), nototheniids (rock cods), achiropsittids and paralichthyids (flounders) and all myxinids (hagfishes). Biomasses of grenadiers, myctophids, dogfishes and flounders extrapolated from the trawl surveys (Falkland Islands Government, 2002b, c, d) conformed with the mass-balance rule for supporting the system, while those of codlings, rock cods and hagfishes were too low, and were thus left to be estimated by the model with an assumed ecotrophic efficiency of 0.95. Assuming that these groups are under-exploited, total mortality, which is an approximation of the P/B ratio of the group, was assumed to be 50 % larger than the mean natural mortality. Diet compositions were estimated from information available for the member species in FishBase (Froese and Pauly 2003). Additional diet information for hagfish was obtained from Martini *et al.* (1997).

Southern hake (*Merluccius australis*) and common hake (*M. hubbsi*)

Populations of southern and common hake inhabit shelf and slope of the Patagonian shelf and undergo seasonal migrations (Tingley *et al.*, 1995). Their abundance in the FIME varies throughout the year (Arkhipkin *et al.*, 2003). Initially biomasses of the two hake groups in the model were averages extrapolated from the fishing surveys. However, biomass of southern hake was found to be too low (0.0013 $t \cdot km^{-2}$). Ratio of catch per unit effort of southern hake to common hake in the FIME was about 186 $kg \cdot h^{-1}$ to 488 $kg \cdot h^{-1}$ (Arkhipkin *et al.*, 2003). Therefore, biomass of southern hake was extrapolated from the biomass of common hake based on this ratio of CPUE (0.028 $t \cdot km^{-2}$). Assuming that the group was between under-exploited to fully-exploited, total mortality, which is an approximate of the P/B ratio of the group, was assumed to be 1.5 times its mean natural mortality. Diet compositions were estimated from information available in FishBase (Froese and Pauly, 2003). Additional diet information was obtained from descriptions in Sanchez and Rosa (1999) and Arkhipkin *et al.* (2003).

Snoek (*Thyrsites atun*)

The group, which undergoes ontogenetic changes in mortality and feeding behavior, was segregated into juveniles and adults. Biomass values extrapolated from the fishing survey data were too low to support the system according to the mass-balance theory and were thus estimated by the model with an assumed ecotrophic efficiency of 0.95. As in other fish groups, assuming that the group was under-exploited to fully-exploited, fishing mortality rate was assumed to be a quarter of natural mortality (Patterson, 1992). Diet composition estimates of snoek off Otago, New Zealand were adopted from O'Driscoll (1998).

Southern blue whiting (*Micromesistius australis*)

Southern blue whiting migrates to the southwest Falkland area to spawn in the spring and then disperses to feed over the shelf (Agnew, 2002). This behavior supports the segregation of this group into juveniles and adults adopted for this model. Biomass of the adult group was obtained from the estimated spawning stock biomass of the species in 1999 reported by the Falkland Islands Government (1999), while biomass of the juvenile group was unclear and was thus left to be estimated by the model. Fishing mortality of adult southern blue whiting was estimated as the catch to biomass ratio of 0.095 (see Falklands Islands Government, 1999) and led to a P/B ratio of 0.355 $year^{-1}$. The P/B ratio of juvenile southern blue whiting was assumed to be the same as the bathypelagic fish group. Diet compositions were obtained from estimates available in FishBase (Froese and Pauly, 2003) and descriptions from Cousseau and Perrotta (1998), Sabatini *et al.* (1999) and Agnew (2002).

Patagonian toothfish (*Dissostichus eleginoides*) and hoki (*Macruronus magellanicus*)

Patagonian toothfish (= Chilean seabass) and hoki (so called in Falkland Island statistics; = Patagonian grenadier, Merluza del cola) are large pelagic species found in the Argentine and Falkland shelves. In this model, because of the large difference in adult and juvenile sizes, and hence in their trophic ecology, both groups were separated into juveniles and adults. Biomasses estimated from extrapolation were found to be too low to support the system in mass-balancing. Therefore, as above, they were estimated by the model based on an assumed ecotrophic efficiency of 0.95. The adult groups were assumed to be under-exploited to fully-exploited, and total mortality, were set at 1.5 times the mean natural mortalities. P/B ratio of the juvenile groups was assumed to be the same as the bathypelagic fish group. Diet compositions were obtained from quantitative estimates available in FishBase (Froese and Pauly, 2003), McKenna (1991), Prenski *et al.* (1996) and Agnew (2002).

Rays and sharks, and basking shark

Biomasses of these two groups were estimated by the model. Assuming that the group was under-exploited to fully-exploited, total mortality, which is an approximate of the P/B ratio of the group, was assumed to be 1.5 times its mean natural mortality. Diet composition of rays was obtained from quantitative stomach content studies in the FIME (Falkland Islands Government, 2002), while diet input for other groups were estimated from information available in FishBase (Froese and Pauly, 2003).

Baleen whales, toothed whales, dolphins and porpoises

The Baleen whales and toothed whales, dolphins and porpoises include all baleen whales and toothed whales, dolphins and porpoises that occur in the FIME (Jefferson *et al.*, 1993; Bingham, 2002a). Because local population estimates were lacking, their populations in FIME were roughly estimated from the average of their regional abundance (Northridge, 1991; Jefferson *et al.*, 1993) and mean body masses of the member species were estimated from a length-to-weight empirical relationship (Jefferson *et al.*, 1993; Trites and Pauly, 1998). Q/B ratio and diet composition were estimated from results of meta-analysis (Trites *et al.*, 1997). P/B ratio of baleen whales was estimated by the model while P/B ratio of the toothed whales, dolphins and porpoises (0.05 $year^{-1}$) was adapted from the 1995-97 'Newfoundland' model (Heymans and Pitcher, 2002).

Seals and sea lions

This group mainly includes the local breeding populations of the South American sea lion (*Otaria byronia*), South American fur seal (*Arctocephalus australis*) and Southern elephant seal (*Mirounga leonine*). Population estimates of the South American sea lion (15,000) and South American fur seal (15,000) in the Falkland Islands were obtained from Reijnders *et al.* (1993) and those of the Southern elephant (500) were estimated from Bingham (2002a). Mean body masses were estimated from a length-to-weight empirical relationship (Jefferson *et al.*, 1993; Trites and Pauly, 1998). Biomass of the group was estimated from the mean body masses and population estimates by assuming a sex ratio of 1:1. P/B ratios for the 3 species of pinnipeds were not available. Average annual mortality rates of the crabeater seals (*Lobodon carcinophagus*) (0.145) and Leopard seals (*Hydrurga leptonyx*) (0.127) (Reijnders *et al.*, 1993), which are visitors to the Falkland Islands, were adopted as the P/B ratio of the group. Q/B ratio and diet composition of the groups were obtained from the weighted estimates for the 3 pinnipeds which were estimated from results of meta-analysis (Trites *et al.*, 1997). Future models might benefit from splitting this group into the proper trophic roles of seals and sea lions.

Penguins

This group includes 5 species of penguins occurred in the Falkland Islands: King penguin (*Aptenodytes patagonicus*), Gentoo penguin (*Pygoscelis papua*), Southern rockhopper (*Eudyptes chrysocome chrysocome*), Macaroni penguin (*Eudyptes chrysolophus*) and Magellanic penguin (*Spheniscus magellanicus*). Biomasses of the penguins which occurred in the Falkland Islands were estimated from the local population estimates (Bingham, 2002a) and mean body weights (Dunning, 1992; Boyd, 2002; www.whaletimes.org/rockhopper.htm; www.penguins.cl/magellanic-penguins.htm). Q/B ratio was estimated from the ratio of annual per capita food consumption of the Macaroni penguin to its average individual body weight. P/B ratio was estimated from an assumed P/Q ratio of 0.05 (Heymans and Pitcher, 2002). Diet compositions were estimated from quantitative stomach content analysis in nearby areas (Moore *et al.*, 1998; Pütz *et al.*, 2001; Clausen and Pütz, 2002) in the 1990s. We also tested the effect of using estimated historical biomasses and diet compositions of penguins in the late 1980s (Pütz *et al.*, 2001) on the ecosystem.

Seabirds and shorebirds

Seabirds include the Black-browed albatross and Southern giant petrel while shorebirds include all shorebirds occurring in the Falkland Islands (Bingham, 2002a). Biomasses of the member species were estimated from local population counts (Bingham, 2002a) and estimated mean body weight (Dunning, 1993; Lorentsen *et al*., 1998). Q/B ratio of seabirds was assumed to be the consumption rate of Southern giant petrel estimated from Lorentsen *et al*.'s (1998) allometric equation. Q/B ratio of shorebirds was adopted from the piscivorous and planktovorous birds group of the 1995-97 'Newfoundland model' (Heymans and Pitcher, 2002). The P/B ratio was estimated from an assumed P/Q ratio of 0.05 (Heymans and Pitcher, 2002). Diet composition of seabirds was estimated from quantitative analysis (Reid *et al*., 1996; Lorentsen *et al*., 1998) while diet of shorebirds was estimated from qualitative descriptions (Bingham, 2002a).

Detritus

Detritus was estimated from the empirical equation (Pauly *et al*., 1993), i.e.,

$$\log_{10}D = -2.41 + 0.954\cdot\log_{10}PP + 0.863\cdot\log_{10}E \qquad \ldots 2)$$

where D is detritus biomass ($gC\cdot m^{-2}$), PP is primary productivity ($gC\cdot m^{-2}year^{-1}$) and E is euphotic depth (m). Primary productivity was estimated from Maranon *et al*. (2001) (13.7 $gC\cdot m^{-2}\cdot year^{-1}$) and euphotic depth was assumed to be 200 m. Therefore, the estimated detritus biomass is 4.59 $gC\cdot m^{-2}$. Assuming a carbon dry to wet weight ratio of 1 to 9 (Bundy *et al*., 2000), detritus biomass of 41.3 $t\cdot km^{-2}$ was used in this model.

Fishery catch

In this model, fishing fleets within the FIMZ were defined by 4 gear types: jigger, trawl, mixed trawl, and longline. Catches of the functional groups per fishing gear were based on the Falkland Islands Government catch statistics in 1999 (Falkland Island Government, 2000; see also Table 2) and scaled to a per km squared basis. Catches for 'Others (Osteichthyes/Chondrichthyes)' reported in the catch statistics (Falkland Islands Government, 2002 b, c, d, e) were allocated to species according to the relative composition in the survey samples because the majority of this category was caught by trawlers.

There was evidence that marine mammals and seabirds might be caught as by-catch (Northridge, 1991; Tasker *et al*., 2000; Barton, 2002). Quantitative estimates of the amount of by-catch were not available, thus, the preliminary model used a guessed value of 0.052 t (0.0000001 $t\cdot km^{-2}$) of each marine mammal and bird group taken by each fishing gear in the FIME.

Model balancing

The input parameters were adjusted using an auto-balancing routine in *Ecopath* with *Ecosim* (Kavanagh *et al*., 2004) so that the constraint of mass-balance in the ecosystem could be met. In this routine, input parameters were adjusted based on a pre-defined range for each input (pedigree, Table 3) until the system was mass-balanced.

RESULTS

The parameters for the mass-balanced FIME model are shown in Table 4 and the adjusted diet matrix in Table 5. This represents a first quantitative description of the Falkland Islands marine ecosystem and provides a tool for understanding the interactions between the living groups in the ecosystem with the local fisheries.

Table 2. Fishery catches (tonnes) used in the FIME model.

Group Name	Mix trawl	Jigger	Longline	Trawl	Total
Phytoplankton	0.000	0.000	0.000	0.000	0
Herbivorous zooplanktons	0.000	0.000	0.000	0.000	0
Carnivorous zooplanktons	0.000	0.000	0.000	0.000	0
Krill	0.000	0.000	0.000	0.000	0
Jellyfish	0.059	0.000	0.001	5.720	6
Small zoobenthos	0.745	0.000	0.018	72.500	73
Large zoobenthos	1.800	0.000	0.043	175.000	177
Benthic crustaceans	0.397	0.000	0.010	38.700	39
Illex Squid	0.000	48816.000	0.000	2346.000	51162
Patagonian squid	0.000	0.000	0.000	6703.000	6703
Small cephalopods	0.000	5.570	0.000	0.000	6
Large cephalopods	0.042	0.000	0.001	4.070	4
Pelagic fish	0.111	0.000	0.003	10.800	11
Small demersal	0.351	0.000	0.008	34.200	35
Large demersal	0.008	0.000	0.000	0.788	1
Bathypelagic fish	0.213	0.000	0.005	20.700	21
Small bathydemersal Fish	0.025	0.000	0.001	2.390	2
Large bathydemesal fish	4.610	0.000	0.000	496.000	501
Grenadier	1.110	0.000	0.027	108.000	109
Myctophidae	0.870	0.000	0.021	84.600	85
Codling	5.960	0.000	0.000	1783.000	1789
Dogfish	0.461	0.000	0.011	44.900	45
Rock cod	0.409	0.000	0.010	39.800	40
Flounder	0.002	0.000	0.000	0.189	0
Hagfish	0.000	0.000	0.000	0.008	0
Merlucius australis	2.650	0.000	0.000	159.000	162
Merlucius hubbsi	10.600	0.000	0.000	638.000	649
Snoek Juvenile	0.183	0.000	0.004	17.800	18
Snoek Adult	0.733	0.000	0.018	71.300	72
Southern blue whiting Juvenile	0.346	0.000	0.008	33.700	34
Southern blue whiting Adult	0.000	0.000	0.000	5464.000	5464
Toothfish Juvenile	0.015	0.000	0.000	1.430	1
Toothfish Adult	8.640	0.000	340.000	219.000	568
Hoki Juvenile	0.183	0.000	0.004	17.800	18
Hoki Adult	14.400	0.000	0.000	3578.000	3592
Rays and sharks	153.000	0.000	0.192	747.000	900
Basking shark	0.011	0.000	0.000	1.070	1
Baleen whales	0.000	0.000	0.000	0.000	0
Toothed whales, dolphins & porpoises	0.001	0.001	0.001	0.010	0
Seals and sea lion	0.010	0.010	0.010	0.010	0
Penguins	0.010	0.010	0.010	0.010	0
Seabirds	0.010	0.010	0.010	0.010	0
Shorebirds	0.010	0.010	0.010	0.010	0
Detritus	0.000	0.000	0.000	0.000	0

Table 3. The distribution range of input parameters, as defined by the Pedigree routine in *Ecopath* with *Ecosim*. a. = the input parameters were either not required or were estimated by the model. Values represent +/- percentage of the estimate of the input parameters.

No.	Group	B	P/B	Q/B	Diet	Catch
1	Phytoplankton	30	20	n.a.	n.a.	n.a.
2	Herbivorous zooplanktons	n.a.	40	40	80	n.a.
3	Carnivorous zooplanktons	60	80	40	40	n.a.
4	Krill	60	40	40	40	n.a.
5	Jellyfish	n.a.	70	70	80	30
6	Small zoobenthos	n.a.	70	70	80	30
7	Large zoobenthos	30	20	80	80	30
8	Benthic crustaceans	n.a.	70	70	80	30
9	*Illex* Squid	10	10	80	40	10
10	Patagonian squid	10	40	80	50	10
11	Small cephalopods	n.a.	30	80	50	10
12	Large cephalopods	n.a.	80	80	50	30
13	Pelagic fish	n.a.	50	50	70	10
14	Small Demersal	60	50	50	70	10
15	Large Demersal	n.a.	50	50	70	10
16	Bathypelagic fish	n.a.	50	50	70	10
17	Small bathydemersal Fish	n.a.	50	50	70	10
18	Large bathydemesal fish	n.a.	50	50	70	10
19	Grenadier	60	50	50	70	10
20	Myctophidae	60	50	50	70	10
21	Codling	n.a.	50	50	70	10
22	Dogfish	60	50	50	80	10
23	Rock cod	60	50	50	70	10
24	Flounder	60	50	50	70	10
25	Hagfish	n.a.	50	50	80	10
26	*Merlucius australis*	60	50	80	70	10
27	*Merlucius hubbsi*	60	50	50	70	10
28	Snoek Juvenile	n.a.	80	80	70	80
29	Snoek Adult	n.a.	50	50	70	10
30	Southern blue whiting Juvenile	n.a.	80	80	80	80
31	Southern blue whiting Adult	10	50	50	70	10
32	Toothfish Juvenile	n.a.	80	80	80	80
33	Toothfish Adult	n.a.	50	50	70	10
34	Hoki Juvenile	n.a.	80	80	80	80
35	Hoki Adult	n.a.	50	50	70	10
36	Rays and sharks	60	50	50	70	10
37	Basking shark	n.a.	50	50	70	10
38	Baleen whales	80	n.a.	50	70	n.a.
39	Toothed whales, dolphins & porpoises	80	70	50	70	80
40	Seals and sea lion	10	50	50	30	80
41	Penguins	10	40	50	30	80
42	Seabirds	30	n.a.	50	30	80
43	Shorebirds	10	70	70	50	n.a.
44	Detritus	n.a.	n.a.	n.a.	n.a.	n.a.

DISCUSSION

As an example of the simple analysis that may be done with the *Ecopath* model, we used the 2000 *Ecopath* model to examine the consequences of reportedly higher penguin biomass in the 1980s. In order to balance, 1980s biomasses and diet compositions of penguins required substantial increases in biomasses for most groups in the model. Biomass increases required are particularly large for cephalopods (Figure 3). Most commercially exploited groups require 20-40 % increase in biomass to support penguins' biomasses and diets in the 1980s.

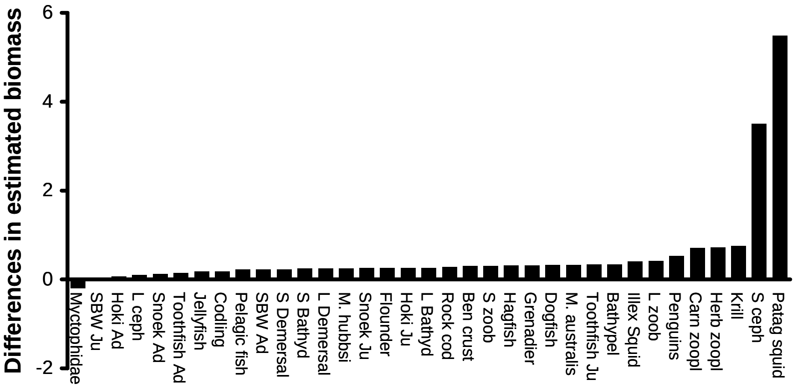

Figure 3. Differences in biomass estimates for the FIME model when biomass and diet estimates for penguins in the 1980s were used (relative to the model using 2000 estimates).

The version of the FIME model that uses historical biomasses and diets of penguins may provide insight into the mechanisms that resulted in such changes. Gentoo, Magallenic and Rockhopper penguins in FIME in the 1980s were more abundant and their diets were composed of a higher proportion of cephalopods – groups that are the primary target of commercial fishing in the regions. The higher biomasses of these groups required to support the 1980s penguin biomass and diets suggest potential competition between commercial fishing and penguins. Such hypothesis may be further investigated by more detailed studies on the bio-energetics of penguins.

The FIME model can be improved by incorporating better local quantitative data for estimating input parameters. These may include data from stock assessments, locally-based diet composition, etc. Priority for data improvement can be based on the 'pedigree' in which higher priority could be given to the least certain inputs, and on the importance of the group to the ecosystem.

Beyond simple mass-balance investigations such as that outlined above, this basic FIME *Ecopath* model can form the starting point for temporal and spatial dynamic simulations of the ecosystem using *Ecosim* and *Ecospace* respectively (Walters *et al.*, 1999; Christensen *et al.*, 2002). Parameters for these dynamic ecosystem models may be refined by fitting the model outputs to time-series biomass, fishing mortality or CPUE data from surveys and annual climate changes. In a related paper, we will use *Ecosim* to test a hypothesis about the dynamics and interactions of the FIME ecosystem and fisheries (see Cheung *et al.*, this volume).

Table 4. Basic parameters of the mass-balanced FIME *Ecopath* model. Numbers in bold represent parameters that were estimated by the model. TL represents the estimated trophic levels for each functional group.

No.	Group name	TL	Biomass	P/B	Q/B	EE	P/Q
1	Phytoplankton	1.00	123.670	243.572	–	**0.114**	–
2	Herbivorous zooplanktons	2.00	**119.009**	8.400	20.670	0.950	**0.406**
3	Carnivorous zooplanktons	3.23	28.917	**5.147**	17.155	**0.971**	0.300
4	Krill	2.53	50.150	5.000	34.310	**0.923**	**0.146**
5	Jellyfish	3.43	**1.845**	3.433	13.732	0.950	**0.250**
6	Small zoobenthos	2.00	**5.272**	2.000	6.330	0.950	**0.316**
7	Large zoobenthos	2.02	12.000	0.261	**1.044**	**0.634**	0.250
8	Benthic crustaceans	2.32	**7.450**	0.820	4.420	0.980	**0.186**
9	Illex Squid	3.80	0.372	2.337	**9.348**	**0.747**	0.250
10	Patagonian squid	3.55	0.239	2.337	**9.348**	**0.904**	0.250
11	Small cephalopods	3.31	**0.051**	2.337	**9.348**	0.980	0.250
12	Large cephalopods	3.99	**0.070**	1.169	**4.676**	0.980	0.250
13	Pelagic fish	3.43	**1.819**	0.930	6.385	0.950	**0.146**
14	Small demersal	3.12	0.146	0.897	8.936	**0.980**	**0.100**
15	Large demersal	3.33	**0.062**	0.370	3.800	0.980	**0.097**
16	Bathypelagic fish	3.93	**0.097**	1.009	6.438	0.951	**0.157**
17	Small bathydemersal Fish	3.15	**0.126**	1.091	9.943	0.980	**0.110**
18	Large bathydemesal fish	4.42	**0.171**	0.300	2.633	0.980	**0.114**
19	Grenadier	3.33	0.463	0.431	4.243	**0.980**	**0.102**
20	Myctophidae	3.63	0.362	1.227	9.420	**0.642**	**0.130**
21	Codling	3.79	**0.130**	0.521	5.025	0.980	**0.104**
22	Dogfish	4.10	0.192	0.383	6.335	**0.980**	**0.060**
23	Rock cod	3.83	**0.285**	0.926	9.300	0.980	**0.100**
24	Flounder	3.15	0.001	0.603	7.300	**0.980**	**0.083**
25	Hagfish	2.93	**0.104**	0.353	4.650	0.980	**0.076**
26	Merlucius australis	4.62	0.028	0.402	1.591	**0.983**	**0.253**
27	Merlucius hubbsi	4.35	0.074	0.360	1.900	**0.997**	**0.189**
28	Snoek Juvenile	4.06	**0.180**	1.009	6.438	0.980	**0.157**
29	Snoek Adult	3.57	**0.039**	0.315	1.300	0.980	**0.242**
30	Southern blue whiting Juvenile	3.72	**3.521**	1.009	6.438	0.951	**0.157**
31	Southern blue whiting Adult	3.44	0.577	0.390	1.900	**0.985**	**0.205**
32	Toothfish Juvenile	3.76	**0.580**	1.009	6.438	0.950	**0.157**
33	Toothfish Adult	4.23	**0.199**	0.150	1.100	0.980	**0.136**
34	Hoki Juvenile	3.79	**0.176**	1.009	6.438	0.980	**0.157**
35	Hoki Adult	3.59	**0.291**	0.194	1.300	0.980	**0.149**
36	Rays and sharks	4.34	**0.022**	0.634	7.200	0.980	**0.088**
37	Basking shark	3.79	**0.00016**	0.090	3.700	0.956	**0.024**
38	Baleen whales	3.82	0.00010	**0.112**	4.430	0.980	**0.025**
39	Toothed whales, dolphins & porpoises	4.64	0.00040	0.050	5.488	**0.501**	**0.009**
40	Seals and sea lion	4.33	0.007	0.136	14.226	**0.537**	**0.010**
41	Penguins	4.35	0.095	**4.000**	80.000	**0.001**	0.050
42	Seabirds	4.08	0.008	**6.687**	133.736	**0.010**	0.050
43	Shorebirds	3.18	0.002	2.500	54.750	**0.114**	**0.046**
44	Detritus	1.00	41.270	–	–	**0.002**	–

Table 5. Diet matrix for the FIME model. Groups 1-10.

Prey\Predator	1	2	3	4	5	6	7	8	9	10
Phytoplankton		1.00		0.56		0.43	0.34			
Herbivorous zooplanktons			0.71	0.33	0.41				0.07	0.01
Carnivorous zooplanktons			0.10	0.04	0.17				0.20	0.02
Krill			0.19	0.06	0.41				0.20	0.95
Jellyfish									0.03	0.02
S zoobenthos						0.00	0.02	0.24		
L zoobenthos							0.01	0.01		
Benthic crustaceans								0.05		
Illex Squid									0.00	
Patagonian squid									0.00	
Small cephalopods									0.00	
Large cephalopods										
Pelagic fish									0.00	
Small demersal										
Large demersal										
Bathypelagic fish										
Small bathydemersal Fish										
Large bathydemesal fish										
Grenadier										
Myctophidae									0.00	
Codling										
Dogfish										
Rock cod										
Flounder										
Hagfish										
Argentine Hake Juvenile									0.00	
Argentine Hake Adult									0.00	
Snoek Juvenile										
Snoek Adult										
Southern blue whiting Juvenile										
Southern blue whiting Adult									0.00	
Toothfish Juvenile										
Toothfish Adult										
Hoki Juvenile										
Hoki Adult										
Rays and sharks										
Basking shark										
Baleen whales										
Toothed whales, dolphins & porpoises										
Seals and sea lion										
Penguins										
Seabirds										
Shorebirds										
Detritus						0.57	0.64	0.70		
Import									0.50	
Sum	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 5. Continued. Groups 11-21

Prey\Predator	11	12	13	14	15	16	17	18	19	20	21
Phytoplankton											
Herbivorous zooplanktons			0.41			0.03				0.19	
Carnivorous zooplanktons		0.21	0.17			0.21			0.04	0.31	0.02
Krill	0.30	0.21	0.41			0.03		0.05	0.13	0.42	0.04
Jellyfish						0.14					0.00
S zoobenthos	0.19			0.34	0.26		0.45		0.24		0.16
L zoobenthos	0.19			0.35	0.26		0.11		0.28		0.16
Benthic crustaceans	0.30	0.21		0.31	0.26	0.38	0.45	0.10	0.23	0.07	0.19
Illex Squid		0.00				0.00		0.03	0.00		0.00
Patagonian squid		0.01				0.00		0.05	0.00		0.00
Small cephalopods	0.01	0.03			0.01	0.00		0.05	0.00		
Large cephalopods		0.02						0.02	0.00		
Pelagic fish		0.21		0.00		0.03			0.02		0.04
Small demersal					0.20			0.05			0.04
Large demersal								0.05			
Bathypelagic fish		0.01							0.00		
Small bathydemersal Fish								0.05	0.02		
Large bathydemesal fish									0.02		
Grenadier						0.10			0.00		0.04
Myctophidae	0.01	0.05				0.01		0.25	0.00		0.01
Codling		0.03				0.00			0.01		
Dogfish						0.06		0.05			
Rock cod	0.02										0.17
Flounder								0.00			
Hagfish								0.00	0.02		
Argentine Hake Juvenile				0.00							0.00
Argentine Hake Adult				0.00							0.00
Snoek Juvenile				0.01							
Snoek Adult											
Southern blue whiting Juvenile								0.10			0.04
Southern blue whiting Adult				0.00							0.01
Toothfish Juvenile								0.14			0.04
Toothfish Adult											0.03
Hoki Juvenile								0.00			
Hoki Adult								0.00			
Rays and sharks											
Basking shark											
Baleen whales											
Toothed whales, dolphins & porpoises											
Seals and sea lion											
Penguins											
Seabirds											
Shorebirds											
Detritus											0.02
Import											
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 5. Continued. Groups 22-32.

Prey\Predator	22	23	24	25	26	27	28	29	30	31	32
Phytoplankton											
Herbivorous zooplanktons		0.13							0.27	0.01	0.25
Carnivorous zooplanktons		0.11				0.05	0.33	0.06	0.27	0.01	0.25
Krill	0.23	0.52				0.05	0.33	0.94	0.27	0.13	0.25
Jellyfish	0.47	0.03					0.33		0.16	0.03	0.21
S zoobenthos	0.02		0.45	0.22							
L zoobenthos	0.02		0.11	0.22							
Benthic crustaceans	0.02		0.45	0.22		0.05			0.03	0.77	0.02
Illex Squid	0.00					0.01			0.00	0.00	0.00
Patagonian squid						0.00			0.00	0.00	0.00
Small cephalopods						0.00			0.00	0.00	0.00
Large cephalopods									0.00	0.00	0.00
Pelagic fish					0.03	0.05		0.00	0.00		0.00
Small demersal										0.01	
Large demersal											
Bathypelagic fish	0.00	0.00								0.00	
Small bathydemersal Fish				0.09							
Large bathydemesal fish											
Grenadier	0.05									0.03	
Myctophidae	0.01	0.00				0.05			0.00	0.01	0.00
Codling		0.01								0.00	
Dogfish											
Rock cod						0.05					
Flounder											
Hagfish											
Argentine Hake Juvenile	0.00	0.00				0.00					
Argentine Hake Adult	0.00	0.00				0.00					
Snoek Juvenile		0.06									
Snoek Adult											
Southern blue whiting Juvenile	0.12	0.08			0.18	0.05					
Southern blue whiting Adult	0.03	0.01			0.20	0.05					
Toothfish Juvenile					0.03						
Toothfish Adult					0.03						
Hoki Juvenile		0.06			0.03	0.05					
Hoki Adult					0.03	0.04					
Rays and sharks											
Basking shark											
Baleen whales											
Toothed whales, dolphins & porpoises											
Seals and sea lion											
Penguins											
Seabirds											
Shorebirds											
Detritus	0.02			0.25							
Import					0.50	0.50					
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 5. Continued. Groups 33-43.

Prey\Predator	33	34	35	36	37	38	39	40	41	42	43
Phytoplankton											
Herbivorous zooplanktons		0.25	0.24		0.28	0.24	0.01	0.03			
Carnivorous zooplanktons		0.25	0.19		0.22	0.24	0.01	0.03	0.11	0.00	
Krill	0.17	0.25	0.24		0.22	0.24	0.01	0.03	0.24	0.41	
Jellyfish		0.25	0.05		0.28	0.24	0.01	0.03			
S zoobenthos							0.01	0.05			0.32
L zoobenthos				0.00			0.01	0.05			0.32
Benthic crustaceans	0.20	0.01	0.24	0.18			0.01	0.05			0.28
Illex Squid	0.01	0.00	0.00	0.12		0.00	0.09	0.05	0.01	0.00	0.00
Patagonian squid	0.01	0.00	0.01	0.08		0.00	0.09	0.05	0.05	0.00	0.00
Small cephalopods	0.01	0.00	0.01	0.07		0.00	0.09	0.05	0.00	0.00	0.00
Large cephalopods			0.01	0.03			0.25	0.10	0.00		
Pelagic fish	0.05	0.00	0.02	0.02		0.00	0.11	0.23	0.12	0.51	0.00
Small demersal							0.01	0.01		0.02	0.07
Large demersal							0.01	0.01			
Bathypelagic fish	0.01					0.00	0.01	0.00	0.01	0.00	
Small bathydemersal Fish				0.16			0.01	0.01			
Large bathydemesal fish				0.01			0.01	0.01			
Grenadier				0.04		0.01	0.01	0.01		0.00	
Myctophidae	0.05	0.00	0.02			0.00	0.03	0.01	0.01	0.00	
Codling	0.00					0.00	0.00	0.00		0.00	
Dogfish	0.05						0.01	0.01			
Rock cod	0.05			0.14		0.00	0.01	0.01	0.01	0.04	
Flounder				0.00			0.00	0.00			
Hagfish							0.00	0.00			
Argentine Hake Juvenile	0.00			0.00		0.00	0.00	0.00	0.00	0.00	
Argentine Hake Adult	0.00			0.01		0.00	0.01	0.01	0.00	0.00	
Snoek Juvenile	0.05					0.01	0.01	0.01		0.00	
Snoek Adult	0.04						0.01	0.01			
Southern blue whiting Juvenile	0.05					0.00	0.01	0.01	0.38	0.00	
Southern blue whiting Adult	0.10			0.13		0.00	0.03	0.03	0.00	0.00	
Toothfish Juvenile	0.05					0.00	0.01	0.01	0.06	0.00	
Toothfish Adult							0.01	0.01			
Hoki Juvenile	0.05					0.01	0.01	0.01		0.00	
Hoki Adult	0.05						0.01	0.01			
Rays and sharks				0.02			0.01	0.01			
Basking shark							0.00				
Baleen whales							0.00				
Toothed whales, dolphins & porpoises							0.00	0.00			
Seals and sea lion							0.00	0.01			
Penguins							0.00	0.01			
Seabirds							0.00	0.01			
Shorebirds							0.00	0.01			
Detritus											
Import											
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

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SIMULATIONS OF THE FALKLAND ISLANDS MARINE ECOSYSTEM: CLIMATE, PENGUINS AND SQUID FISHERIES[1]

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ABSTRACT

Based on a preliminary mass-balance of the marine ecosystem of the Falkland Islands, we simulate, using *Ecosim*, responses of the ecosystem to different levels of fishing and historical changes in primary productivity. The model suggests *Illex* squid, and sharks and rays are most sensitive to changes in fishing rates. The abundance of many model groups changes strongly and positively with historical changes in primary productivity. The abundance of penguins, sea lions and seals increases when fishing is reduced, mainly because of reduction in simulated by-catch, but the value of this parameter needs improving. The model also suggests that *Illex* squid fisheries may be near the maximum possible, but does not lend strong support to the hypothesis that squid fisheries significantly reduce food for penguins. The model is useful for exploring hypotheses about alternative ecological and management scenarios for the Falkland Islands marine ecosystem. Our simulation results are highly sensitive to the values assumed for the *Ecosim* vulnerability factors, and so the next steps should be to improve these parameters by fitting the model using time-series data.

INTRODUCTION

The rich resources in the Falkland Islands marine ecosystem (FIME) attract fishing fleets from around the world. In 2002, a total of 250 fishing licenses were issued for all fisheries in the Falkland Conservation Zones (FCZ) by the Falkland Islands Government, the total annual catch amounting to slightly over 100,000 t (Falkland Islands Government, 2003). A large proportion of the fleets target the lucrative *Illex* and *Loligo* squids in the region; over 140 licenses were issued specifically for these squid fisheries. The remaining fleets mainly targeted finfish such as southern blue whiting (*Micromesistius australis*), southern hake (*Merluccius australis*), tadpole codling (*Salilota australis*) and Patagonian toothfish (*Dissostichus eleginoides*).

Since the designation of the FCZ in the late 1980s, fishing effort has been managed by the Falkland Islands Government (Barton, 2002). Stock assessments of a few major species, such as the *Illex* and *Loligo* squids and the southern blue whiting have been undertaken, with licensing being partly determined by the status of the main stocks. Therefore, as in most stock assessment around the world at present, the approaches used have been based mainly on individual commercially important species. Given the trend towards ecosystem-based management, comparison with well-founded ecosystem modeling has recently begun in many places.

Indeed, there are concerns about the effect of fisheries on the food web of the FIME, with particular attention needed for charismatic species such as penguins and marine mammals at the top of the food chain. For instance, breeding populations of the Magellanic penguin (*Speniscus magellanicus*), Gentoo penguin (*Pygoscelis papua*) and Rockhopper penguin (*Eudyptes chrysocome*) in the Falkland Islands have evidently declined from their early 1980s levels (Bingham, 2002). At the same time, diet analysis has suggested that squid have gradually disappeared from the diet of these penguins and have been replaced by fish (Pütz *et al.*, 2001). Direct trophic competition between these squid predator species and squid fisheries is one hypothesis that might explain these reported changes (Pütz *et al.*, 2001; Bingham, 2002).

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Biota in the FIME correlates significantly with features of the regional oceanography. For example, productivity around the Falkland Islands is affected by the strength of the predominant Falklands current (Longhurst, 1998). Distribution and abundance of *Illex* squid is partly determined by the strength and spatial patterns of planktonic productivities (Basson *et al.*, 1996; Arkhipkin and Middleton, 2002). Recruitment of *Loligo* squid is significantly correlated to sea surface temperature (SST) in the FIME (Agnew *et al.*, 2000, 2002). Meanwhile, the indirect effects of these variations on the trophic system have not been fully understood. However, these climate influences comprise a plausible alternative hypothesis to explain the changes in abundance of some top predators, such as penguins and marine mammals, in the FIME.

In this study, an ecosystem simulation model – *Ecosim* with *Ecosim* (EwE) – was used to explore the effects of fisheries on the FIME. In particular, we evaluate hypotheses that may explain the observed changes in the penguin and pinniped populations. *Ecosim* is a dynamic version of the *Ecopath* ecosystem model which is governed by the basic equations (Christensen *et al.*, 2000):

$$\frac{dB_i}{dt} = g_i \sum_j C_{ji} - \sum_j Cij + I_i - (M_i + F_i + e_i) B_i \qquad \text{... 1)}$$

and

$$C_{ij} = \frac{v_{ij} \cdot a_{ij} \cdot B_i \cdot B_j}{v_{ij} + v'_{ij} + a_{ij} \cdot B_j} \qquad \text{... 2)}$$

where the left side gives the growth rate of group i in terms of its biomass, g_i is growth efficiency, M and F are natural and fishing mortalities, I and e are immigration and emigration rates, C_{ji} is the consumption of group j organisms by group i organism, v and v' parameters represent rates of behavioural exchange between invulnerable and vulnerable states and aij represents rate of effective search by predator j for prey type i. In case of split pools (juveniles vs. adults of the same species), account is kept of the number of recruits from the juvenile to the adult stages using the delay-difference model, which allows the inclusion of stock-recruitment relationships as part of the *Ecosim* outputs. Therefore, changes in biomasses of different groups in the ecosystem could be simulated by forcing changes of harvest rates of the fishing fleets into the model. Moreover, any time-series forcing could be input into the model to force the changes of biomass of any specified groups to the input.

An *Ecosim* model of the late-1990s FIME was constructed (see Cheung and Pitcher, this volume). The model has 44 functional groups and 4 types of fishing fleets categorized according to gear type. Moreover, there were juvenile and adult groups for 4 functional groups: southern blue whiting, hoki, snoek and toothfish, which were linked through delay-difference equations in *Ecosim*.

In this study, we used the FIME *Ecosim* model to initialise *Ecosim* dynamic simulations. Scenarios of different fishing patterns were simulated to obtain insights on interactions between fisheries and the ecosystem, particularly the charismatic species such as penguins and pinnipeds. Using *Ecosim*, we also associated primary productivity with historical variations in oceanography in the region to explore the effects of environmental variability on the FIME.

METHODS

Initial Input Parameters

The late 1990s FIME *Ecopath* model (Cheung and Pitcher, this volume) was used as the base model for dynamic simulations in *Ecosim*. Input parameters that determine the predator-prey behaviour of the functional groups in the ecosystem were required to initialize the simulations. Input parameters: maximum relative production to biomass ratio, feeding time, density dependent catchability and handling time, were set as default of the software because specific knowledge on these parameters for the FIME was lacking (for details, refer to Christensen *et al.*, 2000). For the juvenile and adult split groups of southern blue whiting, hoki, snoek and toothfish, input parameters for the delay-different equations (age at maturation t_K, ratio of mean adult weight mw to weight at maturation mw/w_k, von Bertalanffy growth factor K) were based on data obtained from FishBase (Froese and Pauly, 2003), while others were set as the default (Christensen *et al.*, 2000; Table 1).

The vulnerability determines the rates of behavioural exchange between invulnerable and vulnerable states to the predator (*v and v'*) for the prey group. In EwE, these values are between 0 and 1[2]; a value for vulnerability allows the functional group to spend more time in the vulnerable state (to predators) and thus represents a top-down control system, and *vice versa* for bottom-up control. As information to determine this input parameter for the FIME was not available from time series fitting, we assumed that vulnerabilities were proportional to the trophic level of the functional group (Cheung *et al.*, 2002), with a minimum of 0.1 and maximum of 0.6. The sensitivity of the model results to assumptions about the vulnerability parameters was explored.

Two scenarios on the FIME model were explored using *Ecosim* including different levels of fishing effort and the effect of environmental variability.

Table 1. Parameters for the delay-difference equations in the juvenile and adult split groups. Figures with asterisk are default settings from *Ecosim*.

Juvenile/Adult functional groups Input parameters	Snoek (*Thrsites atun*)	Southern blue whiting (*Micromesistus australis*)	Toothfish (*Dissostichus eleginoides*)	Hoki (*Macruconus magellanicus*)
Minimum time as juvenile (relative to the specified setting)	1*	1*	1*	1*
Maximum time as juvenile (relative to the specified setting)	1.0001*	1.0001*	1.0001*	1.0001*
Recruitment power parameter	1*	1*	1*	1*
Age at transition to adult group (t_K)	2.7	3	7	5
Average adult weight to weight at transition (m_w/w_k)	2*	2*	2*	2*
von Bertalanffy growth factor (K)	0.21	0.21	0.08	0.087
Base fraction of food intake used for reproduction	0.3*	0.3*	0.3*	0.3*
Fraction of increase in food intake used for growth	0.8*	0.8*	0.8*	0.8*

Scenario 1: fishing levels

To explore the possible long-term responses of the FIME to different level of fishing, the harvest rate of all the fishing fleets was varied from 0 to 2.5 times the initial rate specified in the late-1990s FIME model. The resulting biomass of the 43 living functional groups and the annual catches at the end of each 50-year simulation were recorded. Biomasses of the functional groups were plotted against the harvest rates. We explored the sensitivity of the simulated results to different assumptions for the vulnerability factors, representing bottom-up and top-down controlled ecosystems.

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[2] Note that vulnerabilities have been changed to vary from one to infinity in recent releases of the EwE software.

Scenario 2: climate forcing

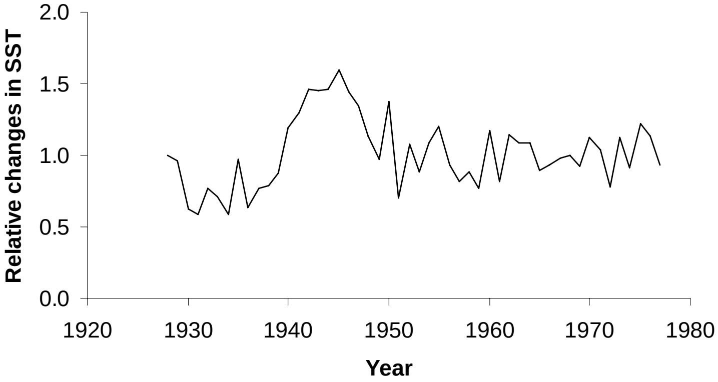

Figure 1. Normalized sea surface temperature (SST) anomalies of the South Atlantic (57.5°S and 52.5°W, between 1928-1977). The time series was fed into the *Ecosim* model as a forcing function and annual phytoplankton abundance was positively associated with it.

This scenario explores the possible effects of oceanographic variability on the biota in the FIME. Sea surface temperature (SST) was used as a proxy for oceanographic conditions around the Falkland Islands (Agnew *et al.*, 2002). Time-series SST anomalies data for the Southeast Atlantic ocean (57.5°S and 52.5°W, between 1928-1977) were obtained from the NGDC, NOAA database[3]. The SST anomaly data were normalized and used in the *Ecosim* model as a forcing function (Figure 1). The annual biomass of phytoplankton was positively associated with this time-series. Harvest rates of all fishing fleets were set to the initial *Ecosim* model values. Changes in biomasses of the functional groups during the 50- year simulations were recorded.

RESULTS

Functional groups in the model responded strongly to the time-series climate-driven changes in primary productivity level (Figure 2). Biomasses of Patagonian squid, *Illex* squid and krill showed large fluctuations under the influence of primary productivity changes. Southern blue whiting and penguin biomasses also responded relatively strongly. Simulated biomasses of most groups appear to correlate positively with primary productivity.

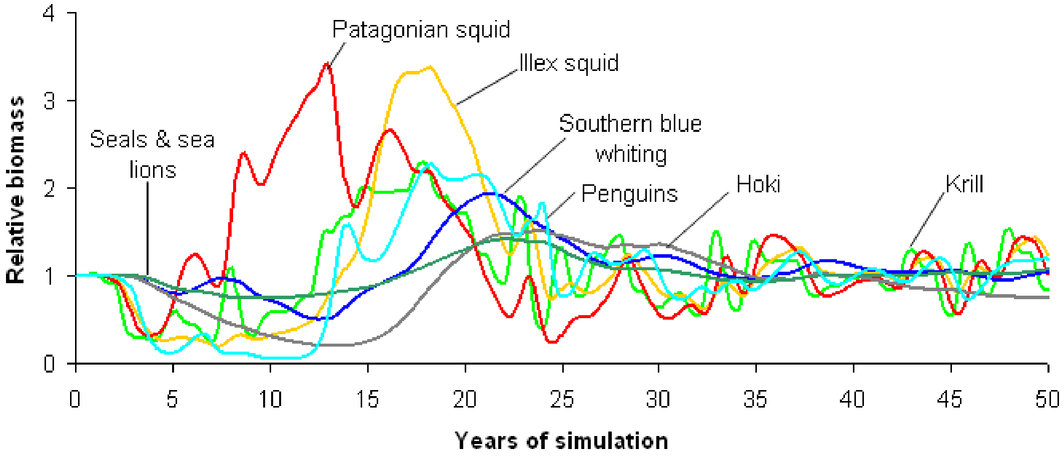

Figure 2. *Ecosim* model of FIME driven over 50 years by primary production changes similar to those reported in Figure 1.

The abundance of commercially targeted groups and groups with vulnerable life history are sensitive to different fishing rates (Figure 3). Biomass of the currently heavily-exploited *Illex* squid responded strongly to changing fishing rate; for example, a 2.5-fold increase led almost to extirpation (Figure 2a). Sharks and

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[3] (http://picasso.ngdc.noaa.gov/cgi-bin/paleo/mannmapxy.pl?lat=-52.5000&lon=-57.5000&gridcell=870&filename=grid870.dat).

rays also responded in a similar fashion. Biomasses of seals, sea lions and penguins increased when fishing was reduced from the 1990s level, but remained relatively stable when fishing increased.

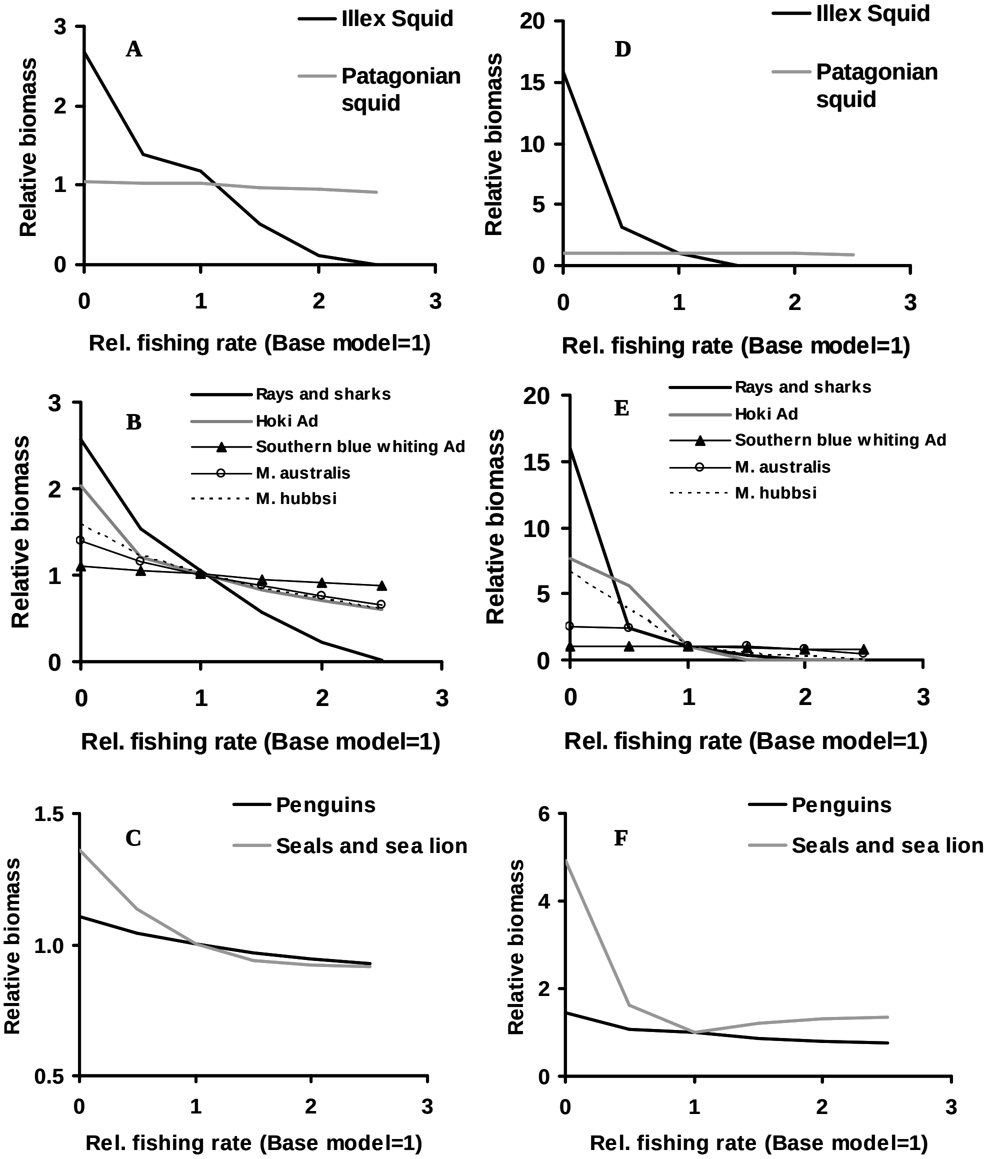

Figure 3. Results of changing relative fishing rates in the FIME *Ecosim* model: (a), (b) and (c) have bottom-up vulnerabilities while (d), (e) and (f) have top-down vulnerabilities.

Results from the simulations are sensitive to our assumptions about the vulnerability factor of the functional groups (Figure 3d, e, f,). A low vulnerability factor (assuming bottom-up control) generally produced smaller changes in biomasses and the converse was true with a high vulnerability factor (assuming top-down control). In many cases (e.g. *Illex* squid), the differences in the simulated results are of an order of magnitude.

DISCUSSION

Our model suggests that the FIME is sensitive to changes in patterns of primary productivity. The FIME is strongly affected by regional oceanography through the various prevailing currents (e.g., Falklands current), which can affect the dynamics of the ecosystem through changes in primary productivity. The simulation exercise proposes a strong linkage between primary productivity to commercial targeted groups and species of conservation concern such as penguins. Detailed analysis of historical population trends and oceanographic records are needed to understand the degree to which environmental factors have contributed to the observed abundance changes of some of these groups.

This preliminary explorative study suggests that commercial fisheries may strongly affect the dynamics of the target populations directly. *Illex* squid populations are heavily exploited by the jigging fisheries and the simulation results suggest that there may be little room for further expansion of the fishery without dramatically increasing the risk of stock collapse.

Non-targeted populations may also be affected by commercial fishing, though to a lesser extent, through by-catch and trophic effects. In the model, penguins and marine mammals such as sea lions and seals are taken as by-catch, but more accurate values for this parameter are required. Thus reducing fishing rates increases biomass of these groups.

Large increases in simulated fisheries for *Illex* squid reduced squid biomass with a much lesser effect on penguins, sea lions and seals. Hence, we do not have enough evidence to support the hypothesis that empirically observed population declines were caused by competition between fisheries and penguins, sea lions and seals (Pűtz et al., 2001; Bingham, 2002). However, our simulation assumed a diet composition of these groups as it was in the 1990s; the energetic costs and benefits resulting from the possible differences in their diet during the 1980s period are not accounted for. These may be important factors in evaluating the hypothesis about the relationship between changes in abundance and competition with fisheries that may be further explored with an improved model.

Results from this simulation studies are preliminary and uncertain. The simulations were based on a very preliminary *Ecosim* model of the FIME (Cheung and Pitcher, this volume). Sensitivity analysis suggests that the simulation results are highly sensitive to the *Ecosim* vulnerability factors. When time-series abundance data for the functional groups are available, they can be used to better estimate these parameters (Christensen *et al.* 2000). But in the meantime, this study allows us to explore ways to understand the dynamics of the FIME. It also helps identify focal areas for more detailed studies to answer some of the ecological and management questions.

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COMMENT ON PENGUINS, SQUID AND FISHERIES IN THE FALKLAND ISLANDS ECOSYSTEM[1]

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The discussion in Cheung and Pitcher (2005, this volume) follows Bingham (2002) in suggesting that penguins may be affected by fishing. Pütz *et al.* (2001) provide information about changes in penguin diet, but this paper is in fact much more circumspect in identifying fisheries as the cause, simply drawing attention to the parallel decline of *Loligo* in catches and in penguin diets.

The hypothesis that fishing caused declines in penguins has several problems. Firstly, the penguins were eating both *Gonatus* and *Loligo*, and both of these squids declined. Only *Loligo* is targeted by the fishery. Putz does not provide a quantitative split between the two in the 1980s penguin diets. Secondly, only juvenile *Loligo* are eaten by penguins; the adult squid are generally found at greater than 100m depth, and are eaten by demersal fish and not penguins, as shown in Table 5 of Cheung and Pitcher (this volume).

Therefore, while it is true that squid abundance seems to have declined in the early 1990s, this is more likely due to overall environmental changes than to a competitive fishery effect reducing squid in penguin diet. In the 1980s there would have to have been more squid of both these groups to have contributed in the recorded way to penguin diets. Fishing is unlikely to have caused the squid declines, as evidenced by the simultaneous declines of both *Gonatus* and *Loligo*.

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NEW ZEALAND

PILOT TROPHIC MODEL FOR SUBANTARCTIC WATER OVER THE SOUTHERN PLATEAU, NEW ZEALAND: A LOW BIOMASS, HIGH TRANSFER EFFICIENCY SYSTEM[1]

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ABSTRACT

The Southern Plateau subantarctic region, southeast of New Zealand, is an important feeding area for birds, seals and fish, and a fishing ground for commercially significant species. The Southern Plateau is a major morphometric feature, covering approximately 433,620 km^2 with average depth of 615 m. The region is noted for its relatively low levels of phytoplankton biomass, and primary production that is iron-limited. In order to evaluate the implications of these attributes for the functioning of this ecosystem a steady-state, 19-compartment model (Figure 1) was constructed using *Ecopath* with *Ecosim* software. The system is driven by primary production that is primarily governed by the supply of iron and light. The total system biomass of 6.28 g C m^{-2} is very low compared with systems so far modeled with a total system throughput of 1136 g C m^{-2} year^{-1}. In the model the Southern Plateau retains 69 % of the biomass in the pelagic system and 99 % of total production. Although fish are caught demersally most of their food is part of production in the pelagic system. Mean transfer efficiencies between trophic levels II and IV of 23 % are at the high end of the range reported in the literature and are partly an artefact of the detail with which the basis of the food web has been portrayed. In the model, adult fish production is almost completely accounted for by the fisheries take (32 %), consumption by seals (7 %), toothed whales (21 %), other adult fish (13 %), and squid (20 %). Fish and squid catches are at the trophic levels of 4.8 and 5.0 respectively. The gross efficiency of the fishery is 0.018 % (catch/primary production), which shows that most of the system's production is not harvested but is going to sustain the system as a whole. Although not all data come from direct knowledge of this system, the model reflects its general characteristics, namely a low biomass and primary production system dominated by the microbial loop, low sedimentation to the seafloor, high transfer efficiencies and a long food web supporting high-level predators. Given that this system appears to be tightly coupled, it is expected that interannual changes in primary production would be quickly transferred to the rest of the system. We might expect fish and other vertebrates to be impacted by a lowering of their production/biomass ratios, by changes to their fecundity and breeding success, or fitness to migrate to breed in the case of hoki, changes to their diets.

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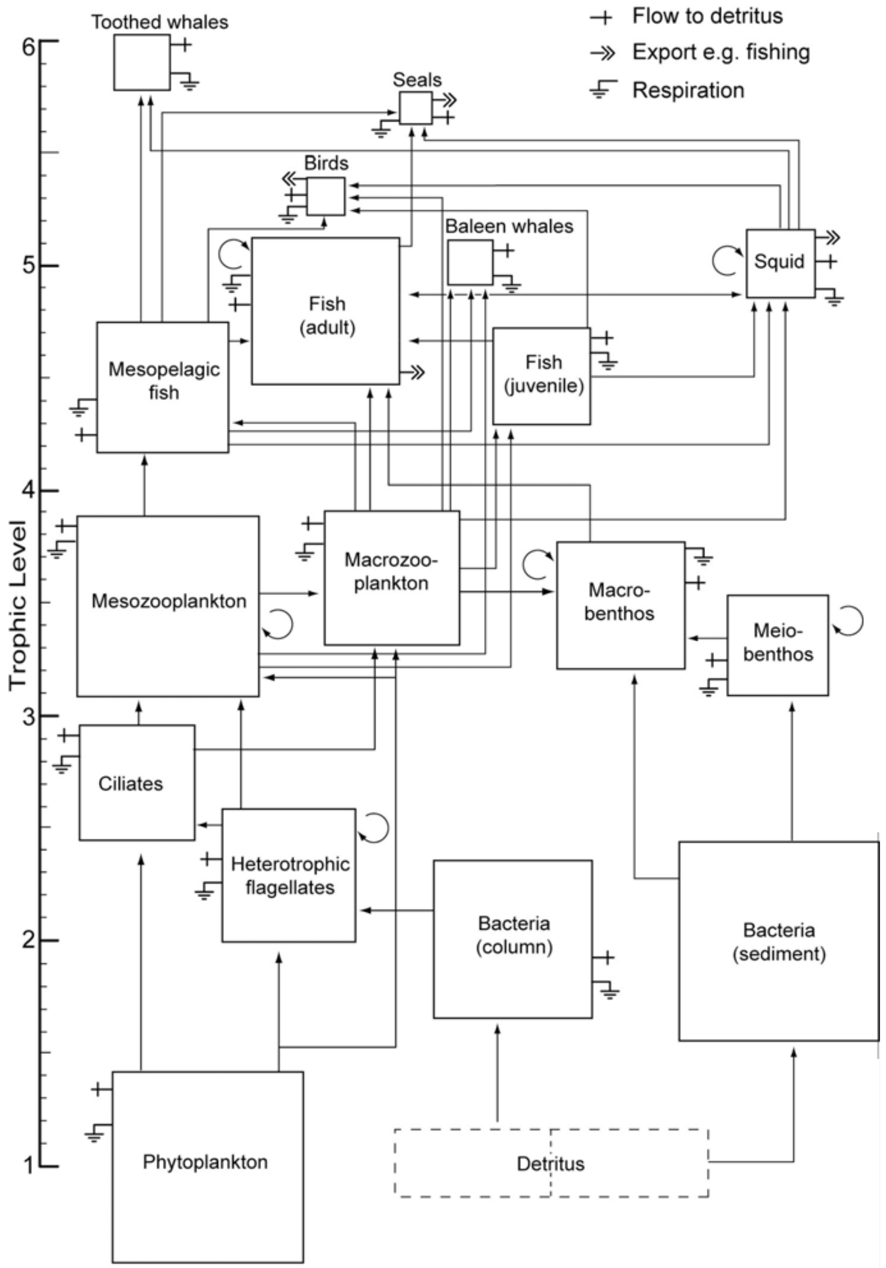

Figure 1. Trophic model for the Southern Plateau, New Zealand. The box size is proportional to the square root of the compartment biomass (from Bradford-Grieve et al., 2003).

APPENDICES

APPENDIX I: MODELING ANTARCTIC ECOSYSTEMS: A UBC FISHERIES CENTRE AND *SEA AROUND US* PROJECT WORKSHOP, VANCOUVER, CANADA, 15-17 APRIL 2003

CONTRIBUTED PAPERS

Preliminary *Ecopath* model of the Kerguelen Islands EEZ. Patrice Pruvost, G. Duhamel, M.L.D. Palomares. Museum Nationale d'Histoire Naturelle, France and *Sea Around Us* project

Predator-prey interactions in the ecosystem at Kerguelen. Mary-Ann Lea, Marine Mammal Research Unit, UBC

Pilot trophic model for sub-Antarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. Janet Bradford-Grieve, NIWA, Wellington, New Zealand

Simulations of ecosystems and fisheries of the Falkland Islands. William Cheung, Tony Pitcher, David Agnew and Tom Marlow Fisheries Centre, UBC and MRAG, London, UK

Preliminary models of minke whale-blue whale-krill interactions in the Antarctic. Mitsuyo Mori and Douglas Butterworth, Cape Town, South Africa

Ecosystem management of South Georgia fisheries. Simeon Hill, British Antarctic Survey, UK

Ecosystem simulations of marine mammal dynamics in the South Georgia region. Emma Bredesen, Marine Mammal Research Unit, UBC

Krill fisheries at the Antarctic Peninsula: spatial simulations addressing conservation concerns for charismatics. Aftab Erfan and Tony Pitcher, Fisheries Centre, UBC

Estimation of illegal and unreported fisheries for Patagonian toothfish in the Antarctic. Louisa Wood and Tony Pitcher, *Sea Around Us* Project, UBC

Mapping global landings: big plans - tiny boxes. Reg Watson and Adrian Kitchingman, *Sea Around Us* project

Mapping marine mammals in the Antarctic. Kristin Kaschner, *Sea Around Us* Project, UBC

Food consumption of seabirds and overlap with fisheries in the Antarctic and adjacent waters. Vasiliki Karpouzi, *Sea Around Us* project, UBC

Modeling the perfect fishery. Tony Pitcher, Fisheries Centre, UBC

DEMONSTRATIONS/PAPERS

Mapping global landings: big plans - tiny boxes. Reg Watson and Adrian Kitchingman, *Sea Around Us* Project

Recent Developments in Ecosystem Simulation Software. Villy Christensen *Sea Around Us* Project, UBC.

ROUND TABLE DISCUSSIONS

Ecosystem simulation modeling: scope and limitations. Sources of information on Antarctic ecosystems and their fisheries

GENERAL AIMS AND SCOPE OF THE WORKSHOP

The workshop will focus on the problems and potential in modeling selected Antarctic ecosystems. Papers on sub-Antarctic regions will be included.

Presented papers and roundtable discussion will aim to address the following issues of modeling, ecology, conservation and management:

- How may the critical features of Antarctic ecology be captured in models?
- In what senses may Antarctic ecosystems said to be fragile?
- What is the extent of fisheries that have operated and are still operating in selected Antarctic regions?
- How does the present differ from the past in selected Antarctic regions?
- How would ecosystems in selected Antarctic regions respond to increased fisheries of various kinds? What are the likely impacts on biodiversity and ecosystem structure and function?
- How might selected ecosystems respond to changes in climate?
- What are the principal management issues for Antarctic fisheries?

Edited proceedings from the workshop will be published as in the Fisheries Centre Research Report series (abstracted in ASFA and available as free PDF downloads on the Web). Written papers should be submitted 3 weeks after the workshop. (Formatting instructions will be distributed at the meeting.)

The Workshop is sponsored by the *Sea Around Us* Project and Fisheries Centre. Limited accommodation is available on campus. Please contact Ms Janice Doyle (Email: j.doyle@fisheries.ubc.ca).

APPENDIX II: ATELIER *ECOPATH* POUR LES ILES KERGUELEN, MUSEUM NATIONAL D'HISTOIRE NATURELLE, PARIS, FRANCE, 29 SEPTEMBRE AU 3 OCTOBRE 2003

PARTICIPANTS

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Jean-Philippe Labat, Patrick Mayzaud. Océanographie Biochimique et Ecologie, Laboratoire d'Océanographie de Villefranche sur mer, UPMC-INSU-CNRS, Paris VI, Observatoire Océanologique BP 28, 06234 Villefranche sur mer, France.

Patrice Pruvost, Guy Duhamel. Muséum National d'Histoire Naturelle, DMPA-USM 403, CP 26, 57 rue Cuvier, Paris, France.

Daniel Pauly, Maria Lourdes D. Palomares. Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver BC V6T 1Z4 Canada.

GENERAL AIMS AND SCOPE OF THE WORKSHOP

To improve the preliminary *Ecopath* model constructed by Patrice Pruvost and Maria L. D. Palomares with inputs from colleagues working on the different components of the Kerguelen Islands' EEZ.

ROUND TABLE DISCUSSIONS (IN FRENCH AS ORIGINALLY SUBMITED BY P. PRUVOST)

Le choix de la période est jugé satisfaisante par l'ensemble des participants dans la mesure où celle-ci correspond à un moment pour lequel nous avons de nombreuses données et à un moment charnière pour les populations des groupes « supérieures » puisque c'est le moment où l'on observe un arrêt du déclin des populations et le début d'une augmentation de certaines colonies.

Les habitats

La discussion a porté sur deux zones :

- le golfe du Morbihan, ne doit pas être considéré dans le modèle en raison de son caractère particulièrement fermé et du peu de relation direct avec l'extérieure. Il peut être étudié comme un écosystème indépendant non lié au système pélagique extérieur et il peut être développer un modèle ecopath spécifique pour cette zone contenu du nombre important de données. L'intégration des biomasses du golfe dans le modèle engendrerait des biomasses beaucoup trop élevées (un rapport 100 peut exister dans certains cas sic. J.-P. Labat).

- la zone côtière, doit être intégrée au modèle dans la mesure ou de nombreux organismes colonisent cette zone à un moment de leur vie et que des transferts de biomasses se font régulièrement entre la côte et le large.

Commentaire par groupe

Top prédateur : il faudrait revoir les publications de Michida mais la composante en céphalopodes semble sous estimée dans la composition alimentaire, car il s'agit essentiellement de cachalot et pas d'orques. La biomasse peut-être cohérente vu le peu d'information que nous avons pour la zone.

- Les animaux filtreurs : La composition alimentaire peut-être vérifiée à partir des études russes de Pervuchine 1968.

- Mammifères chasseurs : le dénombrement et les proportions des différents groupes doivent être disponibles à Chizé. Le régime alimentaire des éléphants de mer doit pouvoir être comparé avec des études menées à Heard. Les otaries doivent être sorties de ce groupe et plutôt associées aux animaux plongeurs tel que les manchots.

- Oiseaux : il faut envisager trois groupes : charognard (pétrels, prions) ; de surface (alabatros) et plongeur (manchots).

- La consommation pour les oiseaux semblent trop élevées si on considère que des oiseaux de 12 Kg environ on une alimentation journalière d'environ 2 Kg. La composition alimentaire pour les manchot est certainement à revoir les prises de poissons mésopélagique doivent représenter près de 0.7 et non 0.51 pour les plongeurs.

- Les requins 2 gros requins sont présents sur la zone dont un le requin dormeur, détritivore et un requin taupe est pélagique sur le plateau + 3 petits requins le régime alimentaire peut-être réévalué à partir des études de Cherel et Duhamel.

- Les calmars biomasse inconnu mais très important dans le réseau trophique. Le cycle est annuel ou dans certains cas de 2 ans le régime alimentaire est essentiellement constitué de mycto, d'euphausiacé et de copépodes.

- Epibenthos profond. Nous nous sommes interrogés sur le bien fondé du groupe d'épibenthos profond dans le modèle vu l'absence de consommateur de ce groupe. Nous pensons qu'il peut–être assimilé à des détritus. Des essais de modélisation sans ce groupe mené le jeudi confirme que la suppression de ce groupe stabilise le modèle.

- Le zooplancton. La répartition par régime alimentaire des différentes espèces doit être revue. Trois groupes peuvent être créés. Les biomasses considérées à partir des campagnes skalp doivent être utilisé avec précaution car le matériel a été fixé au formol préalablement ce qui modifie beaucoup les biomasses. Il doit être envisageable de considérer les données spécifique de la station 5 du programme IOZ qiui se situe à 30 ou 40 miles nautiques dans l'est du golfe du Morbihan et pour laquelle nous avons des séries de données pour la période 1994-1998. La station la plus sud de la campagne antares 3 doit également pouvoir être utilisé pour réévaluer ces données.

Le jeudi matin différents scénarii et modifications ont été testées sur le modèle, notamment la suppression du groupe epi-benthos profond et la modification de certains Q/B.