Trophic interactions between the Patagonian toothfish, its fishery, and seals and seabirds around Macquarie Island

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ABSTRACT: Macquarie Island is a small subantarctic island that supports a variety of breeding seabird and marine mammal populations. A fishery targeting the Patagonian toothfish *Dissostichus elegenoides* was established around the island in 1994. For ecological sustainable development (ESD) of the fishery, this study investigated the trophic interactions based on diet composition and annual consumption between Patagonian toothfish, its fishery, and seals and seabirds within the Macquarie Island Exclusive Economic Zone (MI-EEZ). Annual consumption rates for each predator were estimated from dietary data (mostly published sources), energetic budgets, prey energy content, and population size. Results indicated little predation on toothfish by seals or seabirds, or prey competition between toothfish and other marine predators. The greatest dietary overlap with toothfish was with gentoo penguins (21% dietary overlap) and southern elephant seals (19%). These overlaps in diet were small relative to those among fur seals (3 species, ≥90%), giant petrels (84%), royal and rockhopper penguins (65%), and king and royal penguins and fur seals (>60%). The total annual prey biomass consumed by seabirds, seals, toothfish and the fishery within the MI-EEZ was estimated to be 419 774 t, with the greatest consumption in January, at 2779 t d^{-1}. Pelagic fish (61%, mostly myctophids), followed by pelagic crustaceans (28%, mostly euphausids) and cephalopods (7%) were the major prey. Most prey biomass was consumed by penguins (88%), with comparatively small amounts by toothfish (8%), seals (3%) other seabirds (<1%) and the fishery (0.1%). These results indicate weak trophic linkages between the toothfish, its fishery, and seabirds and seals around Macquarie Island.

KEY WORDS: Patagonian toothfish · Seabirds · Seals · Dietary overlap · Trophic interactions · Prey consumption · Commercial fisheries · Macquarie Island

INTRODUCTION

With major decreases in many of the world′s fish stocks over the last few decades, and the concomitant development of more intensive fishing methods, there has been increased interest in the extent of competition for fish stocks between commercial fisheries and seabirds and marine mammals. Early investigations into this competition were aimed at assessing the extent to which seals and seabirds consumed fishes that could have potentially provided economic benefit to commercial fisheries (Davies 1958, Matthews 1961, Furness & Cooper 1982, Furness 1984). Many of these studies suggested that some seal and seabird populations consumed large quantities of commercially important fish species, and such information has been used to justify reductions in seal and seabird numbers (Davies 1958, Butterworth et al. 1988). More recently,

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with greater efforts to manage fisheries under the principles of Ecological Sustainable Development (ESD), the focus of studies has changed to examine how commercial fishing may effect the conservation status of seabird and marine mammal populations. Some research has suggested that commercial fisheries may be significant competitors with seabirds and marine mammals (Furness & Cooper 1982, Duffy 1983, Hammill et al. 1997, Stenson et al. 1997, Trites et al. 1997), and, in cases of overfishing, cause major decreases in their populations (Anderson & Gress 1984, Burger & Cooper 1984).

The recent rapid expansion of the Patagonian toothfish *Dissostichus eleginoides* (hereafter toothfish) commercial fishery in the Southern Ocean, has raised concerns over the sustainability of the fishery. In addition, the ecological consequences of overfishing, especially on populations of seabirds and marine mammals, is unclear. The dependence of sea birds and marine mammal populations (primarily seals) on marine resources in Southern Ocean and Antarctic waters has been assessed by a number of studies, and some have also estimated the potential competition and impacts that commercial fisheries (mostly for Antarctic krill *Euphausia superba*) may have on their populations (Croxall & Prince 1982, Croxall et al. 1984, 1985, Abrams 1985, Hunt 1985, Brown 1989, Woehler & Green 1992, Adams et al. 1993, Guinet et al. 1996, Ichii et al. 1996, Croll & Tershy 1998, Green et al. 1998, Moore et al. 1998). Studies investigating the consumption of marine resources by seals and seabirds in the South Atlantic Ocean have generally shown the importance of Antarctic krill in these food webs (Croxall & Prince 1982, Croxall et al. 1984, 1985, Croll & Tershy 1998). However, in subantarctic regions of the South Indian and Pacific Oceans, fishes appear to be more important prey than pelagic crustaceans, as such commercial finfisheries (e.g. toothfish, marbled rockcod *Notothenia rossii* and mackerel icefish *Champsocephalus gunnari*) may place seabirds and seals at greater risk of competition for foods (Woehler & Green 1992, Adams et al. 1993, Guinet et al. 1996, Green et al. 1998, Moore et al. 1998).

At Macquarie Island (54° 30′ S, 158° 55′ E) in the South Pacific Ocean, a commercial fishery for toothfish was developed in 1994, and was the first commercial fishery for the region. Current management of the fishery by the Australian Fisheries Management Agency restricts fishing to trawling and to one single vessel in total. Other licensing conditions include the carriage of 2 observers on each fishing voyage to collect scientific data on the fishery, and to monitor environmental impacts. The discharge of factory waste that may attract and provision birds and seals is also prohibited. The fishing season extends from 1 September to 31

August, with most fishing occurring between October and February. To date there has been no illegal or unreported fishing around the island. The average annual catch of toothfish between 1996/97 and 1998/99 was 550 t.

Macquarie Island is an important breeding site for large numbers of land-breeding marine predators, including 86 000 seals and over 3 million seabirds, most of which are penguins. In line with development and management of the fishery under the principles of ESD, it is essential to understand the potential interactions among the fishery, the toothfish population, and other marine predators such as seabirds and seals. This study aims to examine the trophic interactions based on the diet composition and relative consumption rates between the fishery, toothfish, seabirds and seals around Macquarie Island. Dietary overlaps among predators were estimated and used to assess potential food competition among predators. Annual consumption rates on all prey by these predators were also estimated and compared. These estimates will provide useful information for assessing the relative importance of toothfish in the Macquarie Island ecosystem, and can be used to assess potential interactions between the toothfish fishery and other marine predators.

METHODS

Area and species in study. Macquarie Island is a small (12 785 ha) subantarctic island approximately 1500 km south-east of Tasmania, Australia (Fig. 1). The Macquarie Island Exclusive Economic Zone (MI-EEZ) extends from 3 to 200 nautical miles (5.6 to 370 km) from the island. The north-eastern edge of the MI-EEZ is slightly less than 370 km, where it joins the Campbell and Auckland Islands EEZ (New Zealand, Fig.1). The area of ocean within the MI-EEZ is approximately 415 600 km^2. Only those species that undertake a significant portion of their foraging within the MI-EEZ, or have substantial biomass, were included in this study. These include the king *Apenodytes patagonicus*, royal *Eudyptes schlegeli*, and rockhopper *E. chrysocome* penguins, southern elephant seal *Mirounga leonina* and Antarctic *Arctocephalus gazella* and New Zealand *A. forsteri* fur seal, black-browed albatross *Diomedea melanophrys*, northern *Macronectes halli* and southern *M. giganteus* giant petrel and Antarctic prion *Pachyptila desolata*, which are present in the vicinity of the island during the breeding and moulting periods. Gentoo penguins *Pygoscelis papua* and Macquarie shags *Phalacrocorax purpurascens*, are resident year-round, while the subantarctic fur seal *A. tropicalis* is present on the island from December to October. Toothfish were also assumed to be resident.
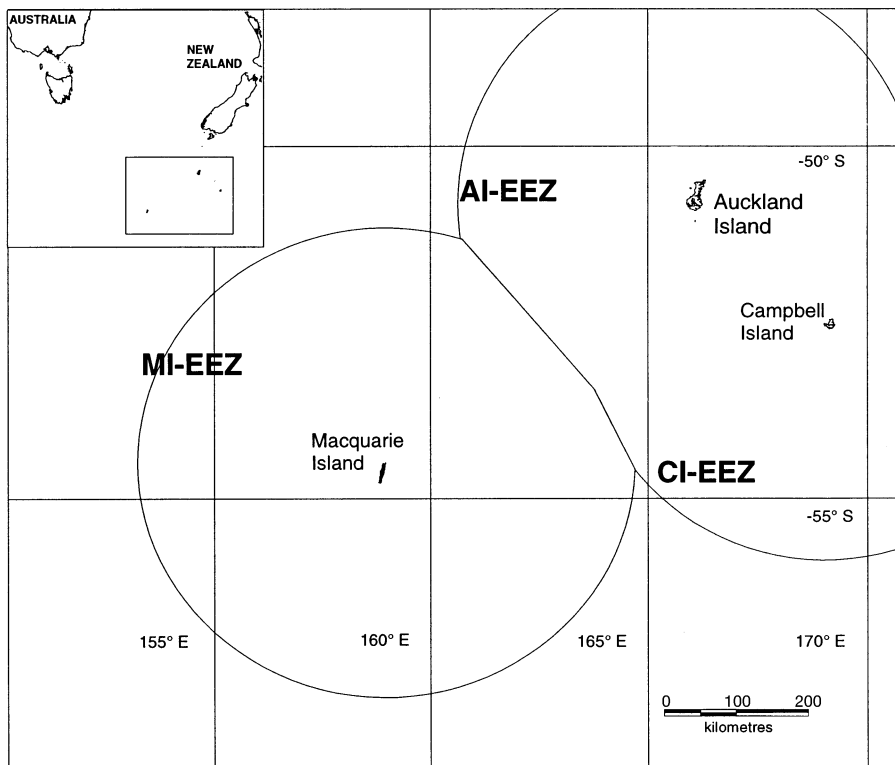
Fig. 1. Location of Macquarie Island and the Macquarie Island Exclusive Economic Zone (MI-EEZ) relative to Campbell (CI) and Auckland (AI) Islands' EEZs

Species, such as several of the small and large petrels that mostly forage outside the MI-EEZ (sooty shearwaters *Puffinus griseus*; white-headed petrel *Pterodroma lessonii*; blue petrel *Halobaena caerulea*; light-mantled sooty albatross *Phoebetria palpebrata*; grey-headed albatross *Diomedea chrysostoma*; and wandering albatross *D. exulans*), other seabirds with very low abundance and biomass (fairy prion *Pachyptila turtur*; common diving petrel *Pelecanoides urinatrix*; South Georgian diving petrel *P. georgicus*; and Wilson's storm petrel *Oceanites oceanicus*), and species that feed mostly along the shoreline and inland (Antarctic terns *Sterna vittata*; kelp gulls *Larus dominicanus*; and subantarctic skua *Catharacta lonnbergi*), were omitted from the study. Because of paucity of data, cetaceans were also excluded.

Population and biomass estimates. The population and biomass estimates of seabirds and seals at Macquarie Island used in this study are presented in Table 1. Population estimates for the southern elephant seal at Macquarie Island were based on an estimated annual pup production of 20 000 (D. Slip, Environment Australia, pers. comm.) and age-specific survival-rate data from Heard Island and South Georgia (McCann 1985, Slip 1997). The biomass of each age class was estimated from the product of the number of individuals in an age class and their mean mass (Slip 1997). For fur seals, population and biomass estimates were based on

pup production and mass data (Goldsworthy et al. 1998, Goldsworthy unpubl. data), and hypothetical age-specific survival rates based on Antarctic and northern *Callorhinus ursinus* fur seal populations (York 1987, Boyd et al. 1995).

For king penguins, population estimates were based on data from D. E. Rounsevell (unpubl. data in Scott 1994) extrapolated through to 1999 based on annual increases in chick production of 5 to 15%, the probable range of population growth based on other populations (E. J. Woehler pers. comm.). A mean growth rate of 10% yr^{-1} was used to calculate the population estimate in this study. Adult population size (individuals) was estimated by multiplying chick production by 3 (i.e. adult population = chick production × 2 [adults] × 1.5 [average of 2 chicks per 3 yr]). For royal, rockhopper, and gentoo penguins, population estimates were based on Warham (1963), Rounsevell & Brothers (1984), Copson & Rounsevell (1987), G. R. Copson (in Scott 1994), and Robinson & Hindell (1996). Biomass estimates for penguins were calculated by multiplying population size by average adult masses (Barrat 1976, Reilly & Kerle 1981, Green & Gales 1990, Hull 1997).

Estimates of the population size of black-browed albatrosses, southern and northern giant petrels and Antarctic prions were derived from Johnstone (1977), Brothers (1984) and Robinson & Scott (1999). Average mass data for these species were obtained from

Table 1. Population and biomass estimates, mean individual mass, metabolic rates and estimated annual days and energy used for 13 marine predators in the Macquarie Island EEZ. Sources of data and estimates are given in second subsection of 'Methods'. M: male; F: female; Juv: juvenile; AM: adult male; SAM: sub-adult males; FMR: field metabolic rate; ME: metabolic energy; ER: energy requirements; ind.: individual; –: no data

	Estimated population range	Population esitimate used (ind.)	Estimated biomass (t)	Sex age class	Mean ind mass (kg)	FMR sea (kJ d^{-1})	FMR shore (kJ d^{-1})	Days in EEZ	ME	Annual ER from EEZ (MJ)
Southern elephant seal	20 000[a]	86 150	39 283					14		809
Antarctic fur seal	106[a]	457	15	M	140.0	76 689	59 996	75	0.74	5949
				F	33.8	33 411	14 483	134	0.74	3847
				SAM	65.0	35 605	27 855	90	0.74	3266
				Juv	16.0	8810	6892	90	0.74	808
Subantarctic fur seal	30[a]	129	4	M	140.0	76 689	59 996	75	0.74	5949
				F	33.8	33 411	14 483	319	0.74	9066
				SAM	65.0	35 605	27 855	90	0.74	3266
				Juv	16.0	8810	6892	90	0.74	808
New Zealand fur seal	2–3000[b]	2500	150	AM-Juv	60.0	32 867	25 713	49	0.74	1634
King penguin	131 863–299 019[c]	323 162	3926	M	12.8	7860	3499	237	0.74	1816
				F	11.5	7275	3256	247	0.74	1704
Royal penguin	850 000[c]	1 700 000	9435	M	5.7	4035	1883	216	0.74	776
				F	5.4	4035	1883	214	0.74	776
Rockhopper penguin	100 000–500 000[c]	600 000	2190	M	3.6	2843	1360	199	0.74	437
				F	3.7	2843	1360	208	0.74	458
Gentoo penguin	4700–6800[c]	11 500	66	Breeding	5.7	4383	2033	150	0.74	574
				Winter	5.7	4383	2033	215	0.74	804
Black-browed albatross	180[c]	360	1	Adults	3.7	2500	945	225	0.69	490
Northern giant petrel	1000[c]	2000	4	M	4.8	2919	1141	180	0.69	472
				F	3.6	2469	931	180	0.69	403
Southern giant petrel	4000[c]	8000	19	M	5.1	3040	1199	280	0.69	757
				F	4.2	2714	1044	280	0.69	679
Antarctic prion	48 900[c]	97 800	7188	Adults	0.15	393	99	156	0.69	52
Macquarie shag	768[c]	1536	2	M	3.6	2905	1367	365	0.69	950
				F	2.6	2366	1113	365	0.69	773
Toothfish	–	–	62 473	–	–	–	–	–	–	–

[a]Annual pup production; [b]total animals; [c]breeding pairs

Johnstone (1977), Voisin & Bester (1981), Weimers-kirch et al. (1986, 1989), and Marchant & Higgins (1990). Population and mass data on the Macquarie shag were derived from Brothers (1985) and Brothers (unpubl. data, in Scott 1994). The biomass of tooth-fish was based on estimates of the available abundance in mid-1995 (1 yr after the commencement of the fishery). The biomass of toothfish available to the fishery was estimated to be 62 474 (95% CI 17 146 to 1 002 728) t (Tuck et al. 1999). For the purpose of this study, where a range of estimates for the population size of species was available, the mid-point of such estimates were used to calculate their energy and food requirements (Table 1).

Diet data sources and prey grouping. Data on the diets of seals and seabirds were obtained from published and unpublished sources, and are summarised in Table 2. With the exception of the Antarctic prion and the species composition of the diet of black-browed albatrosses (although percentage biomass of main prey groups were derived from Macquarie Is-

land), all diet information used in this study came from samples collected at Macquarie Island (Table 2). Dietary composition of all predators was expressed as percentage of wet prey mass. In cases where data were expressed by the numerical abundance of prey, they were converted to mass by multiplying the number of prey items by the estimated mass of the prey items consumed. Data on the composition of the commercial catch at Macquarie Island was based on the mean annual catch of toothfish and bycatch species over a 3 yr period (1996/97 to 1998/99) (Williams unpubl. data). Only major fish and invertebrate bycatch species were included. Corals and sponges were excluded.

Prey species were summarised into 35 groups based mostly on the lowest taxonomic level that could be identified from stomach or faecal data. For many diet studies the lowest taxonomic grouping of fish prey was to the family level (with the exception of toothfish), whereas for cephalopod prey this was generally to the genus level. However, where more detailed identification of fish prey to species level was available, this was

Table 2. Details on the sources of diet information used in this study, and the type, number and timing when samples were collected. The form in which prey composition data were available (FM: frequency by mass; FN: frequency by number; FO: frequency of occurrence), and how data were converted to FM where needed, are also presented

Species	Type of diet samples	No. and location	Year	Month	Data form	Source
Southern elephant seal	Stomach contents from killed and stomach flushed seals	71-MI	1978–85 1987–88 1989–90	Spring & summer	FM-squid FN-fish[a,b]	Green & Burton (1993)
Antarctic fur seal, subantarctic fur seal	Faecal	138-MI	1990–91	Dec-Mar	FN-fish, FO-squid[a,c]	Goldsworthy et al. (1997); Goldsworthy (unpubl. data)
New Zealand fur seal	Faecal	371-MI	1988–89	Nov-Mar	FN-fish FO-squid, birds[a,d]	Green et al. (1990)
King penguin	Stomach contents	144-MI	1984–85	Nov-Nov	FM	Hindell (1988a)
Royal penguin	Stomach contents Stomach contents	258-MI 304-MI	1984–85 1993–96	Nov-Feb Nov-Feb	FM FM	Hindell (1988c) Hull (1997, 1999b)
Rockhopper penguin	Stomach contents Stomach contents	104-MI 236-MI	1984–85 1984–85	Nov-Feb Dec-Feb	FM FM	Hindell (1988b) Hull (1997, 1999b)
Gentoo penguin	Stomach contents Stomach contents	98-MI 82-MI	1985 1993–94	Apr-Nov Oct-Jan	FM FM	Hindell (1989) Robinson & Hindell (1996)
Black-browed albatross	Regurgitations	Unknown-MI	1997–99	Spring-autumn	FM[e]	A. Terauds (pers. comm.)
Northern giant petrel	Regurgitations	341-MI	1969–70 1970–71	Spring-autumn	FO[f]	Johnstone (1977)
Southern giant petrel	Regurgitations	310-MI	1969–70 1970–71	Spring-autumn	FO[f]	Johnstone (1977)
Antarctic prion	Regurgitations	90-South Georgia	1974–75	Dec-Mar	FM	Prince (1980b) Reid et al. (1997)
Macquarie shag	Regurgitations	77-MI	1975–79	Dec-Feb	FM	Kato et al. (1996)
Toothfish	Stomach contents	1423-MI	1995–99	Nov-Mar	FM	Goldsworthy et al. (2001)
Fishery	Commercial hauls	839 hauls	1996/97– 1998/99	Nov-Feb	FM[g]	Williams et al. (unpubl data)

[a] Fish taxa numerical abundance (based on the presence as otoliths) converted to relative biomass using estimates of prey mass
[b] Biomass contribution of cephalopods (55%) and fish (45%) at Macquarie Island based on the estimate by Slip (1997) for Heard Island southern elephant seals
[c] Estimated biomass contribution of fishes (95%) and cephalopods (5%) (Goldsworthy unpubl. data)
[d] Estimated biomass contribution of fishes (85%), cephalopods (5%) and birds (10%) (Goldsworthy unpubl. data)
[e] Estimates of fishes (15%), cephalopods (65%), crustacean, (5%) and carrion (15%) biomass in the diet from A. Terauds (pers. comm.). Cephalopod prey species and their relative contribution based on data from Iles Kerguelen (Cherel & Weimerskirch 1995). Fish component in the diet based on Prince 1980a)
[f] Study used to determine prey composition. Mass contribution of prey items estimated using prey biomass data in Hunter (1983)
[g] Excluding corals and sponges

used (e.g. for fur seals, penguins and the fishery). Diet composition was also summarised into 6 main ecological prey categories: pelagic fishes (Myctophidae, Bathylagidae, Paralepididae), demersal fishes (Nototheniidae, Harpagiferidae, Congiopodidae, Moridae, Macrouridae, Bothidae, Squalidae), cephalopods, pelagic crustaceans (euphausids, amphipods, copepods, and ostracods) and demersal crustaceans (prawns and crabs) and birds/carrion.

Diet overlaps. Diet overlaps between predators were examined using 2 methods. First, an overlap index was used to calculate diet similarities between 2 predators

(i and j). This index, termed percentage similarity index (%PSI), was modified from Schoener (1970):

$$\%\text{PSI}_{ij} = 100 \times \left(1.0 - 0.5\sum_{h=1}^{s}|P_{hi} - P_{hj}|\right) \qquad (1)$$

where P_{hi} is the proportion by mass of prey category h in predator i; P_{hj} the proportion by mass of prey category h in predator j, and s is the number of prey categories. This method produces a similarity matrix for all predator pairs being compared.

The second method applied a hierarchical cluster analysis to diet data in order to classify predator species

into distinct trophic guilds. The Bray-Curtis dissimilarity coefficients were used along with the average linkage clustering algorithm using the software package PRIMER (Plymouth Marine Laboratory, UK). Significant trophic guilds were determined following the methods of Jaksic & Medel (1990).

Energy requirements and food-consumption estimates. The approach in this study was to estimate the daily energy requirements of individuals of each species while in the MI-EEZ based on estimates of activity and field metabolic rate (FMR). Daily energy requirements were then converted to food requirements by first transforming diet data (expressed as proportion of biomass) to proportions of total energy intake using estimates of the energy density of various prey taxa consumed (Table 3). Daily food requirements were then calculated as the sum of the product of the daily energy requirements and prey energy frequencies. The total annual energy requirements and consumption were then estimated by multiplying the daily estimates by total days that animals were estimated to be within the MI-EEZ.

For a particular seabird or fur seal species i, the energy requirements e (kJ) on Day k for animals of a given age-class and/or gender were estimated using the following equation, modified from Croll & Tershy (1998) (see Table 1):

$$e_i^k = \frac{(F_a P_a) + (F_r P_r)}{M} \tag{2}$$

where F_a is the field metabolic rate (kJ) of animals at sea (active) and F_r is the metabolic rate when animals are ashore (resting). The proportion of time spent at sea and on-shore on any given day are given by P_a and P_r, respectively, M is the metabolic energy (assimilation efficiency), assumed to be 0.69 for petrels (Jackson 1986), and 0.74 for other species (Davis et al. 1989) (present Table 1). Metabolic rate (F) values for fur seals were based on those determined for Antarctic fur seals at South Georgia (Costa et al. 1989). The active and resting metabolic rates for penguin and petrels were estimated from regression equations in Green & Gales (1990) and Warham (1996), respectively. The metabolic rate for the Macquarie shag (Table 1) was estimated from allometric equations (Koteja 1991).

The total number of days spent within the MI-EEZ by each species, and the proportion of time spent at sea and on shore during the various stages of the courting,

Table 3. Mean energy content (MJ kg^{-1} wet mass), available standard deviations (SD), and numbers of samples (n) of 16 prey taxa groups used in the analysis

Prey taxon	Energy Content (MJ kg^{-1})	SD	(n)	Source
Fishes				
Bathylagus antarcticus	3.93	1.17	(18)	M. Tierny (unpubl. data)
Protomyctophum spp.[a]	7.54	2.97	(42)	M. Tierny (unpubl. data)
Krefftichthys anderssoni	8.36	0.92	(18)	M. Tierny (unpubl. data)
Electrona antarctica	8.77	2.40	(20)	M. Tierny (unpubl. data)
E. carlsbergi	5.37	1.65	(6)	M. Tierny (unpubl. data)
E. subaspera	7.42	0.59	(6)	M. Tierny (unpubl. data)
Gymnoscopelus spp.[b]	9.05	2.79	(42)	M. Tierny (unpubl. data)
Antimora rostrata (Moridae)	1.26	0.11	(2)	M. Tierny (unpubl. data)
Lepidonotothen squamifrons	5.00			G. Robinson (unpubl. data)
Cephalopods				
Todarodes sp.	4.01		(2)	Clarke et al. (1985)
Moroteuthis sp.	1.84		(1)	Clarke et al. (1985)
Gonatus sp.	3.78		(4)	Clarke et al. (1985)
Histioteuthis sp.	2.65		(5)	Clarke et al. (1985)
Mastigoteuthis sp.	1.82		(3)	Clarke et al. (1985)
Crustaceans	4.68		(–)	Brown (1987)

[a]Includes 12 *P. andriashevi*, 18 *P. bolini*, 6 *P. parellelum*, 6 *P. tenisoni*
[b]Includes 18. *G. fraseri*, 18 *G. braueri*, 6 *G. microlampas*

incubation, brooding, chick feeding, lactation and moulting periods were estimated from accounts of the species annual cycle, breeding and attendance patterns (Brothers 1985, Weimerskirch et al. 1986, 1992, Davis et al. 1989, Marchant & Higgins 1990 and references therein, Hull 1997, Slip 1997 and pers. comm., Goldsworthy 1999 and unpubl. data). For royal, rock-hopper and king penguins undergoing long incubation and pre-moulting foraging trips, most of the foraging was estimated to occur outside of the MI-EEZ (Hull et al. 1977, Hull 1999a, B. Wienecke pers. comm.). As such, the only foraging time included was that estimated to occur from the island to the edge of the MI-EEZ on leaving the island, and from the edge of the EEZ when returning to the island. Penguins were estimated to travel at an average horizontal speed of 3.6 km h^{-1}, and to take about 4.3 d to travel 370 km, assuming continuous swimming at that speed.

Average activity and attendance patterns relative to the mean laying or pupping dates, were used to estimate the daily activity (proportion of time ashore and at sea) of seabird pairs or lactating seals, respectively. However, as not all pairs or animals lay or pup on the same day, data on the timing and spread (standard deviation) of laying and pupping dates were used to calculate a normal distribution around their means. From these, the proportion of pairs or animals undertaking activities on the days either side of the means were calculated in order to provide a more realistic representation of the daily-energy expenditure and

consumption patterns among populations of seabirds and seals.

The total annual energy requirements of predator i (E_i) was thus estimated as,

$$E_i = \sum_{k=1}^{d} \sum_{\substack{age \\ class}} \sum_{sex} e_i^k \qquad (3)$$

where d is the number of days spent in the MI-EEZ each year by predator i.

The daily consumption c_{ij}^k (tonnes), of prey species j by predator i was estimated as

$$c_{ij}^k = e_i^k \frac{f_{ij}}{\sum\limits_{j=1}^{s} f_{ij} d_j} \qquad (4)$$

where f_{ij} is the proportion by mass of prey species j in the diet of predator i, d_j is the energy density (kJ kg^{-1}) of prey species j, and s is total number of prey taxa consumed. The total annual food consumption by predator i, C_i, was calculated as

$$C_i = \sum_{k=1}^{d} \sum_{j=1}^{s} c_{ij}^k \qquad (5)$$

For seabirds, published estimates of the energy requirement or total mass provisioned to chicks by adults were used to calculate the total amount of food fed to chicks from hatching to fledging. For penguins this was estimated to be 119.0, 25.6, 18.0 and 43.8 kg prey mass from hatching to fledging per chick for king, royal, rockhopper and gentoo penguins, respectively (Green & Gales 1990, Moore et al. 1998). For the Antarctic prion this was 0.49 kg per chick (Prince 1980b).

Estimates of the annual energy requirements of southern elephant seals within the MI-EEZ were based on estimates for elephant seals breeding at Heard Island (17 200 MJ seal^{-1} yr^{-1}: Slip 1997). The annual energy requirements for southern elephant seals at Macquarie Island (E'_{es}) was estimated as follows:

$$E'_{es} = E_{es} N_{es} \frac{D_{es}}{365} \qquad (6)$$

where N_{es} is the estimated population size at Macquarie Island, E_{es} is the average annual energy requirements of an elephant seal (17 200 MJ) and D_{es} is the number of days spent by elephant seals in the MI-EEZ waters annually (excluding time hauled out on land).

Satellite and geolocation tracking of approximately 100 elephant seals (juveniles, adult females and males) from Macquarie Island has shown a similar pattern of seals traveling directly to and from the island from foraging grounds that are generally located well outside the MI-EEZ (Slip et al. 1994, Hindell et al. 1999, Bradshaw et al. 2001, J. van den Hoff pers. comm). As such, the only foraging time within the MI-EEZ was assumed to occur when seals were traveling to or from the island. For southern elephant seals, this occurs twice per year, once during the winter for juveniles or during the breeding season for adults, and once for moulting (all seals). Transit times across the MI-EEZ were based on satellite tracking data from 7 transits of 5 yr-old male elephant seals, which traveled on average 4.3 km h^{-1} (SD = 1.2) (J. van den Hoff unpubl. data). Assuming such horizontal swimming speeds, elephant seals were estimated to travel the 370 km to the edge of the EEZ in 3.6 d (2.8 to 4.9) and hence spend a total of 14.4 (11.2 to 19.6) days in the MI-EEZ each year (Table 1).

The 2 annual haul-outs of southern elephant seals are very predictable in their timing, and for each age and sex-class (yearlings, 2 to 3 yr-olds, sub-adults, breeding males and breeding females) can be described by normal curves (Hindell & Burton 1988, Slip 1997). The date of maximum haul-out for the moulting and non-moulting haul-out for the various age and sex-classes, and the standard deviation of these (Slip 1997) were used to estimate the number of seals from each gender and age-class in the MI-EEZ on any given day of the year. Total annual food consumption for southern elephants seals was calculated using Eqs (4) & (5), the ratio of annual consumption per total biomass of the population was used to estimate the annual consumption per age and sex class, and from these the daily food consumption of these classes was calculated throughout the course of a year within the MI-EEZ.

The food consumption of toothfish was estimated using the multiple regression equation developed by Palomares & Pauly (1989) to estimate the consumption per biomass (Q/B) of marine fish populations:

$$\ln Q/B = -0.1775 - 0.2018 \ln W_\infty + 0.6121 \ln T \\ + 0.5156 \ln A + 1.26 F \qquad (7)$$

where Q/B is the daily food consumption by a fish population as a percentage of its biomass, W_∞ is the mean asymptotic mass (g) of the fish, T is the mean habitat temperature (°C), A is the aspect ratio of the caudal fin of the fish species (as a measure of the average activity/and or metabolic rate of the fish), and F is the food type (0 in carnivores, 1 in herbivores). The aspect ratio ($A = h^2/s$) of the caudal fin is estimated using measurements of its height (h) and surface area (s). W_∞ was estimated to be 139 328 g, the water temperature at 400 m depth at Macquarie Island is approximately 2.5°C (unpubl. CTD data: CSIRO Marine Research), and A was estimated to be 1.09. The total annual food consumption, C_t, of the toothfish population in the MI-EEZ was estimated as:

$$C_t = 365 \bar{B}(Q/B) \qquad (8)$$

where $\bar{B}$ is the estimated biomass of the toothfish population. Consumption by toothfish on each prey taxon (j) was calculated by determining:

$$C_{tj} = f_j C_t \tag{9}$$

Sensitivity analysis. A single parameter analysis of sensitivity was undertaken to evaluate the relative importance of input parameters to estimates of annual relative consumption. Parameters examined include population size and metabolic rate, as other parameters such as residence times and predation rates would show the same response as adjusting population size. Each parameter was separately varied by ±10% for the 5 major predators (royal, king, rockhopper penguins, elephant seals and toothfish) and consumption for each prey species were recalculated. The percentage sensitivity ($S_{p,i}$) from the base model for parameter p and predators i was then calculated:

$$S_{p,i} = \frac{100(RC'_{p,i} - RC_{p,i})}{RC_{p,i}} \tag{10}$$

where $RC'_{p,i}$ is the recalculated relative consumption by predator i, with parameter p being varied by 10%, and $RC_{p,i}$ is relative consumption from the base model. Sensitivities ($S_{p,i}$) > 10% indicate high sensitivities, while $S_{p,i}$ < 10% indicate low sensitivity. For example, an $S_{p,i}$ = 5% means that a 10% change of input parameter p for predator i resulted in increasing the base model estimate of consumption for predator i by 5%.

RESULTS

Diet composition

The diet composition of the seals, seabirds, toothfish and the fishery around Macquarie Island, are presented in Tables 4 (35 prey groups), 5 (ecological prey groups) & 6 (to genus and species level for penguins, fur seals and fishery). Pelagic fish (mostly myctophids), were the primary prey (>50%) of fur seals, king, and royal penguins, while demersal fish (mostly notothenids were important in the diets of the Macquarie shag, gentoo penguin and toothfish. Other important fish genera were Bathylagidae (20% by mass in the diet of toothfish) and Harpagiferidae (15% by mass in the diet of Macquarie shags). Squid were a major component of the diets of southern elephant seals and black-browed albatrosses, and accounted for 32% of the diets in toothfish (Table 4). Squid accounted for 24% of the diet of northern giant petrels, 14% of the diet of gentoo penguins, and 11% of the diets of southern giant petrels, and were a minor component (<5%) for all other species examined. Although

Moroteuthis (Onychoteuthidae) was the most widely consumed squid genus (10 of 14 species), it only accounted for ≤8% of the diet in all the predatory species. Three genera of squid were dominant as prey species, *Kondakovia* in elephant seals (23%), and *Todarodes* (39%) and *Martialia* (27%) (family Ommastrephidae) in black-browed albatrosses. *Gonatus* (19%) (family Gonatidae) was the main squid genus taken by toothfish. All predators, with the exception of the Macquarie shag, consumed some squid (i.e. >2%).

Pelagic crustaceans (mostly euphausids and copepods) were the main prey for Antarctic prions and rockhopper penguins (>70%), and were also important in the diet of royal penguins (37%). Demersal crustaceans (mostly prawns) accounted for 10% of the diet in toothfish. Carrion (mostly birds) accounted for most of the diet of northern (72%) and southern giant petrels (84%), and at sea, carrion accounted for 15% of the diet of black-browed albatrosses. About 10% of the diets of New Zealand fur seals were live birds, mostly *Eudyptes* spp. penguins.

Dietary overlap

The highest level of dietary overlap was among the 3 fur seal species (≥89%) and between fur seals and king penguins (≥87%) (Table 7). There were also high levels (>60%) of dietary overlap between royal and rockhopper penguins and between royal and king penguins (Table 7). Other major diet overlaps were between rockhopper penguins and Antarctic prions (>60%), and between northern and southern giant petrels (both >80%). The levels of dietary overlap among other species were generally below 45% (Table 7). There was little dietary overlap between toothfish and other species, the greatest being with the gentoo penguin (22%) and southern elephant seal (19%) (Table 7). There was little dietary overlap with the commercial fishery, the greatest being with its target species, toothfish (4%). Other than the commercial fishery, the only other predator that preyed on toothfish was the gentoo penguin; however, its occurrence in the diet was very low (0.1%) (Table 4).

Indices of dietary overlap were highly sensitive to the taxonomic resolution of prey species groups. For example, when mytophid fishes, a principal component of the diet of several seals and penguins (Table 4), were subdivided to genus or species level (Table 6), diet overlap between Antarctic fur seals and king penguins decreased from 95 to 4.1% (Table 8). This was because although both predators consumed myctophids, the Antarctic fur seal consumed mostly *Electrona subaspera*, while king penguins consumed *E. carlsbergi* and *Krefftichthys anderssoni* (Table 6). Sim-

Table 4. Percentages of prey biomass for 35 prey groups in the diets of 14 marine predators and the fishery in the Macquarie Island EEZ. The 35 prey groups are further aggregated into 4 major groups: fishes, cephalopods, crustaceans, and birds/carrion (bottom of table)

Prey groups	Southern elephant seal	Antarctic fur seal	Subantarctic fur seal	New Zealand fur seal	King penguin	Royal penguin	Rockhopper penguin	Gentoo penguin	Black-browed albatross	Northern giant petrel	Southern giant petrel	Antarctic prion	Macquarie shag	Toothfish	Fishery
Fishes															
Myctophids	37.3	95.0	95.0	84.9	92.7	59.0	27.2	40.7	0	0	0	1.8	0	4.5	0
Bathylagus antarcticus	7.7	0	0	0	0	0	0	0	0	0	0	0	0	19.5	0
Nototheniids	0	0	0	0.1	0	0	0	2.6	15.0	2.0	1.0	0	85.1	12.1	0.1
Dissostichus eleginoides	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	96.4
Harpagiferidae	0	0	0	0	0	0	0	0.3	0	0	0	0	14.9	0	0
Congiopodidae	0	0	0	0	0	0	0	9.0	0	0	0	0	0	0	0
Moridae	0	0	0	0	0	0	0	0	0	0	0	0	0	6.7	0.5
Macrouridae	0	0	0	0	0	0	0	0	0	0	0	0	0	10.6	2.7
Paralepididae	0	0	0	0	5.0	0	0	0.2	0	0	0	0	0	0	0
Bothidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
Shark	0	0	0	0	0	0	0	0	0	0	0	0	0	4.2	0
Cephalopods															
Alluroteuthis sp.	4.4	0	0	0	0	0	0	0	0	0	0	0.6	0	0	0
Brachioteuthis sp.	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiroteuthis sp.	0.2	0	0	0	0	0	0	0	0	0.8	0	0	0	1.9	0
Cirroteuthis sp.	0	1.3	1.3	1.3	0	0	0	0	0	0	0	0	0	0.8	0
Galiteuthis sp.	0.3	0	0	0	0	0	0	0	0	3.2	3.0	0	0	0.6	0
Gonatus antarcticus	0.5	0	0	0	0	0	0	0	0	1.2	0	0	0	19.0	0
Histioteuthis sp.	8.2	0	0	0	0	0	0	0	0	2.0	0	0	0	1.0	0
Kondakovia longimana	23.4	0	0	0	0	0.2	0	0	0	0	2.0	0	0	0	0
Martialia sp.	1.4	0	0	0	0.1	0.2	0.1	6.3	26.5	15.2	6.0	0	0	0	0
Mastigoteuthis sp.	0	0	0	0	0	0	0	0	0	0.4	0	0	0	2.2	0
Moroteuthis sp.	5.6	3.8	3.8	3.8	2.1	3.4	2.2	7.9	0	0.8	0	0	0	5.0	0
Octopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0.8	0
Taonius sp.	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0.2	0
Todarodes sp.	10.9	0	0	0	0	0.1	0	0	38.5	0	0	0	0	0	0
Vampryoteuthis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crustaceans															
Euphausids	0	0	0	0	0	31.9	67.0	0	0	0	0	57.6	0	0	0
Prawns	0	0	0	0	0	0	0	0	0	0	0	0	0	9.3	0
Crabs	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	0.3
Amphipods	0	0	0	0	0	5.2	3.4	0	0	0	0	8.1	0	0	0
Ostracods	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Copepods	0	0	0	0	0	0	0	0	0	0	0	31.9	0	0	0
Others	0	0	0	0	0	0	0	0	5.0	2.0	4.0	0	0	0	0
Birds	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
Carrion	0	0	0	0	0	0	0	0	15.0	72.0	84.0	0	0	0	0
Fishes	45.0	95.0	95.0	85.0	97.8	59.0	27.2	85.9	15.0	2.0	1.0	1.8	100	58.1	99.7
Cephalopods	55.0	5.0	5.0	5.0	2.2	3.9	2.4	14.1	65.0	24.0	11.0	0.6	0	31.6	0
Crustaceans	0	0	0	0	0	37.1	70.3	0	5.0	2.0	4.0	97.6	0	10.3	0.3
Birds/carrion	0	0	0	10	0	0	0	0	15.0	72.0	84.0	0	0	0	0

ilarly, the overlap in diets of Antarctic fur seals with royal, rockhopper and gentoo penguins decreased from 63 to 7, 30 to 5 and 21 to 8%, respectively, when prey were grouped to genus or species levels (Table 8).

Cluster-analysis illustrated that, based on the 35 prey groups, the 14 marine predators and the fishery could be grouped into 7 significantly different trophic guilds (Fig. 2). These comprised: (1) a single-species guild containing the black-browed albatross, (2) a guild containing the giant petrels, (3) a large guild containing the fur seals, king penguin, gentoo penguin and southern elephant seal, (4) a guild including the royal and rockhopper penguin and Antarctic prion,

Table 5. Percentages of prey biomass combined into 6 ecological prey groups, in the diets of 14 marine predators and the fishery in the Macquarie Island EEZ

Prey group	Southern elephant seal	Antarctic fur seal	Subantarctic fur seal	New Zealand fur seal	King penguin	Royal penguin	Rockhopper penguin	Gentoo penguin	Black-browed albatross	Northern giant petrel	Southern giant petrel	Antarctic prion	Macquarie shag	Toothfish	Fishery
Pelagic fishes	45.0	95.0	95.0	84.9	97.8	59.0	27.2	40.8	0.0	0.0	0.0	1.8	0.0	24.0	0.0
Demersal fishes	0	0	0	0.1	0	0	0	45.0	15.0	2.0	1.0	0	100	34.2	99.7
Cephalopods	55.0	5.0	5.0	5.0	2.2	3.9	2.4	14.1	65.0	24.0	11.0	0.6	0	31.6	0
Pelagic crustaceans	0	0	0	0	0	37.1	70.3	0	5.0	2.0	4.0	97.6	0	0	0
Demersal crustaceans	0	0	0	0	0	0	0	0	0	0	0	0	0	10.3	0.3
Birds and carrion	0	0	0	10	0	0	0	0	15.0	72.0	84.0	0	0	0	0

and single-species guilds containing the Macquarie shag (5), toothfish (6) and the fishery (7) (Fig. 2).

Annual prey consumption within the MI-EEZ

Estimates for the population sizes, biomasses, metabolic rates and the annual ER for the MI-EEZ are presented in Table 1. The estimated total annual consumption within the Macquarie Island EEZ by seals, seabirds, toothfish and the fishery is 419 774 t (Table 9). The majority of this is consumed by penguins (88.4%), followed by toothfish (7.6%) and seals (3.1%). Petrels and Macquarie shags consumed only 0.8%, and the commercial fishery 0.1% of the total prey biomass. Royal (51.5%) and king (23.9%) penguins consumed more than 75% of the total annual prey biomass. Of the total prey biomass consumed, 64% was fishes, 29% crustaceans and 7% cephalopods, with <1% being seabirds or carrion (Table 9). Myctophids comprised most (91%) of the fish prey biomass, with the next most important groups being bathylagids (3%), nototheniids (2%) and paralepidids (2%) (Table 9). Euphausids (85%) were the dominant crustacean prey by biomass, followed by amphipods (11%) and prawns (2%) (Table 9). Of the cephalopod prey biomass, squid from the genus *Moroteuthis* (44%), *Gonatus* sp. (20%) and *Kondokvia* sp. (11%) were the most important prey species (Table 9).

Table 6. Percentages of prey biomass in the diets of the major myctophid-consuming predators and the commercial fishery (including bycatch species) in the Macquarie Island EEZ. Taxonomic grouping of prey is to genus or species

Prey species	Antarctic fur seal	Subantarctic fur seal	New Zealand fur seal	King penguin	Royal penguin	Rockhopper penguin	Gentoo penguin	Fishery
Fishes								
Magnisudis prionosa	0	0	0	4.5	0	0	0.2	0
Notolepis sp.	0	0	0	0.5	0	0	0	0
Krefftichthys anderssoni	0	0	4.0	38.0	51.8	23.2	9.2	0
Protomyctophum spp.	0	0	0	0.9	0	0	0.4	0
Electrona antarctica	0	0	0.1	0	0	0	0	0
E. carlsbergi	1.6	0.2	0.5	53.6	4.8	2.8	15.0	0
E. subaspera	92.0	86.7	55.1	0	2.4	1.3	1.2	0
Gymnoscopelus spp.	1.3	8.1	25.3	0.3	0	0	14.7	0
Zanclorhynchus spinifer	0	0	0	0	0	0	9.0	0
Harpagifer georgianus	0	0	0	0	0	0	0.3	0
Macrourus carinatus	0	0	0	0	0	0	0	1.5
Other macrourids	0	0	0	0	0	0	0	1.1
Antimora rostrata	0	0	0	0	0	0	0	0.3
Halargyreus johnsonii	0	0	0	0	0	0	0	0.2
Dissostichus eleginoides	0	0	0	0	0	0	0.1	96.4
Lepidonotothen squamifrons	0	0	0	0	0	0	11.1	0.1
Notothenia rossii	0	0	0	0	0	0	1.0	0
Paranotothenia magellanica	0	0	0.1	0	0	0	23.6	0
Cephalopods								
Kondakovia longimana	0	0	0	0	0.2	0	0	0
Martialia hyadesi	0	0	0	0.1	0.2	0.1	6.3	0
Chiroteuthis spp.	1.3	1.3	1.3	0	0	0	0	0
Moroteuthis spp.	3.8	3.8	3.8	2.1	3.4	2.2	7.9	0
Todarodes spp.	0	0	0	0	0.1	0	0	0
Crustaceans								
Lithodes sp.	0	0	0	0	0	0	0	
Euphausia spp.	0	0	0	0	31.9	67.0	0	0
Themisto gaudichaudii	0	0	0	0	5.2	3.4	0	0
Birds (*Eudyptes* sp.)	0	0	10	0	0	0	0	0

Table 7. Diet overlaps between 14 marine predators and the commercial fishery in the Macquarie Island EEZ based on the 35 prey groups presented in Table 4. Diet overlap is expressed as percentage similarity index (%PSI)

	Southern elephant seal	Antarctic fur seal	Subantarctic fur seal	New Zealand fur seal	King penguin	Royal penguin	Rockhopper penguin	Gentoo penguin	Black-browed albatross	Northern giant petrel	Southern giant petrel	Antarctic prion	Macquarie shag	Toothfish
Antarctic fur seal	41.0													
Subantarctic fur seal	41.0	100												
New Zealand fur seal	41.0	89.9	89.9											
King penguin	39.5	94.9	94.9	87.0										
Royal penguin	41.1	62.5	62.5	62.5	61.2									
Rockhopper penguin	29.7	29.5	29.5	29.5	29.4	64.9								
Gentoo penguin	44.3	44.4	44.4	44.5	43.0	44.3	29.6							
Black-browed albatross	12.4	0	0	0.1	0.1	0.3	0.1	21.3						
Northern giant petrel	5.2	0.8	0.8	0.9	0.9	1.0	0.9	9.1	34.2					
Southern giant petrel	3.7	0	0	0.1	0.1	0.4	0.2	7.0	26.0	84.0				
Antarctic prion	2.4	1.8	1.8	1.8	1.8	38.9	62.8	1.8	0	0	0			
Macquarie shag	0	0	0	0.1	0	0	0	36.0	15.0	2.0	1.0	0		
Toothfish	19.2	9.1	9.1	9.1	6.6	7.9	6.7	21.6	12.1	7.0	1.6	1.8	12.1	
Fishery	0	0	0	0.1	0	0	0	0.2	0.1	0.1	0.1	0	0.1	3.6

The sensitivity of the relative consumption (% of total biomass consumed) by the 14 predators and the fishery to changes (±10%) in population and metabolic parameters are presented in Table 10. The results indicate that relative consumption of the predators and the fishery are generally insensitive to changes in these parameters, with most showing a change of <5% from the base-model estimates. In general, the relative consumption was slightly more sensitive to changes in population parameters than in metabolic parameters (Table 10). Although the overall sensitivity is low, the results also show that the relative consumption of each predator is relatively sensitive to changes in those parameters associated with the same predator as compared to changes in those parameters associated with other predators. For example, the relative consumption by elephant seals had the highest sensitivity to changes in elephant seal population estimates and metabolic rates, but not to changes in other parameters.

Seasonal variation in consumption rates

Seasonal variation in the estimated daily consumption rates of seals and seabirds feeding in the MI-EEZ are presented in Fig. 3. Although the daily consumption rates varied considerably among species, the seasonal trends were similar, with estimated consumption being greatest from October to March (Fig. 3). For many species (royal and rockhopper penguins, Antarctic fur seals and the petrels) daily consumption within the MI-EEZ was zero for part of the year (typically from May to September) when these species feed outside the MI-EEZ. However, when they return to the island in preparation for breeding in September and October, daily consumption rates increase rapidly (Fig. 3f). In the absence of any data on seasonal variation in the consumption rates of toothfish, daily consumption rates were assumed to be constant at about 108 t d^{-1}. Total consumption within the MI-EEZ was lowest in August, when it averaged 176 t d^{-1}, but increased steadily from September (381 t d^{-1}) to January (2779 t d^{-1}), and then declined rapidly through to March (1307 t d^{-1}) (Fig. 3f). The average daily consumption in the MI-EEZ from October to March was 1880 t d^{-1},

Table 8. Diet overlap between predators (fur seals and penguins) and the commercial fishery in the Macquarie Island EEZ based on taxonomic grouping to genus and species level as presented in Table 6. Diet overlap is expressed as percentage similarity index (%PSI)

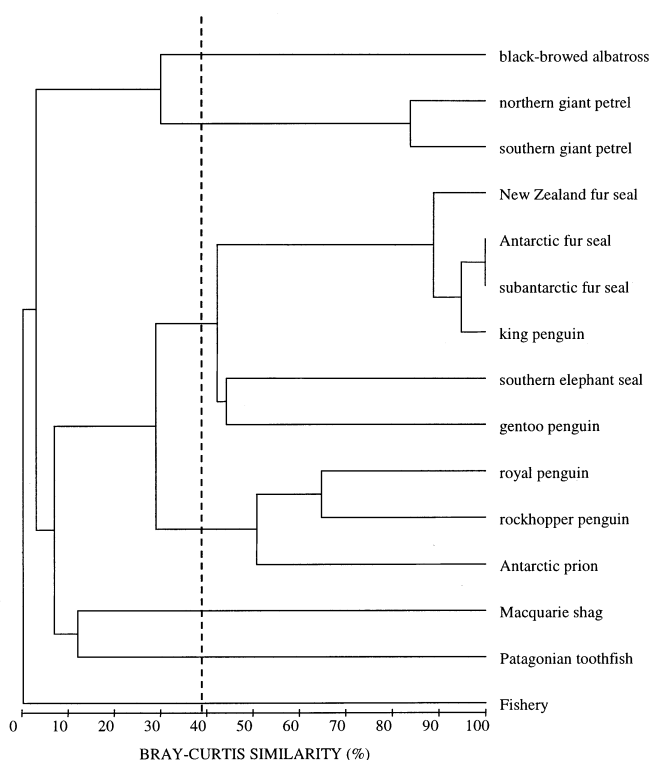|	Antarctic fur seal	Subantarctic fur seal	New Zealand fur seal	King penguin	Royal penguin	Rockhopper penguin	Gentoo penguin
Subantarctic fur seal	93.3						
New Zealand fur seal	62.0	68.4					
King penguin	4.1	2.6	6.8				
Royal penguin	7.4	6.0	10.2	45.0			
Rockhopper penguin	5.1	3.7	7.9	28.2	64.9		
Gentoo penguin	8.0	13.3	24.2	27.4	18.9	15.6	
Fishery	0	0	0	0	0	0	0.1

Fig. 2. Bray-Curtis similarity matrix of the diets of seabirds, seals, toothfish and the commercial fishery around Macquarie Island, based on the percentage contribution by mass of the 35 prey groups. Significant trophic guilds were determined following the methods of Jaksic & Medel (1990), using 5000 randomisations. Dashed line at 38.9% diet similarity indicates that 7 trophic guilds are significant at p < 0.05

peaking at 3045 t d^{-1} in late January (Fig. 3f). Daily consumption rates of fish (91% myctophids) were lowest in August (192 t d^{-1}), and highest in January (1646 t d^{-1}) (Fig. 3f). Crustacean (85% euphausids) and cephalopod consumption were also lowest in August (12 and 37 t d^{-1}, respectively), and highest in January (981 and 146 t d^{-1}, respectively) (Fig. 3f).

DISCUSSION

Data limitations

As with previous studies that have estimated the prey consumption of seals and seabirds, there are many inherent sources of error that must be considered when interpreting our results. These include uncertainties in population estimates, particularly for king, royal and rockhopper penguins, which are the major consumers of marine resources in the MI-EEZ. There are also large uncertainties in estimates of toothfish biomass at Macquarie Island, due to poor understanding of the spatial and temporal dynamics of the population (Tuck et al. 1999). Further, the estimates

used here reflect the biomass available to the fishery and not the total biomass of toothfish in the region.

Much of the diet composition data used have come from studies that were only undertaken over a single season, and sometimes only for part of 1 season. Therefore, we have little understanding of the inter-annual and seasonal variability in the diets of most of the marine predators around Macquarie Island. Furthermore, the taxonomic resolution of prey species for some predators is poor, and as demonstrated here, can significantly bias diet-similarity analyses. There are also likely to be some errors in estimates of the energy requirements of seabirds and seals, as most of these were derived from allometric equations. Further, the calorific values for many of the prey species are unknown and were estimated from values of similar or closely related species.

Uncertainty in estimates of activity budgets (attendance patterns), and assumptions on how much time species spent feeding in the MI-EEZ are also potential sources of error. This may be particularly relevant for the southern elephant seal, for which we assumed that seals feed while in transit through the MI-EEZ between their main feeding grounds and haul-out sites on Macquarie Island. It is possible that the seals are feeding at a much lower rate (or possibly not at all) during these transits.

Because of scant demographic data on all the seabirds, and the unknown number of juveniles feeding within the EEZ at any time, all breeding pairs were assumed to breed annually (with the exception of king penguins) and successfully raise chicks, and all non-breeding, pre-breeding and failed breeders were excluded. The assumption that all pairs breed successfully would inflate estimates of consumption, however the exclusion of non-breeding birds could decrease actual consumption estimates by up to 40% (Croxall et al. 1985). We could have made an estimate of the numbers of juveniles that may return to the island during the breeding season, but because we have no data on this, or the duration that these animals remain in the vicinity of Macquarie Island, we decided that it was better to omit them from our model. Our sensitivity analysis showed that relative consumption of predators and the fishery were generally insensitive to changes in population size, residence times and metabolic rates, with most showing a change of <5% from the base-model estimates. As such, we believe that although the absolute estimates of consumption by predators may not be precise due to the uncertainties described, such errors are unlikely to alter the trophic relationships we have described among predators and the fishery.

One of the strengths of this study is that it has confined estimates of consumption to the period when ani-

Table 9. Estimated annual prey consumption (t) of 14 marine predators and the commercial fishery in the Macquarie Island EEZ on the 35 prey groups, on 6 aggregated prey groups ('Aggregated groups'), and on all prey combined ('Combined prey')

Prey species	Southern elephant seal	Antarctic fur seal	Subantarctic fur seal	New Zealand fur seal	King penguin	Royal penguin	Rockhopper penguin	Gentoo penguin	Black-browed albatross	Northern giant petrel	Southern giant petrel	Antarctic prion	Macquarie shag	Toothfish	Fishery	Total
Pelagic fishes																
Bathylagidae	932	0	0	0	0	0	0	0	0	0	0	0	0	6255	0	7187
Paralepididae	0	0	0	0	5059	0	0	6	0	0	0	0	0	0	0	5065
Myctophidae	4486	151	75	610	93184	127657	13709	1564	0	0	0	25	0	1432	0	242891
Demersal fishes																
Squalidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1357	0	1357
Macrouridae	0	0	0	0	0	0	0	0	0	0	0	0	0	3401	15	3416
Moridae	0	0	0	0	0	0	0	0	0	0	0	0	0	2149	3	2152
Congiopodidae	0	0	0	0	0	0	0	345	0	0	0	0	0	0	0	345
Harpagiferidae	0	0	0	0	0	0	0	10	0	0	0	0	36	0	0	45
Dissostichus eleginoides	0	0	0	0	0	0	0	4	0	0	0	0	0	0	550	553
Other Nototheniidae	0	0	0	1	0	0	0	1373	7	4	11	0	359	3884	1	5641
Bothidae	0	0	0	0	0	0	0	0	0	0	0	0	0	170	0	170
Cephalopods																
Alluroteuthis	535	0	0	0	0	0	0	0	0	0	0	8	0	0	0	543
Brachioteuthis sp.	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Chiroteuthis sp.	25	0	0	0	0	0	0	0	0	2	0	0	0	606	0	633
Cirroteuthis sp.	0	2	1	9	0	0	0	0	0	0	0	0	0	271	0	282
Galiteuthis sp.	36	0	0	0	0	0	0	0	0	7	34	0	0	195	0	272
Gonatus antarcticus	58	0	0	0	0	0	0	0	0	3	0	0	0	6098	0	6158
Histioteuthis sp.	981	0	0	0	0	0	0	0	0	4	0	0	0	317	0	1302
Kondakovia longimana	2813	0	0	0	0	426	23	0	0	0	23	0	0	0	0	3285
Martialia sp.	173	0	0	0	101	420	71	242	13	32	69	0	0	0	0	1121
Mastigoteuthis sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	707	0	708
Moroteuthis sp.	677	6	3	27	2125	7423	1127	302	0	2	0	0	0	1618	0	13310
Taonius sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	71	0	72
Todarodes sp.	1317	0	0	0	0	126	0	0	19	0	0	0	0	0	0	1462
Vampryoteuthis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Octopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	245	0	245
Crustaceans																
Euphausids	0	0	0	0	0	68895	33719	0	0	0	0	788	0	0	0	103402
Prawns	0	0	0	0	0	0	0	0	0	0	0	0	0	2976	0	2976
Crabs	0	0	0	0	0	0	0	0	0	0	0	0	0	328	2	330
Amphipods	0	0	0	0	0	11353	1692	0	0	0	0	111	0	0	0	13156
Ostracods	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	8
Copepods	0	0	0	0	0	0	0	0	0	0	0	436	0	0	0	436
Others	0	0	0	0	0	0	0	0	2	4	46	0	0	0	0	52
Birds	0	0	0	0	72	0	0	0	0	0	0	0	0	0	0	72
Carrion	0	0	0	0	0	0	0	0	0	7	152	961	0	0	0	1120
Aggregated groups																
Pelagic fishes	5418	151	75	610	98242	127657	13709	1569	0	0	0	25	0	7687	0	255143
Demersal fishes	0	0	0	1	0	0	0	1728	7	4	11	0	395	10961	19	13126
Cephalopods	6622	8	4	36	2226	8395	1221	544	32	51	126	8	0	10128	0	29400
Pelagic crustaceans	0	0	0	0	0	80248	35411	0	2	4	46	1335	0	8	0	117054
Demersal crustaceans	0	0	0	0	0	0	0	0	0	0	0	0	0	3304	2	3306
Bird and carrion	0	0	0	72	0	0	0	0	7	152	961	0	0	0	0	1192
Combined prey																
Total consumption	12040	158	79	718	100468	216300	50341	3845	49	211	1144	1368	395	32088	570	419774
Total consumption (%)	2.87	0.04	0.02	0.17	23.93	51.53	11.99	0.92	0.01	0.05	0.27	0.33	0.09	7.64	0.14	

Table 10. Sensitivities of relative consumption estimates of the 14 predators and the fishery to 10% changes in population size and metabolic rate estimates of the 5 main consumers of marine resources in the MI-EEZ used in this study

Parameter and species	% change in para- meter	Sensitivity - percentage (%) change in consumption														
		Southern elephant seal	Antarctic fur seal	Subantarctic fur seal	New Zealand fur seal	King penguin	Royal penguin	Rockhopper penguin	Gentoo penguin	Black-browed albatross	Northern giant petrel	Southern giant petrel	Antarctic prion	Macquarie shag	Toothfish	Fishery
Population size																
Southern elelpahnt seal	10	9.7	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3
	–10	–9.7	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
King penguin	10	–2.3	–2.3	–2.3	–2.3	7.4	–2.3	–2.3	–2.3	–2.3	–2.3	–2.3	–2.3	–2.3	–2.3	–2.3
	–10	2.5	2.5	2.5	2.5	–7.8	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Royal penguin	10	–4.9	–4.9	–4.9	–4.9	–4.9	4.6	–4.9	–4.9	–4.9	–4.9	–4.9	–4.9	–4.9	–4.9	–4.9
	–10	5.4	5.4	5.4	5.4	5.4	–5.1	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4	5.4
Rockhopper penguin	10	–1.2	–1.2	–1.2	–1.2	–1.2	–1.2	8.7	–1.2	–1.2	–1.2	–1.2	–1.2	–1.2	–1.2	–1.2
	–10	1.2	1.2	1.2	1.2	1.2	1.2	–8.9	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2
Toothfish	10	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	–0.8	9.2	–0.8
	–10	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	–9.3	0.8
Metabolic rate																
Southern elelpahnt seal	10	9.7	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3	–0.3
	–10	–9.7	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
King penguin	10	–2.0	–2.0	–2.0	–2.0	6.5	–2.0	–2.0	–2.0	–2.0	–2.0	–2.0	–2.0	–2.0	–2.0	–2.0
	–10	2.1	2.1	2.1	2.1	–6.8	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1	2.1
Royal penguin	10	–4.4	–4.4	–4.4	–4.4	–4.4	4.2	–4.4	–4.4	–4.4	–4.4	–4.4	–4.4	–4.4	–4.4	–4.4
	–10	4.9	4.9	4.9	4.9	4.9	–4.6	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9	4.9
Rockhopper penguin	10	–1.1	–1.1	–1.1	–1.1	–1.1	–1.1	7.8	–1.1	–1.1	–1.1	–1.1	–1.1	–1.1	–1.1	–1.1
	–10	1.1	1.1	1.1	1.1	1.1	1.1	–7.9	1.1	1.1	1.1	1.1	1.1	1.1	1.1	1.1
Toothfish	10	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	–0.4	4.6	–0.4
	–10	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	–4.9	0.4

mals actually feed within the MI-EEZ, where information on the diet was obtained. Most other studies that have estimated the consumption of marine resources in other parts of the Southern Ocean have typically extended estimates of consumption to outside the period when animals are feeding near breeding islands, where information on their diet and spatial distribution is generally lacking.

Competition between commercial fisheries and other marine predators

An approach to evaluating the extent of prey overlap and competition between seabirds and commercial fisheries was developed by Duffy & Schneider (1994). Although developed specifically for seabirds, the model is also applicable to assessing competition between fisheries and marine mammals. It provides a hierarchical assessment of competition, based on ratios, specifically the 'Horn ratio' (that is the same as

the %PSI measure used in this study), 'Schaefer ratio', 'Evans ratio', 'Wiens ratio' and 'Bourne ratio' (Duffy & Schneider 1994). Using this hierarchical approach, a decision is made on the extent of competition at each ratio test; if the competition is low at the first step ('Horn ratio'), then no further analysis is needed. However, if competition is high, then each successive ratio is tested in order to examine the extent and type of competition.

In the case of the toothfish fishery at Macquarie Island, we found the %PSI (or Horn ratio) between the fishery and seabirds and seals to be very low (0.1% for gentoo penguins, ≤0.1% for all other seals and seabirds, Tables 7 & 8), indicating almost no direct overlap between prey species consumed by major marine predators and taken by the commercial fishery. The Schaefer ratio comparing the catch of toothfish by gentoo penguins and the fishery was also very low (0.007). The largest dietary overlap with the commercial fishery was with the target species, Patagonian toothfish, but even this was small (<4%, Table 7).
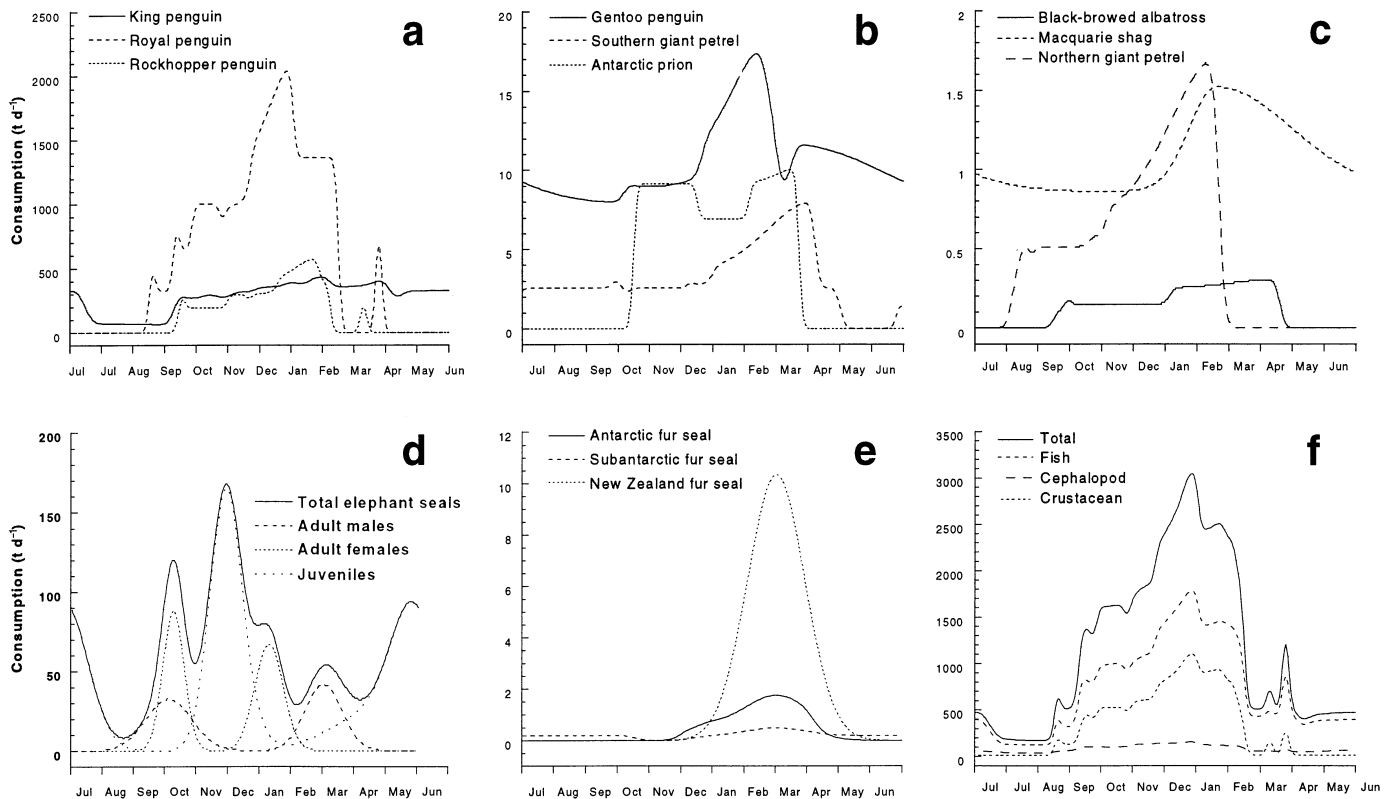
Fig 3. (a–e) Seasonal variation in the estimated daily consumption rates of marine resources by seabirds and seals within the MI-EEZ; (f) estimated total daily consumption, and consumption of fish, crustaceans and cephalopods by seabirds, seals and toothfish within the MI-EEZ

The limited trophic interactions between toothfish, the fishery and seals and seabirds at Macquarie Island, primarily result from limited dietary overlap and the small percentage of total prey biomass consumed by toothfish and the fishery relative to that consumed by seabirds and seals. This is in marked contrast to the fishery for Antarctic krill in the south-west Atlantic, where there is nearly complete overlap in the diets of penguins, fur seals and the fishery, producing correspondingly high Horn and Schaefer ratios (Croll & Tershy 1998).

A recent investigation into the diet of vagrant Hooker's sea-lions *Phocarctos hookerii* that haul-out periodically on Macquarie Island, found that toothfish are a common prey item (42% frequency of occurrence in scats, McMahon et al. 1999). Hooker's sea lions have the greatest diving capacity of all otariid seals, and have been recorded to dive to about 500 m (Gales & Mattlin 1997). However, as only 5 to 15 individuals of this species haul-out annually at Macquarie Island, their consumption is insignificant compared to that of other seals and seabirds that breed on the island. Although cetaceans were not considered in this study due to the paucity of data, sperm *Physeter macro-*

cephalus and killer *Orcinus orca* whales have been reported taking toothfish from active fishing gear (Ashford et al. 1996), and sperm and southern bottlenose *Hyperoodon planifrons* whales (if the latter occur in the MI-EEZ) have the diving capacity to act as natural predators of toothfish (Solyanik & Andriyashev 1964, Vukhov 1972, Hooker & Baird 1999). Greenland sharks *Somniosus microcephalus*, which are occasionally caught as bycatch in the toothfish trawl fishery at Macquarie Island, may also be a natural predator of toothfish; however, examination of the stomach contents of 2 caught as bycatch revealed mostly macrourid and southern elephant seal remains (Williams unpubl. data).

The seal and seabird communities around Macquarie Island prey primarily on pelagic fish (myctophids) and pelagic crustaceans (94% of prey biomass), neither of which form important prey of toothfish or are a target or bycatch of the commercial fishery. For this reason, the ecological impacts of the fishery on seals and seabirds are likely to be minimal, and may in fact bring about the competitive release of some pelagic fishes that could be consumed by seals and seabirds. More detailed ecological modelling would need to be under-

taken to examine this possibility. Although the fishery for toothfish is unlikely to compete for the prey of seals and seabirds, the development of new fisheries in the future may do so. During the 1980s, approximately 75 000 t of the myctophid *Electrona carlsbergi* were taken from the south-western Atlantic and processed into meal and oil (Kock 1992). Interest in this fishery has increased in recent years, and in the 1999/2000 and 2000/2001 fishing season, the CCAMLR set a precautionary catch limit of 109 000 t for *E. carlsbergi* in the south-west Atlantic (CCAMLR Statistical Subarea 48.3: CCAMLR 2000). The rapid development of intensive aquaculture fisheries around the world has meant that the demand for fish-meal has been increasing, and as such it is possible that this fishery may expand to other areas in the Southern Ocean in the future. The estimated annual consumption of *E. carlsbergi* in the MI-EEZ is about 66 000 t, most of which is consumed by king penguins. If such a fishery were to be developed around Macquarie Island, it would compete directly with seabirds and seals and would need to be carefully managed.

Diet overlaps between marine predators

The greatest diet overlap among predators within the MI-EZZ was between the myctophid predators, especially among fur seals, between fur seals and king penguins, and among king, royal and rockhopper penguins. However, closer examination revealed that although the same myctophid species dominated in the diets of all 3 species of fur seal, the penguins (king, royal and rockhopper) consumed different myctophid species (Table 6) and, as such, the perceived high level of overlap was in fact much lower. This highlights how sensitive such analyses are to the taxonomic resolution of the prey species. The likely reason why fur seals take different myctophid species than penguins is that different species may be available near the surface at night when fur seals feed compared to during the day when penguins mostly feed (Robinson & Hindell 1996, Goldsworthy et al. 1997, Hull 1997). The extent of dietary overlap between penguin species at Macquarie Island was much lower (16 to 65%) than that reported between gentoo and macaroni penguins (91%) at South Georgia, where crustaceans (mostly *Euphausia superba*) dominate in the diets of most seabirds (Croxall et al. 1997). With the exception of high levels of dietary overlap between northern and southern giant petrels and moderate overlap between Antarctic prions and rockhopper penguins, the diet overlap among other marine predators was generally low. In general, the extent of resource-partitioning among predators was high within the MI-EEZ relative to similar predator communities in the south-west Atlantic.

None of the seal or seabird species investigated had high diet overlaps with toothfish, the greatest overlap being with gentoo penguins (22%) and southern elephant seals (19%). The real extent to which gentoo penguins actually compete with toothfish for nototheniid fish (their common prey), is probably even lower than indicated by the similarity matrix, as gentoo penguins feed predominantly close inshore and in depths <150 m (Robinson & Hindell 1996), while toothfish are found most abundantly at depths >400 m. Most of the competition between toothfish and southern elephant seals was for squid; however, the main squid species targeted by toothfish was *Gonatus antarcticus*, while for southern elephant seals at Macquarie Island this was *Kondakovia longimana* (Green & Burton 1993, Goldsworthy et al. 2001) (present Table 4).

Consumption of marine resources

The total annual consumption of marine resources within the MI-EEZ by seals, seabirds, toothfish and the fishery was estimated to be 419 774 t, with pelagic fishes, almost entirely myctophids, being the most important prey by biomass (61%), followed by pelagic crustaceans (30%) and cephalopods (7%). Other prey categories, including demersal fishes and crustaceans and birds and carrion, were relatively minor contributors to the estimated annual prey consumption. The consumption of 419 774 t of prey per annum equates to a consumption of approximately 1010 kg km^{-2} yr^{-1} from within the MI-EEZ. However, there is likely to be considerable spatial heterogeneity in this consumption. The importance of fishes in diets of seabirds and seals at Macquarie Island is in marked contrast to many locations south of the Antarctic Polar Front, particularly in the south Atlantic Ocean, where the diets of most seabirds and seals are primarily pelagic crustaceans (Croxall et al. 1984, 1985, 1997, Croll & Tershy 1998). At Heard Island just south of the Antarctic Polar Front in the southern Indian Ocean, seals and seabirds also consume mostly pelagic crustaceans (60%), with smaller quantities of fishes (32%) and squid (8%) (Woehler & Green 1992). Similar results have also been estimated for seabirds and seals at Iles Kerguelen (55% crustacean, 30% fish, 15% cephalopod, Guinet et al. 1996).

Results from Macquarie Island are more similar to those found by Adams et al. (1993) at the Prince Edward Islands, also north of the Antarctic Polar Front, where consumption by 4 species of penguin was mostly of pelagic fishes at 70%, with pelagic crustaceans only making up 18% and cephalopods 11% of total prey biomass. This compares with 65% pelagic fishes, 31% pelagic crustacean and 3% cephalopod of

total prey biomass consumed by the 4 species of penguin at Macquarie Island. At Heard Island, demersal fish species occurred in more than 25% of dietary samples obtained from king, macaroni and gentoo penguins, in 14% of those from Antarctic fur seals, and accounted for most of the fish diet in southern elephant seals (Green et al. 1989, 1991, Woehler & Green 1992, Green & Burton 1993, Moore at al. 1998). This is in marked contrast to Macquarie Island, where demersal fishes were entirely absent from the diets of king and royal penguins, fur seals and the southern elephant seals, although they were present in gentoo penguins. Such differences in diets probably reflect the very large area of continental shelf on the Kerguelen Plateau available to marine predators around Heard Island compared to Macquarie Island.

The greatest consumers of marine resources within the MI-EEZ were penguins, which consumed about 88% of the total prey consumed by seabirds, seals and toothfish; 76% of this was consumed by royal and king penguins. Toothfish were estimated to consume 8% of the total prey biomass, and southern elephants seals 3%, with the remaining species consuming <1% of the total prey biomass each. Of the total prey biomass consumed by seabirds and seals around Macquarie Island, penguins consumed 96% (82% by royal and king penguins). These results are similar to estimates for Heard Island and Iles Kerguelen, where seabird consumption (mostly penguins) makes up 81% and 89% of total seabird and seal consumption, respectively (Guinet et al. 1996, Woehler & Green 1992). Similarly in the South Shetland Islands, consumption by chinstrap (*Pygoscelis antarctica*), Adelie (*P. adeliae*) and gentoo penguins has been estimated to account for 99% of local seabird and seal consumption (Croll & Tershy 1998).

The demand for marine resources by seabirds and seals around Macquarie Island was highly seasonal (Fig. 3). The greatest period of consumption was between October and March, peaking at over 3045 t d^{-1} in late January. This peak coincides with the period of greatest demand and competition for resources (from December to March), when most seabirds are feeding chicks, and fur seals are lactating. At this time, these species are dependant on prey biomass very near the island (<200 km), where they consume on average 2129 t of prey per day. These daily consumption rates are similar to those reported for 4 penguin species breeding at the Prince Edward Islands, ranging from 1900 to 3300 t d^{-1} (Adams et al. 1993).

Estimates of consumption of the various prey groups presented here have assumed static population sizes of various predators. However, the populations of many of the species have changed markedly over the past 200 yr, and for some species large changes in population size may be expected in the near future. The indigenous population of fur seals was completely eliminated by sealers soon after the island's discovery in 1810, when approximately 193 300 seals were killed, with fur seals only re-establishing a breeding population since the mid-1950s (Shaughnessy & Fletcher 1987). Currently, the breeding population only numbers about 600, with pup production increasing at a rate of about 13.9% yr^{-1} (Goldsworthy et al. 1998). Unlike fur seals, the southern elephant seal population has recovered from sealing, but has recently declined to about half that of the estimated population size of the 1960s (Hindell & Burton 1987). King and royal penguins were also taken for oil, but the current status of each species is not well known. The king penguin population is currently increasing, probably at 5 to 15% annually (E. Woehler pers. comm.). The royal penguin population has probably recovered from exploitation, and its population may still be increasing (Scott 1994). Changes in the population size of the various predators will affect the composition and quantity of marine resources consumed around Macquarie Island, and potentially alter the extent of inter-specific competition among predators. Such competition may affect the population sizes of some species and the recovery of others.

This study provides an initial assessment of the ecological linkages among marine predators and the commercial fishery within the MI-EEZ. Inevitably, data limitations, the exclusion of cetaceans, and potential errors in consumption estimates such as the unknown contribution of consumption within the MI-EEZ by non-breeding penguins, will lead to errors in estimates of the magnitude of trophic interaction. However, we believe that our main finding of weak trophic linkages between the commercial fishery and seabirds and seals, and between toothfish and other marine predators are unlikely to change. As more data are accumulated on population estimates, diet composition, predator foraging behavior, energy requirements and prey production, these uncertainties will be reduced. More accurate assessment of the ecological functions of toothfish, the commercial fishery, and other marine predators within the MI-EEZ will then be possible. This study provides an essential food-web model for the region on which further dynamic and integrated models can be developed to assist regional marine management.

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