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## Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica

Received: 26 August 1997 / Accepted: 16 December 1997

**Abstract** Antarctic and sub-Antarctic seabirds, marine mammals, and human fisheries concentrate their foraging efforts on a single species, Antarctic krill (*Euphausia superba*). Because these predators may have a significant effect on krill abundance, we estimated the energy and prey requirements of Adelie (*Pygoscelis adeliae*), chinstrap (*Pygoscelis antarctica*), and gentoo (*Pygoscelis papua*) penguins and female Antarctic fur seals (*Arctocephalus gazella*) breeding on the South Shetland Islands, Antarctica and compared these estimates with catch statistics from the Antarctic krill fishery. Published data on field metabolic rate, population size, diet, prey energy content, and metabolic efficiency were used to estimate prey requirements of these breeding, adult, land-based predators and their dependent offspring. Due to their large population size, chinstrap penguins were the most significant krill predators during the period examined, consuming an estimated  $7.8 \times 10^8$  kg krill, followed by Adelie penguins ( $3.1 \times 10^7$  kg), gentoo penguins ( $1.2 \times 10^7$  kg), and Antarctic fur seals ( $3.6 \times 10^6$  kg). Total consumption of all land-based predators on the South Shetland Islands was estimated at  $8.3 \times 10^8$  kg krill. The commercial krill fishery harvest in the South Shetland Island region ( $1.0 \times 10^8$  kg) was approximately 12% of this. Commercial harvest coincides seasonally and spatially with peak penguin and fur seal prey demands, and may affect prey availability to penguins and fur seals. This differs from the conclusions of Ichii et al. who asserted that the potential for competition between South Shetland predators and the commercial krill fishery is low.

### Introduction

Seabirds, marine mammals, and human fisheries tend to specialize on a limited number of species that are abundant and available relatively close to the surface. Prey consumption models have estimated that seabird populations can consume up to 22–29% of local fish production in some regions (Wiens and Scott 1975; Furness 1978), lending support to the hypothesis that seabird numbers may be limited by intraspecific competition for food during the breeding season (Ashmole 1971; Furness and Birkhead 1984). These types of models also suggest that seabirds and commercial fisheries may be significant competitors (Furness 1978; Furness and Cooper 1982; Duffy 1983; but see Bourne 1983), and a number of empirical studies have demonstrated large declines in seabird numbers due to commercial overfishing (reviewed in Nettleship et al. 1984). In order to prevent seabird population declines due to fisheries competition, Duffy and Schneider (1994) recommended comparing the quantity and timing of the prey requirements of marine predators and commercial fisheries in order to assess the potential for competition. Such comparisons can aid in predicting and understanding potential conflicts between developing fisheries and marine predators before they arise.

In Antarctic and sub-Antarctic waters, seabirds, marine mammals, and human fisheries concentrate their foraging efforts on abundant stocks of a single species, Antarctic krill (*Euphausia superba*). Penguins and fur seals may have a significant impact on krill abundance due to their high numbers, biomass, and metabolic rates. During the breeding season, penguins and fur seals are tied to one location where they return repeatedly throughout a 5–6 month period to feed their dependent offspring. Therefore, they are limited in the distance they are able to forage from the breeding site, and may be particularly sensitive to decreases in local prey availability. Consequently, the Commission for the Conservation of Antarctic Marine Living Resources

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(CCAMLR) is attempting to manage the Antarctic krill fishery in a manner that preserves the diversity and stability of krill predators (CCAMLR 1991).

Several studies have modeled the prey consumption of Antarctic predators (e.g. Croxall and Prince 1981; Croxall and Prince 1987; Woehler and Green 1992). These models have relied almost entirely upon allometric equations of metabolic requirements developed for terrestrial birds (Kendeigh et al. 1977). Several authors (Furness 1978; Weathers and Nagy 1980; Weathers et al. 1984) have found that errors in the estimation of standard and thermoregulatory metabolic rates, time budgets, and activity-specific metabolic rates result in large errors in overall energy requirements. It is difficult to apply laboratory measurements of energetic costs to wild animals which are responding to a myriad of parameters such as weather, reproductive status, food availability, food quality, predation, and competition (Nagy 1987). Thus, good, empirical measurements of field metabolic rates are essential for accurately modeling energy flow in predator populations.

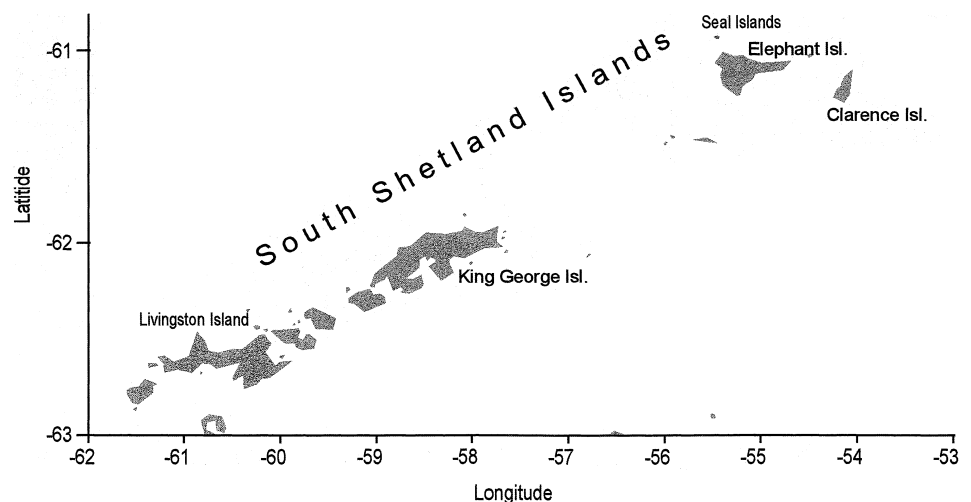
Recently, doubly-labeled water (DLW) has been employed to measure food and energy consumption of free-living marine animals with an accuracy of  $\pm 7\%$  (Nagy 1989; Costa 1991). Doubly-labeled water (DLW) provides a measure of the field metabolic rate (FMR), which is the total energy cost an animal pays in performing its daily activities, and is thus a useful tool for accurately measuring the energy requirements of species in the wild. For example, it has been used to measure the energy requirements of a number of Antarctic predators: chinstrap (Moreno and Sanz 1996), king (*Aptenodytes patagonica*) (Kooyman et al. 1992), Adelie (Nagy 1987), gentoo (Davis et al. 1989), and macaroni penguins (*Eudyptes chrysolophus*) (Davis et al. 1989), and Antarctic fur seals (Costa et al. 1989). In addition, Birt-Friesen et al. (1989) and Nagy (1987) have developed allometric equations that relate FMR to body mass in birds and mammals. These provide more ac-

curate methods to estimate the energy and prey requirements of Antarctic penguin and fur seal populations. Published reports of commercial fisheries catches in the Antarctic by region (Everson and Goss 1989; CCAMLR 1991; SC-CAMLR 1992) allow comparison of predator requirements with commercial fish catches. Recently, Ichii et al. (1996) examined the potential competition between chinstrap penguins and the Antarctic krill fishery, using prey requirement estimates based upon allometric equations and fishery catch statistics. They concluded that there was little potential for competition. In this paper we: (1) apply measurements of field metabolic rates to a model estimating prey requirements of land-based predator populations on the South Shetland Islands, Antarctica (Fig. 1); (2) compare these estimates to published estimates of krill biomass in the vicinity of the South Shetland Islands; (3) examine the potential for interaction between these predator populations and commercial fisheries in the vicinity of the South Shetland Islands; and (4) re-examine the assertion of a low potential for competition proposed by Ichii et al. (1996).

## Materials and methods

Adelie, chinstrap, and gentoo penguins, and female Antarctic fur seals were included in prey consumption estimates. Although additional species, particularly flying seabirds, breed on the South Shetland Islands, their biomass is insignificant compared to the selected species (Trivelpiece et al. 1987; Shuford and Spear 1988; Bengtson et al. 1990; Woehler 1993). Only breeding adults and their offspring that are tied to a land-based breeding colony were included in the estimates. Breeding adult male fur seals were excluded because they fast during the breeding season. Lack of information concerning energy requirements, prey composition, and geographic location during the breeding season excluded other portions of the predator populations from the model (i.e. non-breeding penguins and fur seals). Nevertheless, although unknown, their population numbers are probably significant and thus they are likely important consumers of Antarctic prey resources.

Fig. 1 Study site, South Shetland Islands, Antarctica



The model concentrates on prey consumption during the chick- and pup-rearing months: 1 December to 30 March. Penguin chicks are dependent upon the foraging efforts of their parents for food during most of this period. The post-fledging period is also included as newly fledged chicks and adults undertaking their pre-molting foraging trip are likely to occur close to the breeding colonies (chinstrap and gentoo penguins return to the breeding colonies to molt). Fur seal females suckle their pups ashore throughout the study period.

#### Population estimates

Population estimates for chinstrap, Adelie, and gentoo penguins were taken from Woehler (1993). Antarctic fur seal population estimates were taken from Bengtson et al. (1990) and include only breeding females and their pups. The chick fledging success rate is assumed to be 95%, 99%, and 106% per nest for chinstrap, Adelie, and gentoo penguins, respectively (Trivelpiece et al. 1987).

#### Diet

The diet of penguins was assumed to be the same as those reported by Volkman et al. (1980) on King George Island, although prey composition may vary geographically and temporally. The diet of fur seals on the South Shetland Islands has not been published. We assumed that krill was taken exclusively and in the same age/sex ratios as observed for fur seals on South Georgia (Croxall and Pilcher 1984). However, Green et al. (1989) recently found that Antarctic fur seals breeding at Heard Island fed mainly upon fish, and Daneri and Corin (1992) found that non-breeding male fur seals feed upon krill, fish, and squid during the summer autumn period on the South Orkney Islands. A significant proportion of fish in fur seal diets will lead to an overestimate of krill consumption.

Prey consumption estimate equations, input parameters, and assumptions

Model input parameters and references are summarized in Table 1.

#### Chinstrap penguin – adult

Empirical measurements of FMR for chinstrap penguins have been published for adults at sea and on land (Moreno and Sanz 1996). We combined these measurements with published data on the nest attendance and foraging behavior for chinstrap penguins during the five phases of the study period (26, 34, 25, 15, and 20 days for incubation, brooding, creche, pre-molt, and molt, respectively):

$$\text{Energy Requirement}_{\text{Phase}} = \left( \frac{((\text{FMR}_{\text{Sea}} * \%T_{\text{Sea}}) + (\text{FMR}_{\text{Nest}} * \%T_{\text{Nest}}))}{\text{ME}} \right) \text{No. Days}_{\text{Phase}}$$

where FMR is the activity-specific daily field metabolic rate (Moreno and Sanz 1996), %T is percent time at sea or on nest during time phase (Trivelpiece et al. 1987), ME is metabolic energy, or assimilation efficiency, which we assumed to be the same as that measured for macaroni penguins (Davis et al. 1989), and No. Days is the number of days in the time phase (incubation, brooding, creche, pre-molt) (Lishman 1985). The behavior of adults during the creche period was not determined. Often, adults arrive at the colony to feed their dependent chicks and then move to an area near the colony but some distance from their chicks (D.A. Croll, personal observations). Thus, we assumed that adults spent 50% of their time at sea and 50% resting at the colony during the creche period. Molting metabolic rate was assumed to be the same as that measured for macaroni penguins (a similar-sized penguin) (Davis et al. 1989).

#### Gentoo penguin – adult

Gentoo penguin adult energy requirements were summed from energy requirements calculated for four phases during the study period (35, 30, 60, 10, and 15 days for incubation, early chick-rearing, late chick-rearing, pre-molt, and molt, respectively):

$$\text{Energy Requirement}_{\text{Phase}} = ((\text{FMR}_{\text{Phase}} * \text{Mb}) \text{No. Days}_{\text{Phase}}) / \text{ME}$$

where  $\text{FMR}_{\text{Phase}}$  is the mass-specific daily FMR for the time phase (Davis et al. 1989), Mb is body mass (Davis et al. 1989), No. Days<sub>Phase</sub> is the number of days in the time phase (Davis et al. 1989), and ME is metabolic energy (assumed to be the same as that of macaroni penguins; Davis et al. 1989).

#### Adelie Penguin – adult

The energy requirements of breeding adult Adelie penguins were calculated separately and then summed over each time phase (60, 28, 22, and 10 days for brooding/creche, pre-molt, molt, and post-molt, respectively):

$$\text{Energy Requirement}_{\text{Phase}} = ((\text{FMR}_{\text{Phase}} * \text{Mb}) * \text{No. Days}_{\text{Phase}}) / \text{ME}$$

where  $\text{FMR}_{\text{Phase}}$  is the mass-specific daily FMR during brooding, pre-molt, molt, and post-molt (using field metabolic rates from Nagy 1987 and Birt-Friesen et al. 1989), Mb is adult body mass (Volkman et al. 1980), No. Days<sub>Phase</sub> is the number of days in the time phase (Lishman 1985), and ME is metabolic efficiency (assumed to be the same as that of macaroni penguins; Davis et al. 1989).

#### Chinstrap and gentoo penguin – chick

Chinstrap and gentoo penguin chick energy requirements were calculated separately and summed over two distinct phases: growth and post-fledging:

$$\text{Total Chick Energy Requirement} = \text{Chick Energy}_{\text{Growth}} + \text{Chick Energy}_{\text{Post-fledging}}$$

During the growth phase, energy requirements were further broken down and estimated as energy expended in maintenance and growth:

$$\text{Chick Energy}_{\text{Growth Phase}} = (\text{Maintenance Energy} + \text{Growth Energy}) / \text{ME}$$

Chick metabolic rates change during growth (Taylor 1985), so maintenance energy requirements were summed over distinct time periods (Table 1) during the growth phase:

$$\text{Maintenance Energy}_{\text{Time Period}} = \text{MR}_{\text{Time Period}} * \text{Mb}_{\text{Time Period}} * \text{No. Days}_{\text{Time Period}}$$

where MR is the mass-specific daily metabolic rate for the time period (Taylor 1985), Mb is chick body mass during the time period (calculated from equations in Taylor 1985), and No. Days is the number of days included in the time period (Table 1, Taylor 1985).

$$\text{Growth Energy} = ((\text{Mb}_{\text{Fledge}} - \text{Mb}_{\text{Hatch}}) * (1 - \% \text{BW})) * \text{TC}$$

where Mb<sub>Fledge</sub> is chick body mass at fledging, Mb<sub>Hatch</sub> is chick body mass at hatching (Taylor 1985), %BW is percent water content of chick tissue (assumed to be 75% for all species (Davis et al. 1989), and TC is energy content of dry chick tissue (assumed to be similar to macaroni penguins Brown 1987).

Post-fledging metabolic rates of chicks were assumed to be the same as the at-sea metabolic rate of adult penguins:

$$\text{Chick Energy}_{\text{Post-fledging}} = (\text{MR}_{\text{Adult At-sea}} * \text{Mb} * \text{No. Days}_{\text{Post-fledging}}) / \text{ME}$$

**Table 1** Model input data and assumptions for estimation of South Shetland Islands, Antarctica, land-based predator energy requirements and prey consumption. <sup>1</sup>Birt-Friesen et al. 1989, <sup>2</sup>Volkman et al. 1980, <sup>3</sup>Trivelpiece et al. 1987, <sup>4</sup>Assumed, <sup>5</sup>Davis et al. 1989, <sup>6</sup>Taylor 1985, <sup>7</sup>Ainley 1972, <sup>8</sup>Brown 1987, <sup>9</sup>Costa et al. 1989, <sup>10</sup>Personal communication. M. Goebel, Seal Is., <sup>11</sup>Croxall and Pitcher 1984, <sup>12</sup>Miller 1978, <sup>13</sup>Nagy 1987, <sup>14</sup>Culik et al. 1990, <sup>15</sup>Culik and Wilson 1992, <sup>16</sup>Moreno and Sanz 1996, <sup>17</sup>Adams and Brown 1990)

Chinstrap penguin adult FMR (kJ day <sup>-1</sup> ) <sup>16,17</sup>													
Sea <sup>16</sup>	Nest <sup>16</sup>	Overall <sup>16</sup>	Pre-molt <sup>16</sup>	Molt <sup>17</sup>	Body mass (kg)	% Time incubation		% Time brooding		Adult krill (%) <sup>2</sup>		Metabolic energy (%) <sup>5</sup>	
						Sea	Nest	Sea	Nest	Male	Female		
Male 6423	2124	5597	6423	2431	4.3	53	47	44	56	50	65	35	74
Female 6423	2124	5597	6423	2431	3.7	47	53	56	44	50	65	35	74
Adelie penguin adult FMR (kJ day <sup>-1</sup> ) <sup>1,3,15</sup>													
Brooding <sup>13,15</sup>		Pre molt <sup>1</sup>	Molt	Post-molt	Body mass (kg) <sup>2</sup>	Adult krill (%) <sup>2</sup>		Metabolic energy (%) <sup>5</sup>					
Male 4002	5042	2431	2431	5042	4.5	54	46	54	46	74			
Female 4002	4817	2431	2431	5042	4.2	54	46	54	46	74			
Gentoo penguin adult FMR (kJ day <sup>-1</sup> ) <sup>5</sup>													
Incubation		Brooding		Pre-molt	Body mass (kg) <sup>5</sup>	Adult krill (%) <sup>2</sup>		Fish (%) <sup>2</sup>		Metabolic energy (%) <sup>5</sup>			
		Early	Mid/late			Male	Female	Male	Female				
Male 3888	3584	3900	8538	6.1	38	47	15	38	47	15	74		
Female 3953	3584	3900	8538	6.1	38	47	15	38	47	15	74		
Chinstrap penguin chick Metabolic rate (kJ kg <sup>-1</sup> h <sup>-1</sup> ) <sup>6</sup> at age (days)													
10	15	25	40	55	Chick growth reference		Energy content tissue (kJ g dry mass <sup>-1</sup> ) <sup>7</sup>		Water content tissue (%) <sup>5</sup>		Metabolic energy (%) <sup>5</sup>		
38.7	28.8	21.9	17.9	16.2	6	23.4	75	75	74				
Adelie penguin chick Metabolic rate equation (kJ day <sup>-1</sup> ) <sup>14</sup>													
		Chick growth reference		Chick growth reference		Energy content tissue (kJ g dry mass <sup>-1</sup> ) <sup>7</sup>		Water content tissue (%) <sup>5</sup>		Metabolic energy (%) <sup>5</sup>			
		6,7		6,7		23.4		75		74			
Gentoo penguin chick Metabolic rate (kJ kg <sup>-1</sup> h <sup>-1</sup> ) <sup>6</sup> at age (days)													
10	15	25	40	55	70	Chick growth reference		Energy content tissue (kJ g dry mass <sup>-1</sup> ) <sup>7</sup>		Water content tissue (%) <sup>5</sup>		Metabolic energy (%) <sup>5</sup>	
35.1	31.0	22.2	18.1	14.5	8.7	23.4	6	23.4	75	74			
Antarctic fur seal female with pup FMR (kJ kg <sup>-1</sup> day <sup>-1</sup> ) <sup>9</sup> Time budget (%) <sup>10</sup>													
Sea	Colony	Sea	Colony	Body mass (kg) <sup>10</sup>		Adult krill (%) <sup>11</sup>		Metabolic energy (%) <sup>12</sup>					
988.5	428.5	52	48	40	40	21	79	90					

where  $MR_{Adult\ At-sea}$  is the at-sea metabolic rate of adult penguins (Davis et al. 1989; Moreno and Sanz 1996; for chinstrap and gentoo penguins, respectively),  $Mb$  is body mass at fledging (Trivelpiece et al. 1987), and  $No. Days_{Post-fledging}$  is the number of days from fledging to the end of the study period (Lishman 1985 and Davis et al. 1989 for chinstrap and gentoo penguins, respectively).

#### Adelie Penguin – chick

The energy requirements of Adelie penguin chicks were also separated into growth and post-fledging phases and summed. Energy expended for maintenance during the growth phase was calculated as:

$$\text{Maintenance Energy}_{\text{Growth Phase}} = (839.7Mb^{0.947}) \\ * \text{No. Days}_{\text{Growth Phase}}$$

Chick growth and daily mass-specific metabolic rate equations were taken from Culik et al. (1990);  $No. Days_{\text{Growth Phase}}$  is the number of days from hatching to fledging (Culik et al. 1990).

Energy expended in growth during the growth phase and energy expended during the post-fledging phase were calculated in the same manner as for chinstrap and gentoo penguin chicks. At-sea metabolic rate was estimated from Birt-Friesen et al. (1989); body mass at hatching and fledging were taken from Culik et al. (1990) and Ainley and Schlatter (1972), and brooding and fledging dates were taken from Trivelpiece et al. (1990).

#### Estimation of krill consumption

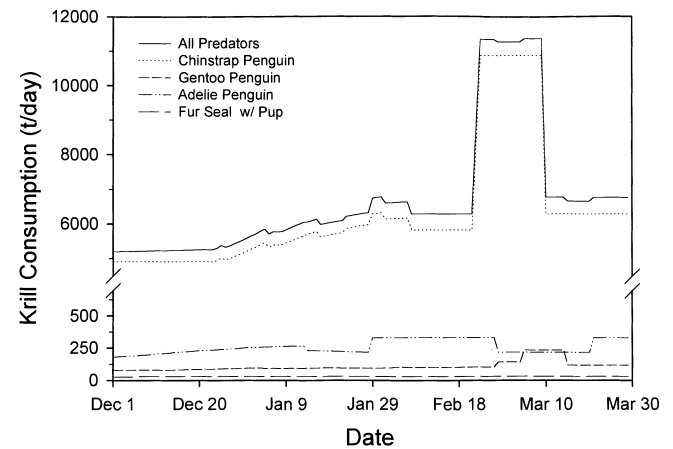
Male and gravid female krill have significantly different energy content, due to the high energy density of the egg mass. The percent of diet by weight composed of gravid female and male krill of penguins was taken from Volkman et al. (1980) (Table 1). The diet composition of Antarctic fur seals was assumed to be similar to that observed on South Georgia (Croxall and Pilcher 1984). Values for the conversion of krill biomass to energy ( $\text{kJ kg wet weight}^{-1}$ ) were taken from Clarke (1980).

## Results and discussion

### Penguin prey requirement estimates

Individual adult prey consumption estimates for the three species of sympatric pygoscelid penguins from 1

December to 30 March were similar (Table 2). Due to the large size of the South Shetland Island population, chinstrap penguins accounted for approximately 92% of the total krill consumed in the South Shetland Islands, followed by Adelie penguins (7%), Antarctic fur seals (less than 1%), and gentoo penguins (less than 1%) (Fig. 2, Table 3). Total estimated daily krill consumption for chinstrap penguins increased from approximately 5 to 6 million  $\text{kg day}^{-1}$ , up to the middle of February when chick feeding ceased and adults began their pre-molt foraging. At that time, estimated consumption decreased to approximately 5 million  $\text{kg day}^{-1}$  (Fig. 2) as the energy requirements of adults increased as more time was spent at sea foraging. Prey consumption increased in mid February at chick fledging when metabolic costs of transport and thermoregulation in water were added to chick energy requirements as fledged chicks foraged at sea. Similar peaks in estimated prey consumption have been reported by others (Croxall and Prince 1987; Brown 1989). Although penguin populations may be especially sensitive to fluctuations in prey



**Fig. 2** Estimated prey consumption of chinstrap, Adelie, and gentoo penguins, and Antarctic fur seals on South Shetland Islands, Antarctica, 1 December to 30 March

**Table 2** Estimated individual energy requirements and krill consumption of South Shetland Island Antarctica, land-based predators, 1 December to 30 March (120 days). Model input parameters summarized in Table 1

Species	Energy (MJ)	Krill (kg)	Fish (kg)
Chinstrap penguin			
Male	360.32	142	–
Female	329.9	130	–
Chick	287.2	113	–
Gentoo penguin			
Male	422.83	128	25
Female	423.74	128	25
Chick	339.09	103	13
Adelie penguin			
Male	431.72	162	–
Female	423.17	158	–
Chick	406.39	917	–
Antarctic fur seal with pup	3433.76	917	–

**Table 3** Estimated population energy requirements and krill consumption of South Shetland Island, Antarctica, land-based predators, 1 December to 30 March. Model input parameters summarized in Table 1

Species	Krill consumption (kg wet weight)	Population adults	Population chicks/pups	Population estimate reference
Chinstrap penguin	$7.8 \times 10^8$	$1.62 \times 10^6$	$7.70 \times 10^5$	Shuford and Spear (1988)
Adelie penguin	$3.1 \times 10^7$	$1.31 \times 10^5$	$1.29 \times 10^5$	Woehler (1993)
Gentoo penguin	$1.2 \times 10^7$	$1.80 \times 10^4$	$1.91 \times 10^4$	Shuford and Spear (1988)
Antarctic fur seal	$3.6 \times 10^6$	$3.96 \times 10^3$	$3.96 \times 10^3$	Bengtson et al. (1990)
Total	$8.3 \times 10^8$	$1.77 \times 10^6$	$9.18 \times 10^5$	

availability at this peak, foraging occurs over a larger area as the birds are no longer closely tied to breeding colonies.

There were large differences in the prey requirements for chick rearing in the three penguin species, with chinstrap penguin parents investing the least energy in chick production and gentoo parents investing the most (Table 4). Trivelpiece et al. (1987) also found that gentoo adults supply more energy to their chicks than do other species, and attributed this to: (1) the longer chick-rearing period (72 days compared to 52 days in the other species), and (2) differences in the fledging weight in the three species (104%, 79%, and 89% of adult weight in gentoo, Adelie, and chinstrap penguins, respectively).

Although chinstrap and Adelie penguin chicks are raised to a similar fledging weight (Trivelpiece et al. 1987), our estimates indicate that Adelie penguin adults must supply more energy to their chicks to meet this growth (Table 4). Two possibilities may explain this difference. Firstly, Adelie penguin chicks have a higher metabolic rate at the nest than do chinstrap and gentoo penguin chicks, due to the higher thermoregulatory costs to the chick associated with the colder temperatures encountered in the earlier breeding season of Adelie penguins (Trivelpiece et al. 1987): this is unlikely, as Chapell et al. (1990) found that thermoregulatory costs in Adelie penguin chicks are small. Secondly, spontaneous activity bouts, included in the metabolic rate measurements for Adelie chicks by Culik et al. (1990), are not included in the measurements of chinstrap and gentoo chick metabolic rates (Taylor 1985). These higher prey requirement estimates for Adelie chicks contrast with those of Trivelpiece et al. (1987), who used food delivery rates to calculate that Adelie penguin adults supply less food to chicks than chinstrap penguin adults. Our estimates (based upon metabolic rate) may be lower because activity of the chick at the nest is not reflected in the resting metabolic rates used in the present model, or some food brought to the colony may not be regurgitated to the chick. Measurements of food consumption of chicks using labeled water would help clarify these differences.

#### Antarctic fur seal prey requirement estimates

As individuals, Antarctic fur seals had a relatively high energy requirement (Table 2), but their impact upon local prey resources and sympatrically breeding penguin populations is limited due to the small size of the South Shetland Island population (Table 3). However, the converse may not be true. Large numbers of chinstrap penguins breed sympatrically and may compete with fur seals for local krill resources. J.L. Bengtson and L.L. Eberhardt (unpublished report, National Marine Mammal Laboratory, Seattle, Washington) found that fur seals forage farther from Seal Island than do chinstrap penguins breeding on the same island. Fur seal females can concentrate food energy as milk, and have longer foraging trips than penguins (Costa et al. 1989; Croll et al. 1991). Thus, they are able to forage further from shore and bring energy back to their pups gained from widely separated (both temporally and spatially) feeding areas. Penguins, which regurgitate whole prey to their young, are unable to concentrate the prey energy captured far from the colony for delivery later to the chick. The greater foraging range of the fur seals would serve to reduce competition with penguins, if it does exist.

#### Errors in prey requirement estimates and model sensitivity

Estimates of energy requirements for penguins based upon allometric equations from Kendeigh et al. (1977) resulted in adult energy consumption estimates 25–30% lower than those estimated in the present study (Croxall and Prince 1981). This leads to similarly lower estimates for prey requirements. Empirically measured energy costs using DLW, or allometric equations derived from field metabolic rate measured using DLW (Birt-Friesen et al. 1989), are probably more accurate than estimates based on allometric equations of basal metabolic rate (Kendeigh et al. 1977) because they include the energy costs of all of the organism's activities, including thermoregulation and locomotion.

**Table 4** Estimated individual breeding energy requirements and prey consumption of species breeding on South Shetland Islands. Energy and krill required from egg laying to fledging in penguins (85, 95, and 95 days for Chinstrap, Adelie, and Gentoo penguins, respectively); from parturition to weaning in Antarctic Fur Seal (117 days)

Species	Energy (MJ)	Krill (kg)	Fish (kg)
Chinstrap penguin			
Male	302.3	125	–
Female	277.9	115	–
Chick	86.0	35	–
Adelie penguin			
Male	380.2	149	–
Female	380.2	149	–
Chick	126.6	52	–
Gentoo penguin			
Male	477.6	190	30
Female	479.9	190	30
Chick	138.9	46	9
Antarctic fur seal with pup	3454.5	952	

Errors in the model estimates of prey consumption due to errors in estimates of the population size and metabolic rates of predators result in proportional errors in the model prey requirement estimates (e.g. a 10% underestimate of population numbers or metabolic rates would result in a 10% underestimate of prey requirements). Overall, model estimates of prey requirements could be improved by accurate estimates of: (1) the breeding population size of predator populations, (2) the population size and distribution, diet, and energy requirements of non-breeding penguins and fur seals during the breeding season, and (3) the energy requirements and diet of all populations during the non-breeding season.

Of the three species examined, Adelie penguins had the highest estimated individual energy requirement (Table 2). This results from the model's assumption that adults and fledglings spend all of their time after fledging at sea, where the costs of swimming and thermoregulation in water result in elevated metabolic rates. Some of the post-fledging time period is likely spent resting on ice floes, so this number may be an overestimate. In addition, Adelie penguins molt on sea ice, not at the breeding rookery, in contrast to the other penguin species (Ainley et al. 1984). As a result, the pre-molt period can be a considerable distance from the breeding colony, which would reduce the dependence of Adelie penguins on prey resources close to the breeding colonies.

Antarctic fur seal females probably use energy stored in their blubber for at least part of the lactation period. This stored energy, if obtained some distance from the colony, would decrease estimates of prey requirements in the South Shetland Island region. While breeding adult male Antarctic fur seals fast during the reproductive period, many non-breeding adult and subadult males forage from the breeding colony (personal observation). It is difficult to estimate the size of this portion of the fur seal population, but if we were able to

include them in our model, it could substantially increase the estimated prey requirements of fur seals in the region.

#### Commercial krill fishery and land-based predators

Duffy and Schneider (1994) provided a model for evaluating the degree of overlap and potential competition between seabirds and commercial fisheries. They proposed ratios to compare: (1) species overlap in predator and fisheries catches ("Horn Ratio"), (2) the magnitude of fisheries catches and predator consumption ("Schaeffer Ratio"), and (3) the magnitude of fisheries and predator catches to prey biomass ("Evans Ratio"). There is nearly complete overlap in the diets of South Shetland penguins and fur seals and the commercial fisheries with both groups taking *Euphausia superba* almost exclusively (high Horn Ratio).

We estimate that penguins and fur seals foraging from the South Shetland Islands consumed an estimated 826,000 t of krill during this period, while Everson and Goss (1989) calculated that the commercial fisheries annual harvest in the South Shetland Island region ranged from 48,765 t in 1991 to 96,750 t in 1989, equal to 6–12% of the estimated penguin and fur seal consumption, or a Schaeffer Ratio of 16.9 to 8.5. A high seabird take relative to fishery catch (Duffy and Schneider suggest  $>0.25$ ) indicates a high potential for competition unless there is low overlap in predator and fishing foraging zones. Everson and Goss (1989) examined the distribution of commercial krill fishing catch statistics by area and found that almost all fishing effort during the Antarctic summer months is concentrated near the South Shetland and South Orkney Islands. From 1988 to 1991, an average of 24% of the Antarctic krill catch occurred in the South Shetland Islands region (Agnew 1992). Fifty percent of this catch was taken within 40 km, and 90% was taken within 80 km of land-based seabird and pinniped colonies between December and March in all years 1988–1991 (Agnew 1992). Thus, it appears that both the commercial fishery and land-based predators are capturing krill in the same area at the same time of year in the South Shetland Island region. Agnew and Phegan (1995) estimated that the overlap is highest between foraging chinstrap penguins and the krill fishery in the South Shetland region. However, Duffy and Schneider (1994) pointed out that a high Schaeffer ratio may also result from a small fishery, and this is likely true of the Antarctic krill fishery which has not undergone significant expansion (SC-CCAMLR 1992).

Siegel (1991) approximately estimated that annual krill biomass in the South Shetland region is about 2 million tons. Our estimates of predator consumption represent approximately 41% of this biomass, or 206% of the natural mortality from predation estimated by Siegel (1991) for this region. This would indicate that: (1) natural mortality estimates are low, (2) South Shet-

land krill biomass estimates are low, or (3) predator consumption rates are high. More reliable estimates of krill biomass based on hydroacoustic surveys are available for the Elephant Island region of the South Shetland Islands (Hewitt and Demer 1993). Using only population estimates of land-based predators breeding in the Elephant Island region (Bengtson et al. 1990; Woehler 1993) in the present model, we calculated 240,000 t of krill biomass was consumed by land-based predators between December and March. This represents 33% (Evans Ratio) of the lowest estimate of krill biomass in the Elephant Island region (721,000 t krill) to 6.5% of the highest estimate (3,720,000 t krill) between 1988 and 1990 (Hewitt and Demer 1993), or 148–33% of the natural mortality based on the Siegel (1991) model. Estimates of predator consumption to biomass ratios for other regions have ranged from 2% in the Benguela ecosystem (Duffy and Siegfried 1987) to 23% in Saldanha Bay, South Africa (Furness and Cooper 1982). Thus it appears that the land-based predator consumption relative to krill biomass or natural mortality in at least the Elephant Island region may be relatively high. Krill populations are likely advected into the South Shetland region (Siegel 1988). Competition would be reduced if a substantial portion of the krill population is advected into the region from areas that are not commercially fished. This seems unlikely, however, as the krill fishery targets the regions of densest aggregation of krill in the vicinity of the South Shetland Islands.

Ichii et al. (1996) concluded that competition between the South Shetland krill fishery and penguins was not significant. They based this conclusion on: (1) a low degree of spatial overlap between the fishery and penguin foraging areas, (2) a low degree of overlap between trawl depth and penguin foraging depth, and (3) an incomplete overlap between the size of krill taken by the fishery and penguins. We disagree with their conclusions because firstly, while spatial overlap between the fishery and penguin foraging areas is incomplete, it is likely that krill populations are dynamic, and not static as Ichii et al. assume. Thus, krill populations fished by the commercial fishery are likely advected into the range of breeding penguins (Siegel 1988). Intense fishing in areas adjacent to penguin foraging areas would serve to reduce the biomass of krill that is advected into the penguin foraging range. Further, Agnew and Phegan (1995) recently found a high degree of overlap between penguin and krill fishery takes in a refined model of foraging ranges of penguins. Secondly Croll et al. (1993) found that mean and median foraging dive depth in chinstrap penguins in the Elephant Island region correlates with the upper, less dense portion of the distribution of krill swarms. Diving no deeper than necessary to encounter sufficient prey density for foraging is logical as penguins must surface in order to breathe. A number of studies have demonstrated a decreasing feeding rate for predators with increasing swarm density (reviewed in Milinski 1984). Chinstrap penguins may circumvent these

avoidance strategies by concentrating their efforts where krill is more dispersed (i.e. the upper portion of the distribution of krill in the water column). In contrast, the logical strategy for a krill trawler when encountering the same swarm would be to trawl the deeper, denser portion of the krill swarm. Thus, we would predict a penguin to dive to shallower depths than a trawler would optimally fish given the identical krill swarm; Thirdly, while the average size of krill taken by penguins in the South Shetland region was higher than that taken by trawlers, this is a result of trawlers taking a high proportion of small krill as well as larger krill. The distribution of krill size taken by penguins presented by Ichii et al. was contained entirely within the distribution of krill size taken by the fishery. Thus, the overlap with the fishery is actually complete, contrary to the conclusion of Ichii et al.

Our estimates provide additional evidence that top marine predators, with their high metabolic rates and population sizes, are significant consumers of offshore prey resources. The high degree of overlap between land-based predators and the krill fishery in the quantity, species, timing, and location of catches indicates that there is a high potential for competition. Coupling this with the relatively high estimates of consumption relative to krill biomass in the South Shetland Island region increases the potential for conflict. To the extent that penguins and fur seals are food limited, and krill availability is limited by the commercial fishery, populations of these predators will be affected. It is logical, therefore, that they be considered important components of the marine ecosystem when considering fisheries management strategies.

**Acknowledgements** The authors wish to thank D. Agnew, J.L. Bengtson, R.L. Gentry, E.V. Miller, and two anonymous reviewers for useful comments on the manuscript. The Asociación de Biólogos Ambulantes helped in the development of the energetic model. Support for model preparation was provided by the U.S. National Oceanic and Atmospheric Administration (NOAA) as part of its Antarctic Marine Living Resources (AMLR), and U.S. Office of Naval Research Grant N00014-95-10646 to D. Croll.

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