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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[1] Cite as: Pruvost, P., Duhamel, G., Palomares, M.L.D., 2005. An ecosystem model of the Kerguelen Islands' EEZ. *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. 40-64.

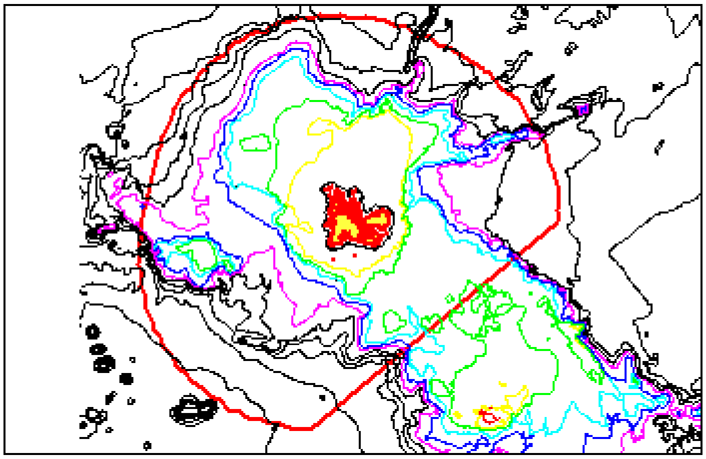

Figure 1. The Kerguelen Peninsula showing its depth contour and the EEZ claimed by the French government.

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.

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$\cdot m^{-2}$) and biomasses ($g\cdot m^{-2}$) as reported in Pakhomov (1993a). An average individual zooplankton (summer 1988) dry weight was estimated as $1.92\ g\cdot m^{-2}/105$ individuals$\cdot m^{-2}=0.018$ g. In order to estimate the zooplankton biomass for 1987, data presented in Table 5 were converted to $g\cdot m^{-2}$ 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 $22.2\ t\cdot km^{-2}$ (Table 5).

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

Order	Taxon	Number of ind. per m^2	Biomass ($g\cdot m^{-2}$)
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 ($19.8\ t\cdot km^{-2}$) from that obtained for the northwest ($22.1\ t\cdot km^{-2}$) and the eastern regions ($17.6\ t\cdot km^{-2}$). 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$\cdot m^{-2}$)	178.56	320.710	146.66	320.710
Average weight in 1988 (g)	0.0183	–	–	–
Omnivorous Zooplankton ($g\cdot m^{-2}$)	3.276	5.884	2.691	5.884
Average biomass in 1987 ($g\cdot m^{-2}$)				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): $M=10\text{^}(0.566-0.718 \cdot \log_{10} L_\infty+0.02 \cdot T$; 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.

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.

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

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·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·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 chororhynchos	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.

ACKNOWLEDGEMENTS

We would like to thank Drs Daniel Pauly and Villy Christensen for their guidance and useful comments in the construction of this model, and Ms Vasiliki Karpouzi and Dr Kristin Kashner for providing data on sea birds and marine mammals on our first modeling attempt. We also thank *The Sea Around Us* Project for making possible the participation of the first author at the workshop on 'Modeling Antarctic Ecosystems' held April 15-17 at the Fisheries Centre, UBC, Vancouver, Canada; and the Muséum National d'Histoire Naturelle (Paris) for making possible the participation of the authors in the workshop on 'The Kerguelen Islands' EEZ' held 29-30 September 2003 at the MNHN, in Paris.

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