

Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem

K. Reid* and J. P. Croxall

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Long-term changes in the physical environment in the Antarctic Peninsula region have significant potential for affecting populations of Antarctic krill (*Euphausia superba*), a keystone food web species. In order to investigate this, we analysed data on krill-eating predators at South Georgia from 1980 to 2000. Indices of population size and reproductive performance showed declines in all species and an increase in the frequency of years of low reproductive output. Changes in the population structure of krill and its relationship with reproductive performance suggested that the biomass of krill within the largest size class was sufficient to support predator demand in the 1980s but not in the 1990s. We suggest that the effects of underlying changes in the system on the krill population structure have been amplified by predator-induced mortality, resulting in breeding predators now regularly operating close to the limit of krill availability. Understanding how krill demography is affected by changes in physical environmental factors and by predator consumption and how, in turn, this influences predator performance and survival, is one of the keys to predicting future change in Antarctic marine ecosystems.

Keywords: Antarctic krill *Euphausia superba*; South Georgia; predators; system change

1. INTRODUCTION

Detecting and understanding the causes and consequences of long-term change in marine ecosystems is fundamental to many global concerns, not least to successful management of marine resources. Determining how large-scale physical processes influence smaller scale ecological, in particular trophodynamic, processes is crucial in interpreting natural ecosystem variability. Given the substantial within- and between-year variation inherent in large marine ecosystems, even detection of systematic changes in physical processes, such as climate warming, is very difficult. These problems are greatly magnified in detecting progressive changes in the biological environment and/or in the species and systems dependent on this. However, only by understanding the natural variability of a marine ecosystem can the significance of long-term systematic changes, including those of potentially anthropogenic origin, be assessed.

There is evidence for a warming trend of 4–5 °C in the mean annual air temperature in the Antarctic Peninsula region over the past 50 years (King 1994), as well as a trend of decreasing duration of fast-ice over a 90-year time-series in the South Orkney Islands (Murphy *et al.* 1995). Given such changes in the physical environment, we might expect to see indications of responses in key biological species or processes. Although there have been major, systematic changes in the abundances of some top predators (e.g. Antarctic fur seals *Arctocephalus gazella* (Payne 1977; Boyd 1993) and king penguins *Aptenodytes patagonicus* (Woehler & Croxall 1999)) and fluctuations and/or regional trends in others (e.g. Adelie penguins *Pygoscelis adeliae* and chinstrap penguins *Pygoscelis antarctica* (Fraser *et al.* 1992; Trathan *et al.* 1996)), information on the population dynamics of key prey species is crucial to interpreting

these changes. A keystone prey species throughout most of the Southern Ocean, in particular the Antarctic Peninsula/Scotia Sea region, is Antarctic krill (*Euphausia superba*). It has been suggested that krill reproduction and survival are significantly affected by the extent and duration of ice cover (Loeb *et al.* 1997) and that there may have been an overall decrease in krill biomass, at least in the South Atlantic sector, over the last decade (Siegel & Loeb 1995). Such changes could obviously have adverse effects on populations and/or the reproductive performance of the main krill predators, which include Antarctic fur seals and Adelie and chinstrap penguins. However, testing these hypotheses requires lengthy time-series of data for several species of predominantly krill-eating predators. Such data are only available from one site, South Georgia, in the northern Scotia Sea (northeast of the Antarctic Peninsula), where studies of four such species have been undertaken for the last 20 years.

The aim of this paper is to combine and analyse data on reproductive performance and the diet of krill-eating predators at South Georgia in order to (i) identify changes or trends over the course of the study and, in particular, over the last decade; (ii) relate these to evidence for changes in krill abundance and/or demography; and (iii) assess the potential impact of predators on the krill population, as well as the implications for predators of changes in krill populations.

2. METHODS

A 23-year time-series of the reproductive performance of krill-dependent predators at South Georgia has shown that the performance of top trophic-level predators reflects interannual changes in the availability of krill on a regional scale (Croxall *et al.* 1988, 1999). The level of concordance between predator performance and krill availability, when measured simultaneously, indicates that the performance of predators represents a

*Author for correspondence (k.reid@bas.ac.uk).

Table 1. *Description and availability of population size and reproductive success parameters for Antarctic fur seals (A. gazella), gentoo penguins (P. papua), macaroni penguins (E. chrysolophus) and black-browed albatrosses (T. melanophrys) breeding on Bird Island, South Georgia*

(The timing indicates the period over which each parameter integrates with respect to the arrival condition (AC) and reproductive output (RO).)

species	parameter	timing	description	availability
Antarctic fur seal	population size	AC	number of pups born on study beach	1984–2000
Antarctic fur seal	birth mass	AC	mean mass of pups at birth	1984–2000
Antarctic fur seal	survival	RO	number of pups surviving to age <i>ca.</i> 30 days	1979, 1981, 1982 and 1984–2000
Antarctic fur seal	weaning mass	RO	mean mass of all pups at <i>ca.</i> 120 days	1979, 1981, 1982 and 1984–2000
gentoo penguin	population size	AC	number of pairs nesting on Bird Island	1980 and 1982–2000
gentoo penguin	breeding success	RO	number of chicks fledged per pair	1980 and 1982–2000
gentoo penguin	fledging mass	RO	mean mass of chicks at peak of fledging	1989–2000
macaroni penguin	population size	AC	number of pairs in Fairy Point colony	1980–2000
macaroni penguin	arrival mass	AC	mean mass of adults on arrival in colony	1989–2000
macaroni penguin	breeding success	RO	number of chicks fledged per pair	1980–2000
macaroni penguin	fledging mass	RO	mean mass of chicks at peak of fledging	1989–2000
black-browed albatross	population size	AC	number of pairs nesting in colony H	1980–2000
black-browed albatross	breeding success	RO	number of chicks fledged per pair	1980–2000
black-browed albatross	fledging mass	RO	mean mass of chicks at peak of fledging	1989–2000

realistic proxy for krill availability in this region (Brierley *et al.* 1997; Croxall *et al.* 1999).

Long-term monitoring data from Antarctic fur seals, macaroni penguins (*Eudyptes chrysolophus*), gentoo penguins (*Pygoscelis papua*) and black-browed albatrosses (*Thalassarche melanophrys*) breeding on Bird Island, South Georgia, were used to examine changes in the population size and reproductive performance of predators. For definitions of each parameter see table 1.

Each individual parameter reflects the conditions experienced by predators over different temporal windows. However, these fall into two main groups. The conditions prior to the onset of breeding were examined using an index of arrival condition (AC), i.e.

$$AC_i = P_i + M_A, \quad (1)$$

where P is the initial population size and M_A is the mass at arrival in the colony in the case of macaroni penguins and the birth mass of fur seal pups in the i th year (there were no arrival mass indices for either gentoo penguins or black-browed albatrosses). In order to consider the conditions pertaining to the breeding season (which is highly synchronous across all four species) a reproductive output index (RO) was calculated for all four species:

$$RO_i S_{Ii} + M_{Ii}, \quad (2)$$

where S_I is the number of offspring reaching independence and M_I is the mass at independence of those offspring in the i th year.

All parameters used in the composite indices were standardized to $\bar{x} = 0$ and $\delta = 1$. Individual parameters were smoothed with locally weighted regression using Minitab (Minitab, Inc.) in order to examine long-term trends.

In order to examine the relationship between predator performance, diet and krill population, we used data from a number of studies on the diet of Antarctic fur seals and macaroni and gentoo penguins conducted throughout the period 1980–2000 (Croxall *et al.* 1988, 1999; Reid & Arnould

1996; Reid *et al.* 1996, 1999b; British Antarctic Survey, unpublished data) to examine changes in the overall composition and length–frequency distribution of krill. The latter data, which were available for Antarctic fur seals (1983, 1986 and 1989–2000) and macaroni and gentoo penguins (1986 and 1989–2000), were used to produce composite krill length–frequency distributions for the period up to and including 1990 and from 1991 to 2000 inclusive (proportions were summed across size classes in order to normalize the samples with respect to sample size).

3. RESULTS

(a) *Predator populations and performance*

The population size of all species showed a negative trend over the time-series with two highly and two very nearly significant values at the 0.05 level; a composite index of predator population size showed a highly significant decline over time (table 2). Despite considerable interannual variation, the smoothed data consistently showed a period of increase or stability in the 1980s compared with a decline in the 1990s (figure 1).

The birth mass of both male and female Antarctic fur seals showed a negative trend during the 1990s compared to an increase during the period 1984–1990; similarly the arrival mass of both sexes of macaroni penguins showed negative trends (figure 2). The AC for both Antarctic fur seals and macaroni penguins showed significant negative trends (Antarctic fur seals, $F_{1,17} = 5.91$ and $p < 0.05$ and macaroni penguins $F_{1,10} = 15.92$ and $p < 0.01$) and there was a significant correlation between the indices for the two species ($r = 0.751$ and $p < 0.05$).

The RO index (figure 3) showed a high level of correlation between Antarctic fur seals, gentoo penguins and black-browed albatrosses (table 3), although not between these species and macaroni penguins (table 3) in which the RO index showed a significant negative trend over time ($F_{1,10} = 5.74$ and $p < 0.05$) (figure 3). The amplitude

Table 2. Population changes in Antarctic fur seals, macaroni penguins, gentoo penguins and black-browed albatrosses at Bird Island, South Georgia

(The overall index uses the population data for each species standardized to mean = 0 and s.d. = 1 and summed across species.)

species	rate of change (number year ⁻¹)	s.d.	<i>t</i>	<i>p</i> -value
Antarctic fur seal	-7.33	3.97	-1.84	0.082
macaroni penguin	-35.88	4.86	-7.38	< 0.001
gentoo penguin	-67.81	34.09	-0.98	0.061
black-browed albatross	-7.02	0.98	-7.14	< 0.001
overall	-0.37	0.08	-4.50	< 0.001

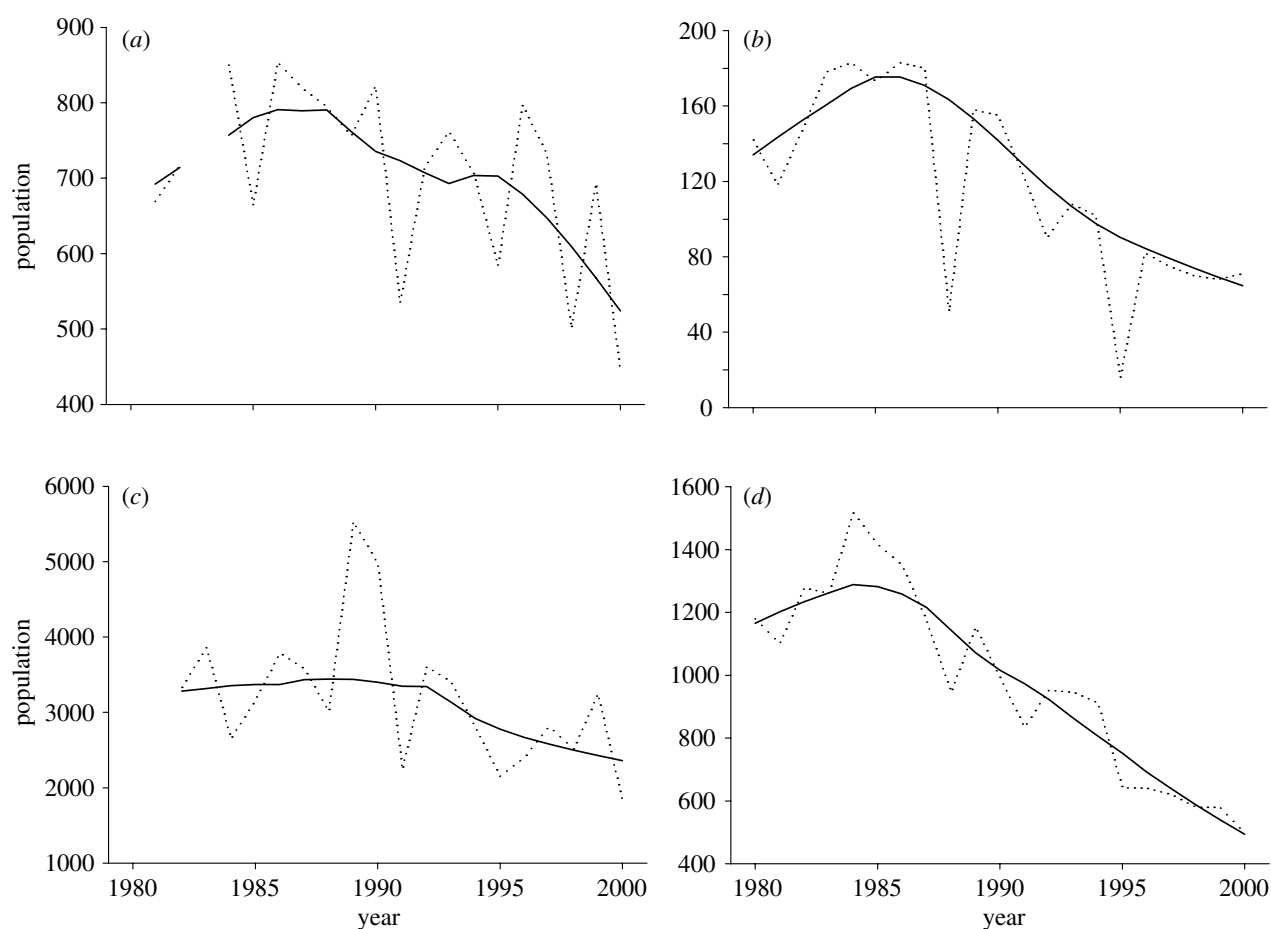


Figure 1. Population changes in (a) Antarctic fur seals, (b) black-browed albatrosses, (c) gentoo penguins, and (d) macaroni penguins breeding at Bird Island, South Georgia, 1980–2000 (for a definition of populations see table 1).

of variation in the RO index for Antarctic fur seals showed a significant increase over the time-series ($F_{1,17}=4.84$ and $p < 0.05$), with an increase in the frequency of years with a negative RO index in the latter part of the time-series.

(b) Krill demographics

Krill remained a key element in the diet of all species throughout (table 4), although there was a significant decline in its contribution to the diet of macaroni penguins, particularly in the period after 1995 (figure 4). There was a significant difference in the population

structure of krill in the diet of Antarctic fur seals (Kolmogorov–Smirnov two-sample test, $D_{\max}=0.462$ and $p < 0.01$), gentoo penguins (Kolmogorov–Smirnov two-sample test, $D_{\max}=0.453$ and $p < 0.01$) and macaroni penguins (Kolmogorov–Smirnov two-sample test, $D_{\max}=0.610$ and $p < 0.01$) between the period up to 1990 and 1991–2000 (figure 5). During the early part of the time-series the dominant modal size of krill taken by predators was 54–56 mm and during the period 1991–1998 the dominant modal size of krill was 42–44 mm in all three predator species, with only a small proportion of krill in the larger size class.

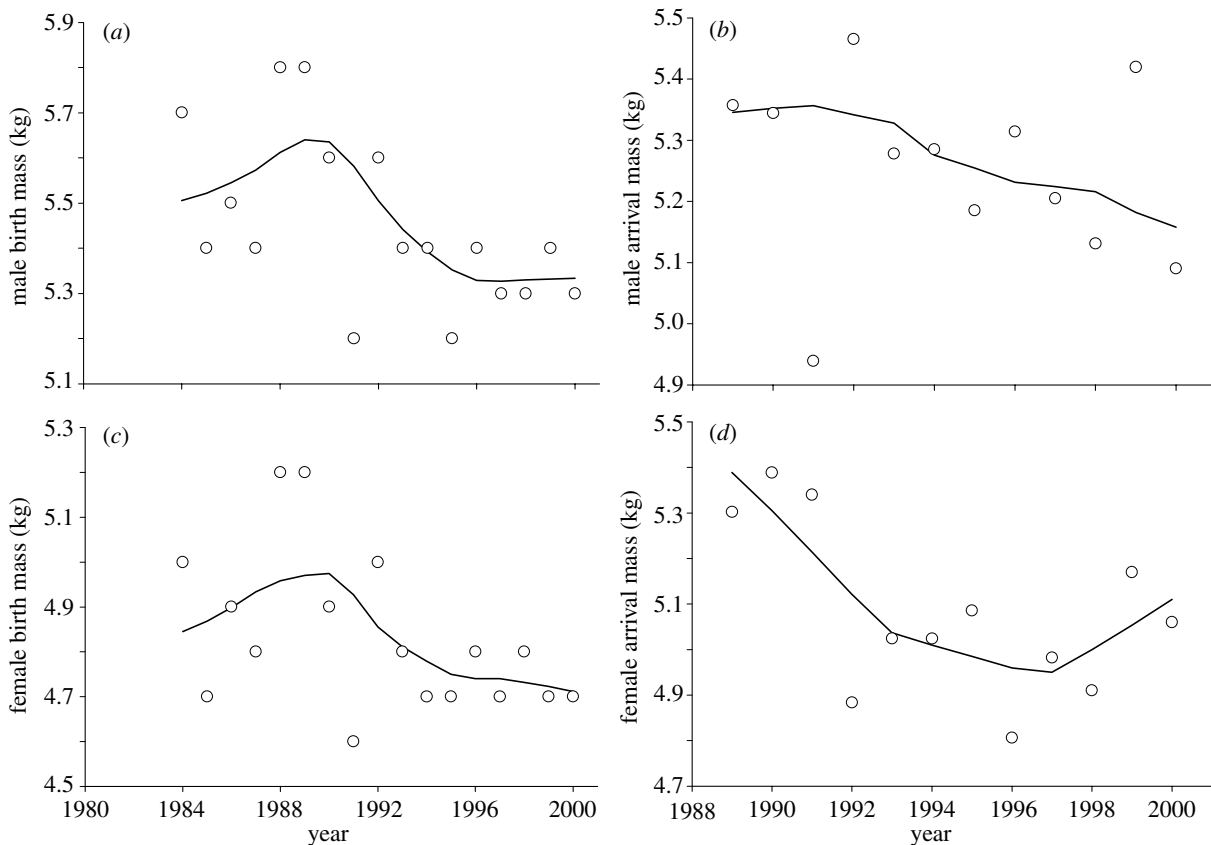


Figure 2. (a,c) Birth mass of Antarctic fur seal pups at Bird Island, South Georgia, 1984–2000. (b,d) Arrival mass of adult macaroni penguins at Bird Island, South Georgia 1989–2000.

Table 3. Correlation matrix for reproductive output indices of Antarctic fur seals, black-browed albatrosses, macaroni penguins and gentoo penguins

	Antarctic fur seal	black-browed albatross	gentoo penguin
black-browed albatross	0.885**	—	—
gentoo penguin	0.877**	0.827**	—
macaroni penguin	0.262	0.326	0.314

** $p < 0.01$.

4. DISCUSSION

(a) Changes in predator population size and reproductive performance

The population sizes of all four predator species declined during the 1990s after a period of relative stability or increase in the 1980s. The largest changes in population size occurred in macaroni penguins and black-browed albatrosses, where populations declined by ca. 50%. However, some of these changes may reflect other processes. Thus, black-browed albatross populations are declining, at least in part, due to incidental mortality of birds as a result of long-line fishing operations (Croxall *et al.* 1998). Although the Antarctic fur seal population has declined at our study colony on Bird Island, increasing populations are still a characteristic of newly colonized areas of South Georgia (Boyd 1993). Nevertheless, the broad pattern of changes across species of very

different ecologies and interactions with the marine environment and with human activity suggests that there may be substantial underlying changes in system-wide processes involving prey and the environment. There is no evidence (and good evidence to the contrary) that any of these species are limited by quality or availability of breeding habitat (Croxall & Prince 1980; Boyd 1993).

In this study, we have assessed changes in the Southern Ocean using two main indices, one largely reflecting conditions at the start of the breeding season and the other reflecting events throughout all of, or the offspring-rearing part of, the breeding season. For the species involved, the spatial scales range from a few hundred kilometres (penguins and fur seals) to a few thousand kilometres (black-browed albatrosses) and ecologies as different as feeding only while diving and being restricted to obtaining food from the surface of the sea. Therefore, even during the breeding season, the scale on which the krill-eating predators are being affected, while mainly reflecting events in the vicinity of South Georgia, is also directly influenced by processes operating over large areas and time-frames, in particular with respect to the advection of food from outside the South Georgia region itself (Murphy *et al.* 1998). Furthermore, the changes in population size, a variable that also integrates annual (e.g. adult survival) and multiyear (e.g. recruitment) processes, also suggests that causal factors probably operate on fairly large spatial and temporal scales.

Therefore, taken together, we feel that the relative similarity and synchrony of changes involving several different kinds of indices of population performance

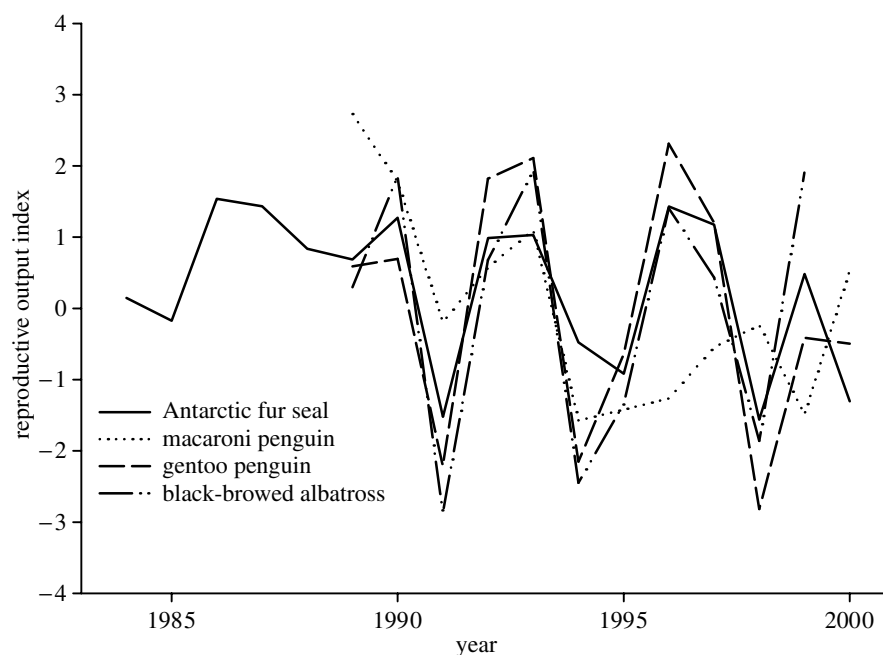


Figure 3. The RO index for Antarctic fur seals, gentoo penguins, macaroni penguins and black-browed albatrosses breeding at Bird Island, South Georgia.

Table 4. Occurrence of krill in the diet of predators at Bird Island, South Georgia 1980–2000

species	measure of % krill in diet	mean (s.e.)	years	trend
Antarctic fur seal	frequency of occurrence	95 (2.4)	10	none
macaroni penguin	percentage by mass	56 (5.3)	18	none
gentoo penguin	percentage by mass	76 (7.7)	16	decline ($F_{1,14} = 6.59$ and $p < 0.05$)
black-browed albatross	percentage by mass	33 (7.1)	7	none

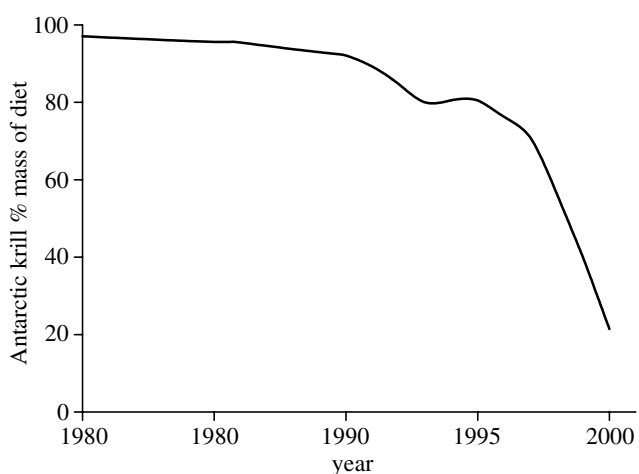


Figure 4. The contribution by mass of Antarctic krill to the diet of macaroni penguins at Bird Island, South Georgia.

across a group of species of very different physiologies and ecologies, whose main common feature is that they breed at South Georgia and eat krill, suggest a change in the processes affecting the availability of their principal prey, namely krill.

(b) Changes in the population of krill at South Georgia

Krill in the diet of predators at South Georgia consistently showed three modal sizes (28, 42 and 56 mm); the relative contributions of these modes to the population showed a consistent pattern of both intra- and inter-annual variation, with distinctive changes associated with periods of low krill abundance between 1991 and 1998 (Reid *et al.* 1999a,b). The length–frequency distribution of krill in the diet showed a consistent change from the upper mode to the central mode for all three species between the two halves of the study period (figure 5). During 1991–1998 the only times when the largest size mode dominated the length–frequency distribution of krill were December 1991, December 1994 and December 1998 and these were always associated with low krill biomass and subsequent negative RO indices (Reid *et al.* 1999a,b). However, before 1990 this largest size class of krill regularly dominated in years of good reproductive performance, i.e. in 1983, 1986, 1989 and 1990 and was associated with positive RO index values. This indicates that there have been changes in both the population structure of krill in the diet of predators and also in the relationship between the population structure and availability of krill to predators. Whereas the biomass of

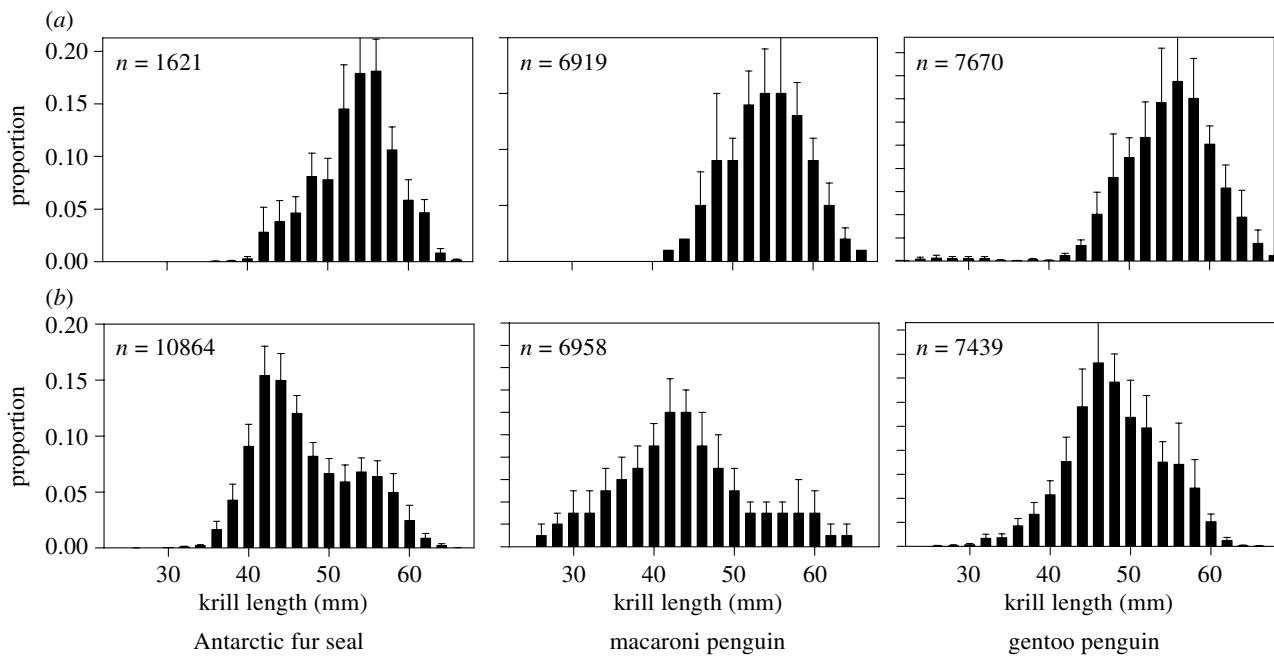


Figure 5. The length–frequency distribution of krill in the diet of Antarctic fur seals and gentoo and macaroni penguins at Bird Island, South Georgia (a) up to and including 1990 and (b) 1991–2000 (see §2 for details of years included).

krill in the largest size class of krill was sufficient for supporting predator demand in the early part of the time-series, this seems not to have been the case during the 1990s.

(c) *Causes of changes in the krill population structure at South Georgia*

The status of the krill population at South Georgia is a function of recruitment into the area, which is generally considered to be an influx from the Antarctic Peninsula region (Murphy *et al.* 1998), growth within the region and the local mortality rate. The effect of reduced recruitment as a consequence of lower biomass in the source region would be that fewer krill enter the population; however, the same proportion of those krill would be expected to enter the older/larger size classes, assuming no change in the growth rate or adult mortality. Therefore, the change we observed in the krill population structure suggests that fewer krill are entering the larger/older size classes as a result of either a reduction in the growth rate or an increase in the adult mortality rate. While there is considerable scope for variability in growth rates of krill (Rosenberg *et al.* 1986) such variability would probably result in a coalescing of the two modes rather than a distinct shift from one modal size to another. This suggests that changes in local krill mortality at South Georgia may be mainly responsible for the observed changes in the krill population structure.

A comparison of the krill population structure generated using a standard growth model and the local South Georgia population (from net-caught krill between 1991 and 1997) found that an instantaneous rate of mortality (M) of 1.25 (or 71% mortality per annum) produced the best fit (Murphy & Reid 2001). This is considerably higher than the generally accepted value of $M=0.6$ (or 45% mortality per annum) used in previous models developed from the Antarctic Peninsula region

(Butterworth *et al.* 1994) and suggests that, within the foraging range of predators at South Georgia, the krill mortality rate may be considerably higher than the overall population mean.

Where the supply of krill far exceeds demand, the amount of krill consumed as a proportion of the local population will be small, i.e. the rate of mortality will be low. However, if the supply and demand values converge due to some combination of reduced supply and/or an increase in local demand, this will increase the mortality rate. Such a change would be consistent with the observed changes in the diet of predators. One effect of a higher mortality rate of krill associated with variable recruitment rates will be to increase the variation in population size, which will be reflected in a greater amplitude of variation in the response of dependent species.

(d) *Potential impacts of predators on krill at South Georgia*

Inferring to what extent this change in the balance of supply and demand can be attributed to fewer krill or to an increase in predator demand is complicated by a lack of data. The relationship between krill reproduction and sea-ice cover (Loeb *et al.* 1997) and the long-term reduction in sea-ice extent (Murphy *et al.* 1995) predict a decline in the krill population size. Indeed, Siegel *et al.* (1998) presented a krill biomass index from the Antarctic Peninsula region over the period 1978–1996 that showed a change from positive values up to 1985 to consistently negative values during the period 1988–1995. Although there are few comparable data from South Georgia, there is strong evidence of concordance in the pattern of inter-annual changes in krill biomass at South Georgia and the Antarctic Peninsula (Brierley *et al.* 1999), suggesting that similar trends may be operating in both locations. In 1991, 1994 and 1998, when the predator reproductive output indices were negative, acoustic estimates of krill

biomass within the foraging range of predators were also very low (Brierley *et al.* 1999). The increase in the frequency of negative indices over the predator time-series suggests an increase in the frequency of periods of low krill biomass.

Assessing changes in demand for krill involves estimating changes in demand from both fisheries and predators. The commercial fishery for krill at South Georgia is relatively small (*ca.* 100 000 t per annum) and total catches decreased by almost 50% from the 1980s to the 1990s (CCAMLR 1995). However, these changes are attributed to changing market forces rather than to changes in the availability of krill to the fishery. The dominant mammalian and avian krill predators, *i.e.* Antarctic fur seals and macaroni penguins, have undergone considerable reciprocal changes in their overall population sizes over the past two decades. Combining the population changes with the output from a generalized model of krill consumption (Boyd & Croxall 1996) indicates that there may even have been an overall decrease in the demand for krill by these two species. Unfortunately, changes in demand from other krill predators, such as fish (Kock *et al.* 1994), squid and baleen whales, remain unclear and limit our ability to estimate changes in the overall predator demand.

Given the complexity of the system, uncertainty about the relative magnitude of changes in krill supply and/or predator demand is inevitable. However, we believe that our data indicate that the balance between them has altered substantially over the past two decades. Within the time-series considered we infer that (i) there has been a change from a situation with a relatively large krill supply compared to the predator demand, linked to a krill population structure that effectively buffered predators against the underlying variability in krill recruitment; (ii) a distinct change occurred around 1990, since when the supply of krill appears to have been sufficiently close to the level of predator demand to cause the local mortality rate of krill and, consequently, the local krill population structure to be substantially altered; and (iii) predator-induced mortality of krill has effectively removed the buffering that previously existed, with a consequent increase in the frequency of years where the amount of krill is insufficient to support predator demand. These interlinked shifts in predator response and prey demographics suggest that the operations of top predators may be magnifying the effects of the slower, gradual change in the underlying ecosystem.

Current management strategies for Antarctic krill fisheries were developed in order to take into account the relationship between predator demand and krill population size (see Everson & de La Mare 1996; Constable *et al.* 2000). If this relationship has changed substantially, then assessment of the amount of krill available to commercial fisheries without adversely affecting predators may need to be reconsidered. This is particularly important where there is a high degree of spatial overlap in the operation of fisheries and predator demand, such as areas on the shelf break to the north of South Georgia (Trathan *et al.* 1998). Overall, krill predators at South Georgia now appear to be operating much closer to the limits of krill availability than previously assumed and this may have become the dominant influence, at least on their

reproductive performance. For krill-dependent predators at South Georgia the time of 'krill-surplus' (the increased availability of krill to other predators following the removal of the great whales from the Southern Ocean) (Laws 1977) may now be at an end. Continuing multi-species studies of these predator-prey interactions may be crucial in understanding the consequences of long-term change in the Antarctic marine ecosystem.

We thank all the staff who worked at Bird Island over the period of this study and Professor I. L. Boyd and Dr E. J. Murphy for helpful comments and discussion. We thank three anonymous referees for constructive comments on an earlier draft of the manuscript.

REFERENCES

- Boyd, I. 1993 Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Sci.* **5**, 17–24.
- Boyd, I. L. & Croxall, J. P. 1996 *Preliminary estimates of krill consumption by Antarctic fur seals and macaroni penguins at South Georgia*. Hobart, Australia: CCAMLR (WG-EMM 96/66).
- Brierley, A. S., Watkins, J. L. & Murray, A. W. A. 1997 Interannual variability in krill abundance at South Georgia. *Mar. Ecol. Prog. Ser.* **150**, 87–98.
- Brierley, A. S., Demer, D. A., Hewitt, R. P. & Watkins, J. L. 1999 Concordance of inter-annual fluctuations in densities of krill around South Georgia and Elephant Islands: biological evidence of same-year teleconnections across the Scotia Sea. *Mar. Biol.* **134**, 675–681.
- Butterworth, D. S., Gluckman, G. R., Thomson, R. B., Chalis, S., Hiramatsu, K. & Agnew, D. J. 1994 Further computations of the consequences of setting the annual catch limit to a fraction of the estimate of krill biomass from a survey. *CCAMLR Sci.* **1**, 81–106.
- CCAMLR 1995 *Statistical bulletin*. Hobart, Australia: CCAMLR.
- Constable, A. J., de la Mare, W. K., Agnew, D. J., Everson, I. & Miller, D. 2000 Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.* **57**, 778–791.
- Croxall, J. P. & Prince, P. A. 1980 Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol. J. Linn. Soc. Lond.* **14**, 103–131.
- Croxall, J. P., McCann, T. S., Prince, P. A. & Rothery, P. 1988 Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. In *Antarctic Ocean and resources variability* (ed. D. Sahrhage), pp. 261–285. Berlin: Springer.
- Croxall, J. P., Prince, P. A., Rothery, P. & Wood, A. G. 1998 Population changes in albatrosses at South Georgia. In *Albatross biology and conservation* (ed. G. Robertson & R. Gales), pp. 69–83. Chipping Norton, UK: Surrey Beatty & Sons.
- Croxall, J. P., Prince, P. A. & Reid, K. 1999 Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar. Ecol. Prog. Ser.* **177**, 115–131.
- Everson, I. & de la Mare, W. K. 1996 Some thoughts on precautionary measures for the krill fishery. *CCAMLR Sci.* **3**, 1–11.
- Fraser, W. R., Trivelpiece, W. Z., Ainley, D. G. & Trivelpiece, S. G. 1992 Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol.* **11**, 525–531.
- King, J. C. 1994 Recent climate variability in the vicinity of the Antarctic Peninsula. *Int. J. Climatol.* **14**, 357–369.

- Kock, K.-H., Wilhelms, S., Everson, I. & Groger, J. 1994 Variation in the diet composition and feeding intensity of mackerel icefish *Champsocephalus gunnari* at South Georgia (Antarctic). *Mar. Ecol. Prog. Ser.* **108**, 43–57.
- Laws, R. M. 1977 Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. Lond. B* **279**, 81–96.
- Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W. & Trivelpiece, S. 1997 Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* **387**, 897–900.
- Murphy, E. J. & Reid, K. 2001 Biological processes generating fluctuations in large-scale ecosystems: modelling Southern Ocean krill population dynamics. *Mar. Ecol. Prog. Ser.* (In the press.)
- Murphy, E. J., Clarke, A., Symon, C. & Priddle, J. 1995 Temporal variation in Antarctic sea-ice: analysis of a long term fast-ice record from the South Orkney Islands. *Deep-Sea Res.* **42**, 1045–1062.
- Murphy, E. J., Watkins, J. L., Reid, K., Trathan, P. N., Everson, I., Croxall, J. P., Priddle, J., Brandon, M. A., Brierley, A. S. & 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, M. R. 1977 Growth of a fur seal population. *Phil. Trans. R. Soc. Lond. B* **279**, 67–79.
- Reid, K. & Arnould, J. P. Y. 1996 The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biol.* **16**, 105–114.
- Reid, K., Trathan, P. N., Croxall, J. P. & Hill, H. J. 1996 Krill caught by predators and nets: differences between species and techniques. *Mar. Ecol. Prog. Ser.* **140**, 13–20.
- Reid, K., Barlow, K., Croxall, J. P. & Taylor, R. 1999a Predicting changes in the Antarctic krill *Euphausia superba* population at South Georgia. *Mar. Biol.* **135**, 647–652.
- Reid, K., Watkins, J. L., Croxall, J. P. & Murphy, E. J. 1999b Krill population dynamics at South Georgia 1991–1997, based on data from predators and nets. *Mar. Ecol. Prog. Ser.* **177**, 103–114.
- Rosenberg, A. A., Beddington, J. R. & Basson, M. 1986 Growth and longevity of krill during the first decade of pelagic whaling. *Nature* **324**, 152–154.
- Siegel, V. & Loeb, V. 1995 Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.* **123**, 45–56.
- Siegel, V., Loeb, V. & Groger, J. 1998 Krill *Euphausia superba* density, proportional and absolute recruitment and biomass in the Elephant Island region (Antarctic Peninsula) during the period 1977 to 1997. *Polar Biol.* **16**, 393–398.
- Trathan, P. N., Croxall, J. P. & Murphy, E. J. 1996 Dynamics of Antarctic penguin populations in relation to the inter-annual variability in sea-ice distribution. *Polar Biol.* **16**, 321–330.
- Trathan, P. N., Murphy, E. J., Everson, I. & Parkes, G. B. 1998 Analysis of haul data from the South Georgia krill fishery. *CCAMLR Sci.* **5**, 9–30.
- Woehler, E. J. & Croxall, J. P. 1999 The status and trends of Antarctic and sub-Antarctic seabirds. *Mar. Ornithol.* **25**, 43–66.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.