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Are penguins and seals in competition for Antarctic krill at South Georgia?

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Abstract The Antarctic fur seal (*Arctocephalus gazella*) and macaroni penguin (*Eudyptes chrysolophus*) are sympatric top predators that occur in the Southern Ocean around South Georgia where they are, respectively, the main mammal and bird consumers of Antarctic krill (*Euphausia superba*). In recent years the population of fur seals has increased, whereas that of macaroni penguins has declined. Both species feed on krill of similar size ranges, dive to similar depths and are restricted in their foraging range at least while provisioning their offspring. In this study we test the hypothesis that the increased fur seal population at South Georgia may have resulted in greater competition for the prey of macaroni penguins, leading to the decline in their population. We used: (1) satellite-tracking data to investigate the spatial separation of the Bird Island populations of these two species whilst at sea during the breeding seasons of 1999 and 2000 and (2) diet data to assess potential changes in their trophic niches between 1989 and 2000. Foraging ranges of the two species showed considerable overlap in both years, but the concentrations of foraging activity were significantly

segregated spatially. The size of krill taken by both species was very similar, but over the last 12 years the prevalence of krill in their diets has diverged, with nowadays less krill in the diet of macaroni penguins than in that of Antarctic fur seals. Despite a significant degree of segregation in spatial resource use by the study populations, it is likely that the South Georgia populations of Antarctic fur seal and macaroni penguin exploit the same krill population during their breeding season. For explaining the opposing population trends of the two species, the relative contributions of independent differential response to interannual variation in krill availability and of interspecies competition cannot be resolved with available evidence. The likely competitive advantage of Antarctic fur seals will be enhanced as their population continues to increase, particularly in years of krill scarcity.

Introduction

Interspecific competition may play a significant role in community structure (e.g. Connell 1983; Schoener 1983; Diamond and Case 1986; Roughgarden 1989). If species are to avoid competition and to coexist stably whilst exploiting similar, limiting resources, they are expected to show partitioning along at least one resource axis (Hutchinson 1957). The existence of competition between species is extremely difficult to assess, but we can often determine overlap in resource use between species. The Southern Ocean ecosystem, especially in the South Atlantic sector, is largely dependent on Antarctic krill, *Euphausia superba* Dana, as the key prey item. Based upon spatial analysis, resource partitioning appears to exist amongst several groups of seabird species in the Southern Ocean, many of which feed on krill (e.g. Croxall and Prince 1980a; Weimerskirch et al. 1988; Croxall et al. 1997; Waugh et al. 1999; González-Solis et al. 2000). Several studies have investigated resource partitioning between

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sympatric penguin species, and mainly found differences in diet and breeding chronology (Trivelpiece et al. 1987; Cooper et al. 1990; Hindell et al. 1995; Hull 1999). The local availability of krill varies enormously between years, and at least in some years at South Georgia it is a limiting factor that can affect reproductive success of the top predators in the ecosystem (Croxall et al. 1999). Recently, it has been shown that years of low reproductive output by predators at South Georgia have become more frequent in the last decade (Reid and Croxall 2001), suggesting that their populations may now be having greater difficulty in avoiding limiting conditions. Coexisting predators reliant on this limited prey population might therefore be expected to be in competition.

There are two sympatric, particularly abundant predators in the Southern Ocean around South Georgia, the Antarctic fur seal (*Arctocephalus gazella*) and the macaroni penguin (*Eudyptes chrysolophus*), respectively, the main mammal and bird consumers of krill (Croxall et al. 1985). There are an estimated five million breeding macaroni penguins around South Georgia (Trathan et al. 1998) and more than three million Antarctic fur seals (Boyd 1993; British Antarctic Survey data). Both feed mainly on Antarctic krill in the same size range (Croxall and Prince 1980b; Reid and Arnould 1996; Croxall et al. 1999; Reid et al. 1999a,b) by diving to depths of 10–60 m on average (Croxall et al. 1988a, 1993; Boyd and Croxall 1992). The breeding seasons of these two species are highly synchronous and coincident (Gentry and Kooyman 1986; Williams and Croxall 1991) and both rear one offspring per year. During this time both species are restricted in their foraging ranges by the need to return at regular intervals to the colony to feed their offspring.

There are differences in the constraints on foraging behaviour of these two predators, at least during the breeding season, some of which will relate to the difference in size between macaroni penguins (3.5–4.0 kg) and female fur seals (30–40 kg). Both macaroni penguin parents provision their offspring and regurgitate stomach contents directly to their chick. This places an upper limit (the stomach capacity) to the volume of food brought back after each foraging trip. In contrast, only female fur seals provision their offspring and do this by storing fat on a foraging trip and converting this to milk before being given to the pup. Consequently, fur seals can deliver a larger quantity of energy per visit to the offspring and can adjust the delivery rate more precisely. This could place fur seals at an energetic advantage compared with penguins, because less efficient delivery and the requirement on penguins to return to the offspring at greater frequency than fur seals will involve a greater energetic cost due to additional travel (Boyd 1999). The time spent at sea, the distance travelled and therefore the potential foraging area available to the two species may differ as a result of these differences in energetic requirements; we predict that fur seals will be able to forage at greater distances from their breeding colonies than penguins.

The extent of segregation between the trophic niches of these two sympatric predators has not been investigated previously. The effects of competition on coexistence are usually studied among taxonomically similar species, based on the assumption that the ability to detect and process food is dependent on morphology (Stevens and Willig 2000) and that morphological similarity therefore reflects ecological similarity. Although penguins and seals are not very similar taxonomically, there are numerous morphological similarities between them, reflecting convergence with respect to adaptations for life underwater. Although little is known about how these two groups of animals detect and catch their prey, considerable potential for competition between them must exist.

Over the last two or three decades, the population of macaroni penguins at South Georgia has declined (Ellis et al. 1998; Trathan et al. 1998; Fig. 1), and the current number of breeding pairs may be only half the five and a half million estimated by Croxall and Prince (1979). In contrast, the population of Antarctic fur seals has increased at a very rapid rate since the late 1950s (Payne 1977), recovering from virtual extinction during the first half of the nineteenth century to about 400,000 in 1972 and to a present day estimate of more than three million individuals. There has also been a breeding range expansion across the north-west end of South Georgia (Boyd 1993). Understanding the extent and importance of interactions in foraging behaviour between these two species is an essential part of determining factors that may be influencing these observed population changes and therefore of predicting likely future changes.

Has the expanding fur seal population at South Georgia resulted in greater competition for the prey of macaroni penguins and a concomitant decrease in their population? In this study we investigate this question by assessing the trophic niches of the two species from breeding colonies at Bird Island, which lies 1 km off the north-west tip of South Georgia. This site has breeding populations of about 90,000 macaroni penguins and

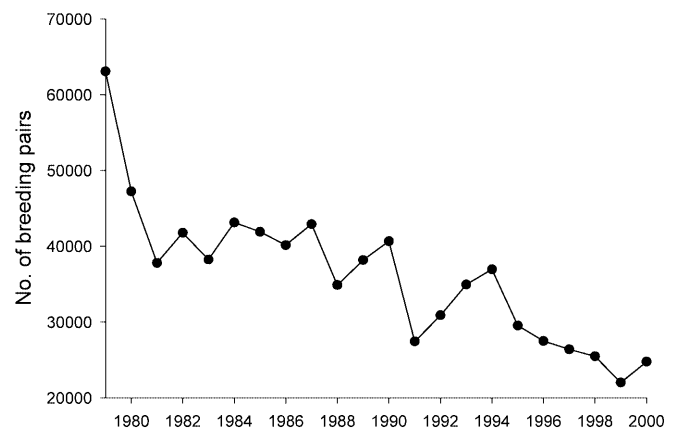


Fig. 1 *Eudyptes chrysolophus*. Estimated (methods as described in Croxall and Prince 1979) population changes of macaroni penguins in the colony at Goldcrest Point, Bird Island from 1979–2000

100,000 Antarctic fur seals, and is close to the main South Georgia population centres of these species. Thus within a radius of 50 km of Bird Island, 85% of the South Georgia macaroni penguin population (mainly on the Willis Islands 5–10 km to the west) and 75% of the South Georgia fur seal population (on the mainland to the east) breed. The foraging areas of female fur seals from Bird Island during the breeding season have recently been determined using satellite-tracking techniques (Boyd et al. 1998), but there are only limited data on the foraging ranges of macaroni penguins in the area, estimated from distributions of penguins observed at sea (Trathan et al. 1998). The aims of the present study were: (1) to examine the foraging areas of the two species during the breeding season and to assess the extent of spatial overlap between them by satellite-tracking them simultaneously from Bird Island and (2) to determine the contribution of krill to the diets of the two species during the breeding season, with a view to assessing trophic resource partitioning and the potential for competition between them.

Materials and methods

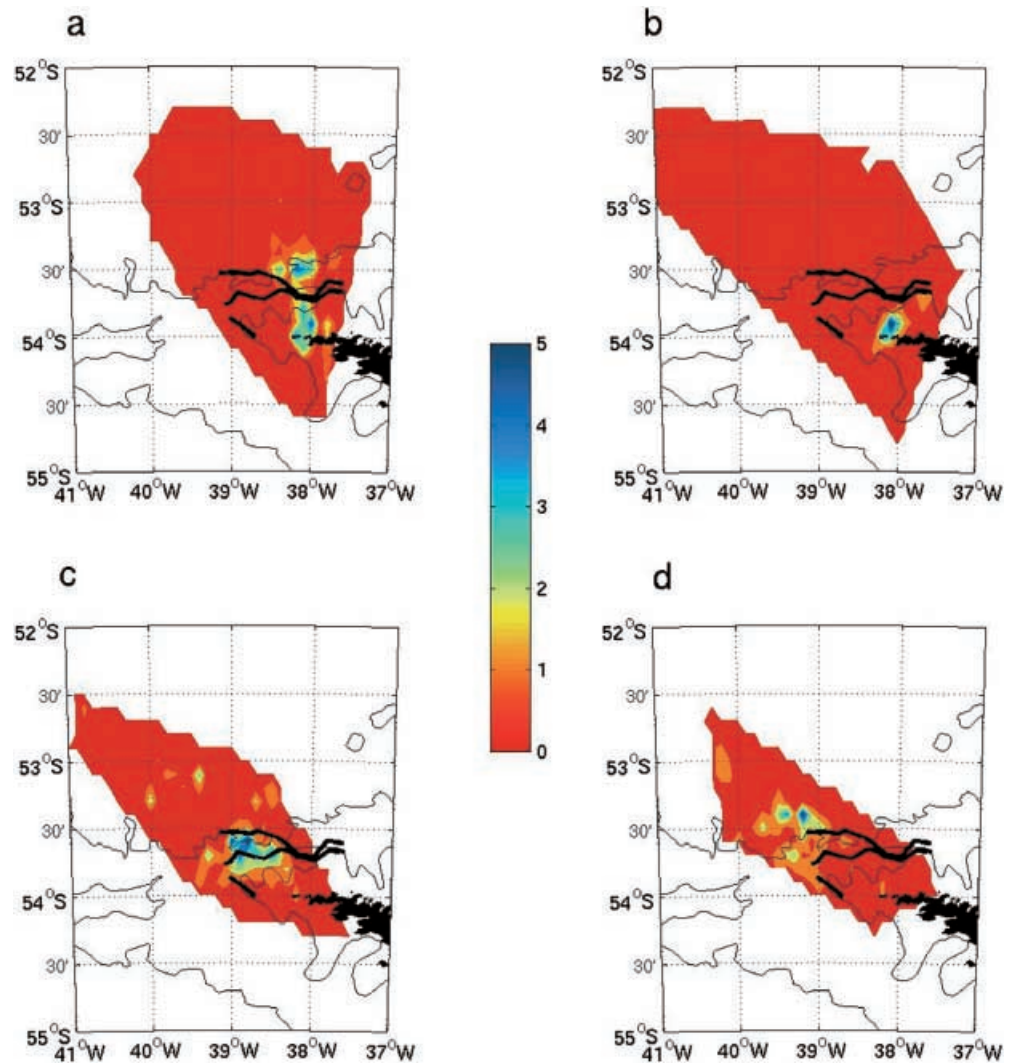
Study site

The study was carried out at Bird Island, South Georgia (54°00'S; 38°02'W; Fig. 2) during January and February 1999 and 2000. Breeding birds at the Fairy Point macaroni penguin (*Eudyptes chrysolophus*) colony were marked during the first part of the breeding season with a number painted on the chest feathers with a black dye, so that they could be identified individually. Study birds were selected randomly from nests in the outer part of the colony to minimise disturbance. Breeding female fur seals (*Arctocephalus gazella*) from the beach at Freshwater Inlet were given flipper tags (Dalton Supplies, Henley-on-Thames, UK) for identification.

Satellite tracking instruments

Marked penguins were captured at the colony during the chick-rearing period in January and February. When possible, birds were captured once they had fed the chick and left the nest to start to return to sea, in order to reduce disturbance. A platform transmitter terminal (ST-10 PTT; Telonics, USA, packaged by Sirtrack, New Zealand) was attached to the lower medial portion

Fig. 2a–d *Eudyptes chrysolophus* (a, b), *Arctocephalus gazella* (c, d). Maps of density distributions during January and February 1999 (a, c) and 2000 (b, d) on foraging trips from Bird Island during the breeding season. The maps show the northern end of South Georgia, the 200 and 2,000 m depth contours [General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas, 1994] with the frontal positions to the north of South Georgia overlain in **bold** (Brandon et al. 2000). The area to the south of the two **lines** is South Georgia Shelf Water, the area to the north is Antarctic Zone water and the area in between is the approximate position of the frontal region, although it may vary between years (Brandon et al. 2000). The density distributions are constructed from contour plots of five contours with a linear spline interpolation (**red** lowest density; **blue** highest)



of the back of the penguin using waterproof tape and epoxy resin, following methods described by Wilson et al. (1997). The PTTs (mass 85 g, dimensions 95×42×20 mm) were streamlined at the front of the device to reduce hydrodynamic drag (Culik et al. 1994). Each bird was weighed and sexed by bill measurements, following Williams and Croxall (1991). Sex was confirmed by the pattern of attendance at the nest. The attachment procedure took <20 min in total, and penguins were then released close to their nest or capture site. Devices were attached to female penguins during the guard stage and to male and female penguins during the creche stage of the chick-rearing period. Each device was deployed on an individual bird for one to six foraging trips (about 2–12 days).

ST-10 PTTs were also deployed on marked, lactating female fur seals captured on the breeding beach, following the method described in Boyd et al. (1998). Devices were deployed during the same time period as for the penguins, in January and February. Each device was deployed on an individual seal for one or two foraging trips (about 3–12 days).

Location data and analysis

Locations of penguins and seals carrying devices were provided by the ARGOS system and assigned to one of six classes (3, 2, 1, 0, A, B) depending on their accuracy. Classes 1–3 gave positions accurate to within 1–2 km on average, class 0 gave positions accurate to 3.8 km on average and only these four classes were used in analysis (Boyd et al. 1998). The individual animal was used as the unit of analysis, but the number of foraging trips was greater than the number of animals in some cases, as more than one trip was recorded from some individuals. To verify the location data, the speed (km h^{-1}) travelled between adjacent locations within each foraging trip was calculated. If the calculated speed from a previous location was $> 10 \text{ km h}^{-1}$ for macaroni penguins, this location was deleted. Estimated swimming speed for the macaroni penguins is 7.5 km h^{-1} on average (Brown 1987), and 10 km h^{-1} was used as a conservative cut off speed to avoid overestimating distance travelled during foraging trips. The same method was used to verify the location data from fur seals; average swim speed of Antarctic fur seals is around 6.5 km h^{-1} (Boyd 1996).

The location data were used to determine foraging density distributions of macaroni penguins and Antarctic fur seals during the breeding season. Percentage frequency tables of the distribution of locations within 0.1 degree squares (approximately $11 \times 9 \text{ km}$) were constructed for each individual. The 0.1 degree square was selected as a much smaller square would be lower than the level of location accuracy and a much larger square would significantly lessen the resolution of the analysis. The mean proportion of locations from all individuals was used to create a contour plot of the distribution density for each species in each year. The contour plots were constructed using a linear spline interpolation of the distribution data on a 0.1 degree square grid in Matlab (The MathWorks, USA).

The distribution of positions was compared between years and between species using a bootstrapping procedure on the Pearson product-moment correlation coefficient between the density of seals versus the density of penguins on a 0.1 degree grid. Bootstrapping was carried out by repeatedly re-creating spatial distributions using random selection (with replacement) of the foraging patterns of individual birds or seals and by allocating them at random to the

groups being compared in the analysis. The number of animals allocated to each group was the same as in the original sample. This procedure allowed us to determine the probability that the observed seal/penguin correlation could occur by chance, without the need to make specific assumptions about parameter distribution. By using the individual bird or seal as the sampling unit, this method also overcame the problems associated with autocorrelation between locations within the tracks of individuals (see White and Garrott 1990; Priede and Swift 1992). Two comparisons were carried out, one to determine differences between the density distributions of the two species between years and one to determine differences between species. The more negative the correlation between the two density distributions, the more different they were; the more positive the correlation, the more similar the distributions. Therefore, the density distribution of the two groups was assumed to be significantly different if $< 5\%$ of the 1,000 bootstrapped correlation coefficients had a more negative value than that calculated from the original data.

Diet

The diet of macaroni penguins was examined in breeding seasons between 1989 and 2000 by food sampling ten birds each week during January and February from the breeding colony, following the methods described in Wilson (1984) and Williams (1991). The amount of krill (*Euphausia superba*) in the diet was determined by calculating the percentage wet mass of krill in each sample and averaging these to determine the mean for each year.

The diet of fur seals was examined in the breeding seasons of 1989 and between 1991 and 2000 by collecting ten scats each week during January and February from the Freshwater Bay breeding beach, following the methods described in Reid and Arnould (1996). The amount of krill in the diet was determined by calculating the percentage of scats that contained krill for each year.

The amount of krill in the diets could not be compared statistically between the two species due to differences in the sampling techniques used. For penguins, the percentage wet mass of krill directly represents the proportion of krill in the diet. For seals, however, the potential bias of differing digestive rates may affect the proportions of different prey groups found in faecal samples (e.g. Pierce and Boyle 1991). The estimated contribution of krill to the diet of seals is basically therefore only a frequency of occurrence measure; its relationship with krill abundance cannot be quantified or investigated statistically.

In order to consider the component of the krill population exploited, the length-frequency distribution of krill taken by both species was compared during the period when data were available for both species. The length-frequency distribution of krill in the diet was estimated following the methods described in Reid et al. (1999b).

Results

Spatial distribution of predators

The numbers of penguins (*Eudyptes chrysolophus*) and seals (*Arctocephalus gazella*) that carried devices and the number of trips recorded during each stage of the

Table 1 *Eudyptes chrysolophus*, *Arctocephalus gazella*. Number of penguins and number of seals instrumented during 1999 and 2000 at each stage of the breeding season and the total number of foraging trips recorded in each group

Taxon	Stage	1999		2000	
		Individuals	Trips	Individuals	Trips
Penguins	Guard (female)	17	44	12	38
	Creche (male)	9	24	5	13
	Creche (female)	–	–	4	8
Seals	Females	11	27	14	14

breeding season in each year are shown in Table 1. There was overlap in the density distributions of macaroni penguins and Antarctic fur seals during the 2 years of the study (Fig. 2). In 1999 and 2000, 25% and 16%, respectively, of 0.1 degree squares in which locations were recorded were used by both species. Both distributions covered an area to the north-west of Bird Island, over and beyond the continental shelf. However, the areas of the highest density of locations differed between the two species (Fig. 2). The main concentrations of fur seal activity were found around the 2,000 m depth contour, whereas the main concentration of locations from macaroni penguins, particularly in the year 2000, was closer to Bird Island. The overall area of the foraging range used by penguins, however, was greater than that used by seals. The bootstrap analysis showed that the density distribution of the two species differed significantly ($P=0.001$), but that there was no significant difference in the density distributions of the two species between years ($P=0.113$).

Diet

The percentage of krill in the diet of macaroni penguins varied between years from 11.2% in 1994 to 99.9% in 1996; the average over the 10 years was 69.1% (Fig. 3). The percentage of fur seal scats containing krill ranged from 71% in 1994 to 100% in 1992, 1993, 1999 and 2000 (Fig. 3; Reid and Arnould 1996; McCafferty et al. 1998). In 1994, the contribution of krill to the diet of both species was low (fur seals 71% of scats, penguins 11.2% by mass). From 1994 to 2000, however, the overall amount of krill in the diet of macaroni penguins was much lower than in fur seals (fur seal mean=93%, penguin mean=55%, Fig. 3). In 1999 the length-frequency distributions of krill taken by Antarctic fur

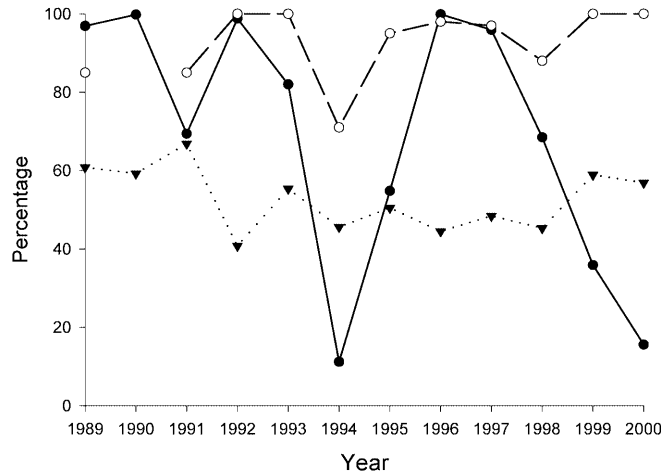
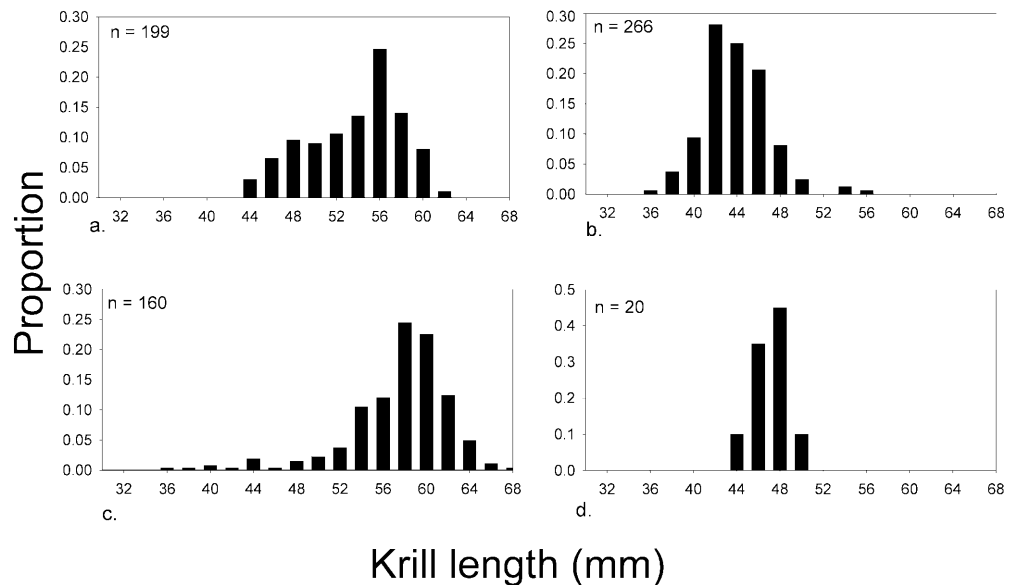


Fig. 3 *Eudyptes chrysolophus*, *Arctocephalus gazella*. The contribution of krill (*Euphausia superba*) to the diets of macaroni penguins (filled circles) and Antarctic fur seals (open circles), and the reproductive success of macaroni penguins (inverted triangles) at Bird Island, South Georgia from 1989 to 2000. Diet data are the percentage by wet mass of krill in the diet of macaroni penguins during the breeding season and the percentage of fur seal scats collected during the breeding season that contained krill. Reproductive success is expressed as the proportion of chicks fledged per breeding pair

seals and macaroni penguins had modal sizes of 56 and 58 mm, respectively, and in both species <20% of krill taken were smaller than 50 mm (Fig. 4). In 2000, >90% of the krill in the length-frequency distribution from both species was smaller than 50 mm, and while the modal sizes differed by 6 mm, all of the krill taken by macaroni penguins were within the size range taken by Antarctic fur seals. This is consistent with the conclusions derived from similar comparisons in other years (Reid et al. 1996, 1999a,b). Taken together, these results suggest that both species were exploiting the same population of krill at South Georgia.

Fig. 4a–d *Arctocephalus gazella*, *Eudyptes chrysolophus*. Length-frequency distribution of Antarctic krill (*Euphausia superba*) in the diet of Antarctic fur seals in 1999 (a) and 2000 (b) and of macaroni penguins in 1999 (c) and 2000 (d)



Krill length (mm)

Discussion

Over the last 12 years, the population of macaroni penguins (*Eudyptes chrysolophus*) at the main (Goldcrest Point) colony on Bird Island, measured as the number of breeding pairs, has decreased significantly (Fig. 5). This decrease has been mirrored in the other colonies at Bird Island and at the main colonies elsewhere at north-west South Georgia (Trathan et al. 1998; S. Poncet, unpublished data). In contrast, the population of fur seals (*Arctocephalus gazella*), measured as pup production at the Bird Island study beach, has shown no significant change during this period (Fig. 5). The overall Bird Island fur seal population, which has been increasing since counts began in 1957 (Boyd et al. 1990), also showed no significant trend from 1983 to 1991 when it reached assumed carrying capacity (Boyd et al. 1990; Boyd 1993); however the fur seal population around South Georgia has continued to increase. It is, therefore, a plausible hypothesis that the increasing predator populations have begun to reach the maximum that finite prey resources can support (Reid and Croxall 2001) and that increased krill consumption by seals may have led to reduced krill availability for penguins. Our new data on the foraging ranges and areas of the two species during their breeding season, together with a re-examination of the nature and proportion of krill in their diets, provides a fresh basis for re-evaluation of the hypothesis that interspecies competition may have contributed to the recent decrease in macaroni penguin populations at South Georgia.

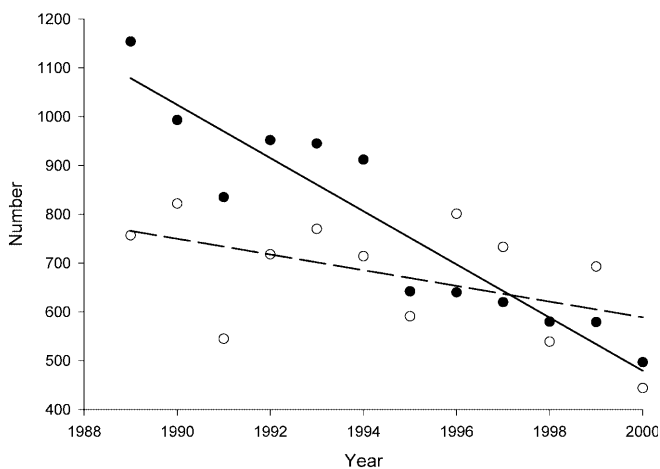


Fig. 5 *Eudyptes chrysolophus*, *Arctocephalus gazella*. Population changes of macaroni penguins in the Fairy Point study colony (filled circles) and Antarctic fur seals at the study beach (open circles), Bird Island between 1989 and 2000. The number of breeding pairs of macaroni penguins at the Fairy Point colony declined significantly ($r^2=0.87$, $F_{1,10}=67.7$, $P<0.0001$), whereas there was no significant change in Antarctic fur seal pup production (equivalent to the number of breeding females) at the study beach ($r^2=0.24$, $F_{1,10}=3.11$, $P=0.108$)

Spatial distribution

There are some biases in using satellite location data to construct density distributions. For example, locations are only obtained from instrumented animals at times of day when sufficient satellites are in view (e.g. Georges et al. 1997) and when the animal is at the surface for a period long enough to obtain a location. However, as both species in this study are diving predators, with similar dive durations and inter-dive surface intervals, we expect the biases to be similar. Additionally, satellite locations can only be considered as a measure of activity rather than foraging, as it is not possible to relate locations to diving behaviour (Georges et al. 1997). However, the density distributions of fur seal activity calculated in this study from satellite locations were very similar to those constructed from interpolated foraging locations using diving data and satellite-tracking data combined (Boyd et al. 1998), so we believe position to be a good proxy for foraging effort. The effects of the devices themselves on the foraging behaviour of both species have previously been shown to be small (Boyd et al. 1998; Barlow and Croxall, in press).

The density distributions of macaroni penguins and Antarctic fur seals during the 2 years of this study showed that there was substantial overlap between their foraging areas. Although much of the overall foraging range of the Bird Island populations of the two species was similar, there was significant separation in the regions in which their activity was concentrated. The concentration of activity of macaroni penguins was closer to Bird Island than was that of Antarctic fur seals. This is consistent with our prediction that fur seals would be able to forage at a greater range from their offspring than would macaroni penguins. The overall foraging range of both species was mainly restricted to an area to the north and north-west of Bird Island, which represents only a small fraction of the potential area available to them if they were to travel in all possible directions from Bird Island. Therefore, when foraging from Bird Island, the populations of both species are only using part of the potential foraging area available to them, and the parts of this area used differ between them.

The distribution of fur seals and macaroni penguins found in the present study differs from distributions derived from at-sea observations (Hunt et al. 1992; Trathan et al. 1998), which show a much more even radial distribution of fur seals and penguins from the northern end of South Georgia, including major concentrations to the south of Bird Island. The distributions seen in our study suggest non-random use of their potential foraging range. However, we only tracked fur seals and penguins from Bird Island. It is probable that the large numbers of penguins breeding at other colonies at the northern end of South Georgia, for example the Willis Islands (Prince and Poncet 1996), and the major colonies of fur seals on the north-west South Georgia mainland, use other areas during their foraging trips. However, given that these main breeding concentrations

lie to the west (macaroni penguin) and east (Antarctic fur seal) of the study sites, there is no reason why the spatial segregation of the main foraging areas of the two species should not be maintained at a level similar to that shown by the study populations.

Indeed, the location of concentrations of activity of macaroni penguins and Antarctic fur seals may be related to the bathymetry and oceanography around the northern end of South Georgia, which in turn influences prey distribution. Brandon et al. (2000) show that there are two main water masses around the northern tip of the island, one of water from the South Georgia shelf, the other of Antarctic Zone water, with a frontal region between which there is a strong upwelling zone (Fig. 2). In the 2 years of this study, the concentrations of activity of macaroni penguins were mainly found within the South Georgia shelf water, whereas the concentrations of fur seal activity were within the frontal zone. It is possible that characteristics of the prey available to the two predators in foraging in different water masses may differ.

Trophic niche separation

The size-distributions of krill taken by Antarctic fur seal and macaroni penguins are very similar, especially in terms of the sizes which contribute most to the biomass of krill in their diets. However, whereas during the 1980s, both fur seals and penguins were considered to be reliant on krill as their key prey item (Croxall et al. 1988b), diet data from the last 12 years suggest that this has recently been less so for macaroni penguins. Moreover, during the 2 years in which penguins and fur seals were tracked in this study, the percentage of krill in the diet of macaroni penguins was lower than in 9 of the previous 10 years, whereas the frequency of occurrence of krill in fur seals was the highest recorded. This low occurrence of krill in the macaroni penguin diet presumably reflects low krill availability in their foraging area, whereby penguins are forced to switch to alternative prey sources (Croxall et al. 1999).

Indeed, over the last 6 years the proportion of krill in macaroni penguin diet has been significantly correlated with the density of krill around north-west South Georgia as estimated from krill acoustic surveys (Fig. 6). Unfortunately, because of the limitations of their diet samples, we cannot undertake a similar analysis for fur seals. This prevents critical comparison of the nature and magnitude of species-specific dietary responses to interannual fluctuations in krill abundance and/or availability.

However, both penguins and fur seals have been shown to respond to years of low krill availability through changes in foraging and reproductive performance (Croxall et al. 1999; Reid and Croxall 2001). In such years fur seals show obvious effects on reproductive success, with high mortality of offspring, particularly early in the breeding season, but no apparent effect on adult survival (Boyd et al. 1995; Croxall et al. 1999). Reproductive success of macaroni penguins, however,

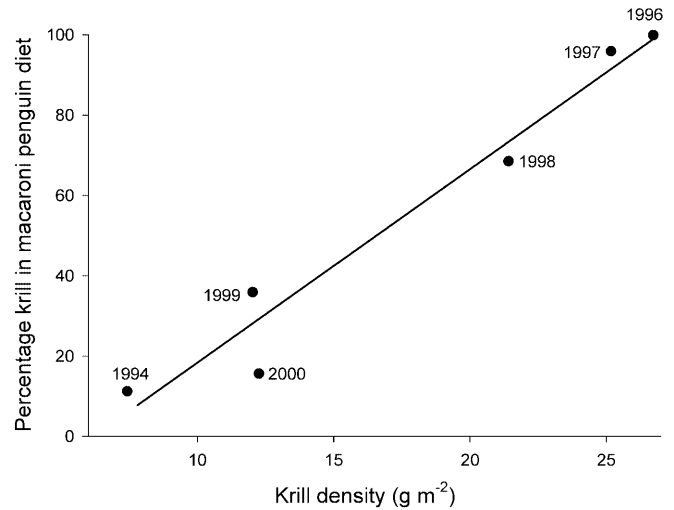


Fig. 6 *Eudyptes chrysolophus*, *Euphausia superba*. Relationship between the percentage by wet mass of krill in the diet of macaroni penguins and estimated krill density (g m^{-2}) at the north-western end of South Georgia between 1994 and 2000 ($r^2=0.96$, $F_{1,5}=92.9$, $P=0.0006$). Diet data from Fig. 3; krill density data from Brierley et al. (1997, 1999), Brierley and Goss (1999) and AtlantNIRO/BAS (unpublished data)

has shown no significant trend over the past 12 years ($r^2=0.09$, $F_{1,10}=0.93$, $P=0.357$, Fig. 3), although in years of low krill availability the mass of chicks at fledging was reduced (Croxall et al. 1999), which may prejudice their future survival. It would, however, be misleading to conclude that, in terms of long-term fitness, macaroni penguins are better able to cope with low levels of krill availability than fur seals, especially without data on adult survival and juvenile recruitment of penguins.

Conclusions

It is rarely possible to determine directly whether resource partitioning between species is a result of evolutionary avoidance of competition (Connell 1980) or of other selective pressures acting independently on each species (Begon et al. 1990). In the present situation it is impossible to determine whether the contemporaneous increase in South Georgia fur seal populations and decrease in macaroni penguin populations simply reflect different and independent species-specific responses to variation in krill availability, or whether (or to what extent) they have been substantially influenced by direct interspecific competition.

We have shown that the foraging range of the Bird Island populations of macaroni penguin and Antarctic fur seal when breeding show substantial overlap, but that the main foraging areas show a significant degree of separation. Nevertheless, the nature and size of the krill eaten by both species are very similar. Together with existing knowledge on the transport of krill to the South Georgia region (Murphy et al. 1998) and its population structure and dynamics, this suggests that both preda-

tors are very likely to be consuming krill from the same overall population.

We have also shown that fur seals, as predicted by the duration of their foraging trips and their adaptations for offspring provisioning, are able to forage further afield, particularly at adjacent frontal systems, than macaroni penguins. It is likely that this confers an important potential competitive advantage, perhaps particularly in years when krill are scarce. In such circumstances macaroni penguins may have to exploit alternative prey sources (as suggested by their progressively reduced reliance on krill in recent years), at a cost of reduced efficiency in provisioning offspring (Croxall et al. 1999) and possibly also of overall fitness.

On the basis of this assessment and interpretation it seems highly probable that, in the exploitation of krill around South Georgia in summer, there is a dynamic interaction between the populations of macaroni penguins and Antarctic fur seals which currently favours fur seals. The level and importance of direct interspecific competition is still uncertain, but it is very likely to increase markedly as fur seal populations continue to increase and if the recent frequency of years of low krill availability (Reid and Croxall 2001) is maintained. Continued studies of the demography and resource use of these two species will be essential for understanding the species' interactions and their longer term prospects in the Southern Ocean ecosystem.

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References

- Barlow KE, Croxall JP (in press) Seasonal and interannual variation in foraging range and habitat of macaroni penguins at South Georgia. *Mar Ecol Prog Ser*
- Begon M, Harper JL, Townsend CR (1990) *Ecology. Individuals, populations and communities*, 2nd edn. Blackwell, Oxford
- Boyd IL (1993) Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarc Sci* 5:17–24
- Boyd IL (1996) Temporal scales of foraging in a marine predator. *Ecology* 77:426–434
- Boyd IL (1999) Foraging and provisioning in Antarctic fur seals: interannual variability in time–energy budgets. *Behav Ecol* 10:198–208
- Boyd IL, Croxall JP (1992) Diving behaviour of lactating Antarctic fur seals. *Can J Zool* 70:919–928
- Boyd IL, Lunn NJ, Rothery P, Croxall JP (1990) Age distribution of breeding female Antarctic fur seals in relation to changes in population growth rate. *Can J Zool* 68:2209–2213
- Boyd IL, Croxall JP, Lunn NJ, Reid K (1995) Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *J Anim Ecol* 64:505–518
- Boyd IL, McCafferty DJ, Reid K, Taylor RI, Walker TR (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Can J Fish Aquat Sci* 55:845–852
- Brandon M, Murphy EJ, Trathan PN, Bone DG (2000) Physical oceanographic conditions to the northwest of the sub-Antarctic Island of South Georgia. *J Geophys Res* 105:23983–23986
- Brierley AS, Goss C (1999) Acoustic estimates of krill density at South Georgia, Dec/Jan 1998/99. In: CCAMLR Scientific Abstracts, WG-EMM-99/20, CCAMLR, Hobart
- Brierley AS, Watkins JL, Murray AWA (1997) Interannual variability in krill abundance at South Georgia. *Mar Ecol Prog Ser* 150:87–98
- Brierley AS, Watkins JL, Goss C, Wilkinson MT, Everson I (1999) Acoustic estimates of krill density at South Georgia, 1981 to 1998. *CCAMLR Sci* 6:47–57
- Brown CR (1987) Travelling speed and foraging range of macaroni and rockhopper penguins at Marion Island. *J Field Ornithol* 58:118–125
- Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Cooper J, Brown CR, Gales RP, Hindell MA, Klages NTW, Moors PJ, Pemberton D, Ridoux V, Thompson KR, van Heezik YM (1990) Diets and dietary segregation of crested penguins. In: Davis LS, Darby JT (eds) *Penguin biology*. Academic, San Diego, pp 129–156
- Croxall JP, Prince PA (1979) Antarctic seabird and seal monitoring studies. *Polar Rec* 19:573–595
- Croxall JP, Prince PA (1980a) Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol J Linn Soc* 14:103–131
- Croxall JP, Prince PA (1980b) The food of gentoo penguins *Pygoscelis papua* and macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Ibis* 122:245–253
- Croxall JP, Prince PA, Ricketts C (1985) Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. In: Siegfried WR, Condy PR, Laws RM (eds) *Antarctic nutrient cycles and food webs*. Springer, Berlin Heidelberg New York, pp 516–533
- Croxall JP, Davis RW, O'Connell MJ (1988a) Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia. *Condor* 90:157–167
- Croxall JP, McCann TS, Prince PA, Rothery P (1988b) Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. In: Sahrhage D (ed) *Antarctic Ocean and resources variability*. Springer, Berlin Heidelberg New York, pp 261–285
- Croxall JP, Briggs DR, Kato A, Naito Y, Watanuki Y, Williams TD (1993) Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J Zool (Lond)* 230:31–47
- Croxall JP, Prince PA, Reid K (1997) Dietary segregation of krill-eating South Georgia seabirds. *J Zool (Lond)* 242:531–556
- Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar Ecol Prog Ser* 177: 115–131
- Culik BM, Bannasch R, Wilson RP (1994) External devices on penguins: how important is shape? *Mar Biol* 118:353–357
- Diamond J, Case TJ (1986) *Community ecology*. Harper and Row, New York
- Ellis S, Croxall JP, Cooper J (1998) *Penguin conservation and management plan*. Report of IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, Minn.
- Gentry RL, Kooyman GL (1986) *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton
- Georges J-Y, Guinet C, Jouventin P, Weimerskirch H (1997) Satellite tracking of seabirds: interpretation of activity pattern from the frequency of satellite locations. *Ibis* 139:403–405
- González-Solís J, Croxall JP, Wood AG (2000) Foraging partitioning between giant petrels *Macronectes* spp. and its rela-

- tionship with breeding population changes at Bird Island, South Georgia. *Mar Ecol Prog Ser* 204:279–288
- Hindell MA, Robertson GG, Williams R (1995) Resource partitioning in four species of sympatrically breeding penguins. In: Dann P, Norman I, Reilly P (eds) *The penguins: ecology and management*. Surrey Beatty, Chipping Norton, pp 196–215
- Hull CL (1999) Comparison of the diets of breeding royal *Eudyptes schlegeli* and rockhopper *E. chrysochome* penguins at Macquarie Island over three years. *J Zool (Lond)* 247:507–529
- Hunt GL, Heinemann D, Everson I (1992) Distribution and predator–prey interactions of macaroni penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. *Mar Ecol Prog Ser* 86:15–30
- Hutchinson GE (1957) Concluding remarks. In: *Proceedings of the Cold Spring Harbor symposia of quantitative biology*, vol 22. Cold Spring Harbor Press, New York, pp 284–294
- McCafferty DJ, Boyd IL, Walker TR, Taylor RI (1998) Foraging responses of Antarctic fur seals to changes in the marine environment. *Mar Ecol Prog Ser* 166:285–299
- Murphy EJ, Watkins JL, Reid K, Trathan P, Everson I, Croxall JP, Priddle J, Brandon MA, Brierley AS, Hofmann E (1998) Interannual variability of the South Georgia marine ecosystem: biological and physical sources of variation in the abundance of krill. *Fish Oceanogr* 7:381–390
- Payne MR (1977) Growth of a fur seal population. *Philos Trans R Soc Lond Ser B Biol Sci* 279:67–79
- Pierce GJ, Boyle PR (1991) A review of methods for diet analysis in piscivorous marine mammals. *Oceanogr Mar Biol Annu Rev* 29:409–486
- Priede IG, Swift SM (1992) *Wildlife telemetry: remote monitoring and tracking of animals*. Ellis Horwood, Chichester
- Prince PA, Poncet S (1996) South Georgia bird distributions. In: Trathan, PN, Daunt FHJ, Murphy EJ (eds) *South Georgia: an ecological atlas*, section 2. British Antarctic Survey, Cambridge, maps 2.1–2.33
- Reid K, Arnould JPY (1996) The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol* 16:105–114
- Reid K, Croxall JP (2001) Environmental response of upper trophic level predators reveals a system change in an Antarctic marine ecosystem. *Proc R Soc Lond Ser B Biol Sci* 268:377–384
- Reid K, Trathan PN, Croxall JP, Hill HJ (1996) Krill caught by predators and nets: differences between species and techniques. *Mar Ecol Prog Ser* 140:13–20
- Reid K, Barlow KE, Croxall JP, Taylor RI (1999a) Predicting changes in the Antarctic krill, *Euphausia superba*, population at South Georgia. *Mar Biol* 135:647–652
- Reid K, Watkins JL, Croxall JP, Murphy EJ (1999b) Krill population dynamics at South Georgia 1991–1997, based on data from predators and nets. *Mar Ecol Prog Ser* 177:103–114
- Roughgarden J (1989) The structure and assembly of communities. In: Roughgarden J, May RM, Levin SA (eds) *Perspectives in ecological theory*. Princeton University Press, Princeton, pp 203–226
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Stevens RD, Willig MR (2000) Community structure, abundance, and morphology. *Oikos* 88:48–56
- Trathan PN, Murphy EJ, Croxall JP, Everson I (1998) Use of at-sea distribution data to derive potential foraging ranges of macaroni penguins during the breeding season. *Mar Ecol Prog Ser* 169:263–275
- Trivelpiece WZ, Trivelpiece SG, Volkmann NJ (1987) Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68:351–361
- Waugh SM, Weimerskirch H, Cherel Y, Shankar U, Prince PA, Sagar PM (1999) Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Mar Ecol Prog Ser* 177:243–254
- Weimerskirch H, Bartle JA, Jouventin P, Stahl J-C (1988) Foraging ranges and partitioning of feeding zones in three species of southern albatross. *Condor* 90:214–219
- White LC, Garrott RA (1990) *Analysis of wildlife radiotracking data*. Academic, San Diego
- Williams TD (1991) Foraging ecology and diet of gentoo penguins *Pygoscelis papua* at South Georgia during winter and an assessment of their winter prey consumption. *Ibis* 133:3–13
- Williams TD (1995) *The penguins*. Oxford University Press, Oxford
- Williams TD, Croxall JP (1991) Annual variation in breeding biology of macaroni penguins, *Eudyptes chrysolophus*, at Bird Island, South Georgia. *J Zool (Lond)* 223:189–202
- Wilson RP (1984) An improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55:109–112
- Wilson RP, Putz K, Peters G, Culik B, Sclaro JA, Charrassin J-B, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull* 25:101–106