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Concordance of interannual fluctuations in acoustically estimated densities of Antarctic krill around South Georgia and Elephant Island: biological evidence of same-year teleconnections across the Scotia Sea

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Abstract Acoustic estimates of the densities of Antarctic krill, *Euphausia superba*, in areas around South Georgia (SG) and Elephant Island (EI) were compared for seven austral summers between 1981 and 1997. Estimated densities of krill at SG were most often lower than at EI, although this may simply have been a function of differences in the survey and data-analysis techniques used at each site. More interestingly, the magnitudes of density and between-year gradients of density at each site were mirrored by those at the other location; for example 1991 and 1994 were years of very low krill density at both SG and EI. There was no apparent lag in changes in density between sites, and ranked between-year gradients in density at both locations were closely correlated. These pronounced similarities suggest that densities of krill at both locations are linked directly, and may be impacted by the same gross physical and biological factors (e.g. recruitment, dispersal and environmental variability) acting over the same temporal and spatial scales. The observed concordance also implies that the pelagic ecosystems at these widely separated sites (≈ 1500 km distant at opposite sides of the Scotia Sea) are not operating in isolation. Fluctuations in krill density were investigated with reference to cyclical variations in sea ice extent, and in air and sea-surface temperature. The resulting model suggests that the 1999/2000 austral summer will be one of low krill density.

Introduction

The Antarctic krill *Euphausia superba* is a keystone species in the Southern Ocean (Miller and Hampton 1989) that is also sought by fisheries (Everson and Goss 1991; Nicol and Endo 1997). For effective management of this ecologically and commercially important species within the context of the dynamic Antarctic marine environment (Everson 1992), abundance estimates are required. In 1981, the “First International Biomass Experiment” was conducted (FIBEX; see Everson and Miller 1994), and an estimate of krill abundance for all the southwest Atlantic Ocean has been derived from the acoustic data gathered synoptically by the multi-ship, multi-national team of participants (see Trathan et al. 1995). Subsequent surveys of krill abundance have been on a smaller scale and have tended to focus on areas of specific interest to individual nation’s Antarctic research programs. Since the FIBEX study, acoustic surveys of krill density have been conducted around Elephant Island (see Fig. 1) by the United States Antarctic Marine Living Resources Program nearly every austral summer (Hewitt and Demer 1994). During the same period, acoustic surveys have also been conducted around South Georgia (Fig. 1) by the British Antarctic Survey, although these were repeated at less regular intervals in earlier years (Brierley et al. 1998). Surveys at both locations have revealed substantial inter-annual variability in krill density (Hewitt and Demer 1994; Brierley et al. 1997, 1998).

The South Georgia (SG) area is not considered to be a krill breeding-site (Ward et al. 1990), and the island is not believed to support a self-sustaining krill population. Rather, it has been variously proposed that krill at SG have their origins at the Antarctic Peninsula or in the Weddell Sea (Fig. 1), and are transported to SG via the prevailing north-easterly flowing ocean currents (reviewed by Murphy et al. 1998). Similarly, there is evidence to suggest that some krill at Elephant Island (EI) may originate from further south along the Antarctic Peninsula (Kawaguchi and Satake 1994; Siegel and Loeb

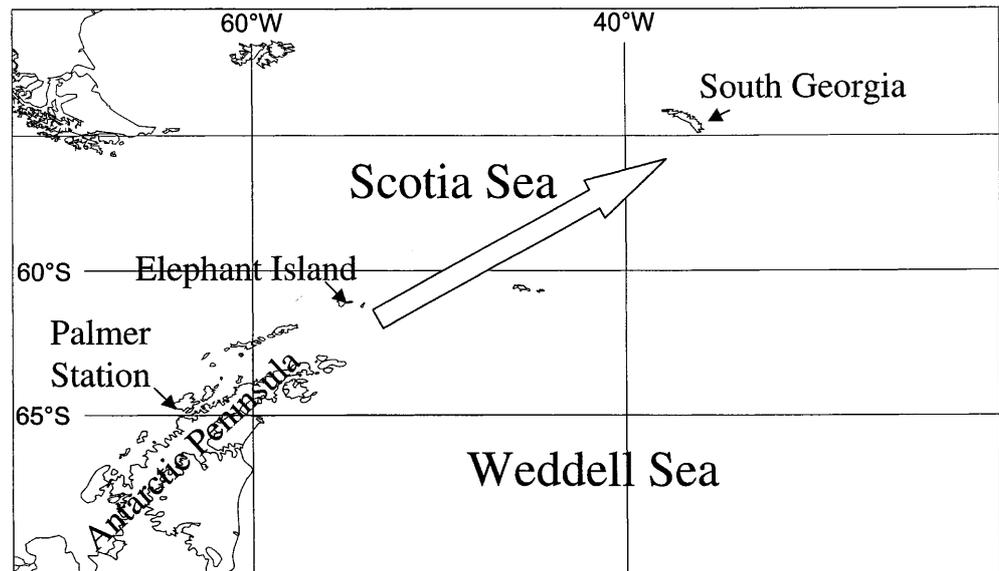
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Fig. 1 Map of Scotia Sea showing South Georgia and Elephant Island (arrow shows direction of flow of prevailing ocean currents from Peninsula towards South Georgia)



1995). Thus, there is reason to believe that krill abundances at both SG and EI – whether one stock, separate stocks, or a mixture (the genetic status of krill throughout Antarctica remains unresolved; see for example Fevolden and Schneppenheim 1989) – are influenced by the same biological and environmental processes (e.g. Loeb et al. 1997). Furthermore, it is possible that despite the separating distances (of the order of 1500 km between South Georgia and Elephant Island) krill populations throughout the Scotia Sea may not exist in biological isolation. To date, because of the geographically isolated nature of surveys conducted since FIBEX, there has been little evidence available to substantiate or refute such a claim.

To investigate the fluctuations of krill populations at sites at opposite sides of the Scotia Sea, time series of acoustic estimates of krill biomass in study areas around South Georgia and Elephant Island are examined here together. This comparison of variations in krill density enables the theory of teleconnection between both locations to be explored quantitatively for the first time, and allows the possible effects of processes of ecosystem variability in both regions to be viewed within a common framework. Understanding processes of krill population fluctuation throughout the Scotia Sea as a whole could lead to improved resource management there, and to greater understanding of the probable responses by krill-dependent predator populations to natural environmental variability and to potential increases in krill-fishing pressure (see Croxall et al. 1988).

Materials and methods

Acoustic surveys to estimate density of Antarctic krill, *Euphausia superba*, were conducted near Elephant Island in 14 of the 17 austral summer seasons between 1981 and 1997 (austral summers span two calendar years: by convention the given year refers to that in which the season ended). In some seasons, multiple surveys were

conducted and, on such occasions, the mean krill-density value used in the present study is based on the large area-surveys conducted during the months January through March (see Macaulay et al. 1984; Hewitt and Demer 1994). Over the same period, acoustic data were collected during ten seasons at South Georgia. Specific to this analysis, single weighted density estimates (Jolly and Hampton 1990) for 1990, 1994, 1996 and 1997 were calculated for SG by combining data from transects run within separate areas to the north-east and north-west of the island (Brierley et al. 1997). Survey and data-analysis techniques adopted at each site in each year have been described in detail by Hewitt and Demer (1993) and Brierley et al. (1998) and references therein. Despite many similarities, there are also some fundamental differences between the survey and analysis techniques that have been employed at South Georgia and Elephant Island over the years. The methodological differences are primarily the result of conflicting efforts to: (1) reduce the uncertainty in acoustic biomass estimates; and (2) adhere to the current guidelines for reporting data for comparative purposes (SC-CAMLR 1996). Table 1 gives some of the most salient of these, and their potential impact on relative density estimates. The components of uncertainty associated with these differences are primarily systematic (MacLennan and Simmonds 1992; Demer 1994). Consequently, while each time series is believed to quantify changes in krill density within a region, the two series are not necessarily unbiased relative to each other. However, since the measurement techniques used within each site remained virtually consistent between years, any observed concordance in the fluctuations of krill density between the two areas may reasonably be considered to be independent of the absolute densities.

The multi-year longevity of krill (Siegel 1987) results in significant autocorrelation of the density time series because year-classes propagate inter-annually through the population (Siegel and Loeb 1995; Reid et al. 1998). Moreover, there is growing support for a hypothesis that the magnitude of krill recruitment in any given year is significantly influenced by annually-varying environmental factors such as sea ice extent, which in turn is highly correlated with air temperature (e.g. Loeb et al. 1997; Murphy et al. 1998). Therefore, a power spectral analysis was conducted for the annual ice index at Elephant Island (Hewitt 1997), air temperature at Palmer Station on Anvers Island to the west of the Peninsula (Loeb et al. 1997; see present Fig. 1) and sea-surface temperature (SST) from the western South Georgia area (Trathan and Murphy 1998) during the periods 1981 to 1997, 1981 to 1995, and 1982 to 1996, respectively. The high-energy cyclical components of the interannual variability within the time series of these environmental factors were then used to create a krill density model [$d(t)$] of the form

Table 1 *Euphausia superba*. Similarities and differences in survey and data-analysis techniques used at South Georgia (SG) and Elephant Island (EI), with assessment of likely direction of change

Component of uncertainty	Survey method		EI rel SG
	SG	EI	
Krill identification	Visual scrutiny; $\Delta MVBS$	Visual scrutiny; all signals included	Greater
Survey time	Day only	Day and night	Less
Target strength	Greene et al. 1991	Greene et al. 1991	Equal
Depth range	10–256 m	15–250 m, 15–225 m	Approx equal
Overall			Less

$$d(t) = A + B \cos\left(\frac{2\pi t}{T_1} + \Phi_1\right) + C \cos\left(\frac{2\pi t}{T_2} + \Phi_2\right) + D \cos\left(\frac{2\pi t}{T_3} + \Phi_3\right) + E \cos\left(\frac{2\pi t}{T_4} + \Phi_4\right) + \dots + Z \cos\left(\frac{2\pi t}{T_n} + \Phi_n\right) \quad (1)$$

to describe the interrelations of annual estimates, where t = time (years), A = mean density (g m^{-2}), and B – Z Φ_1 – Φ_n and T_1 – T_n = amplitudes (g m^{-2}), phases (radians) and periods (years) of each cyclical component. The model can be used to provide an aid to the visual interpretation of time-series fluctuations, as well as constituting a provisional method for quantitative analysis of the potential environmental links.

For the time series of krill abundance at South Georgia and Elephant Island, there exist seven seasons for which data are available from both locations (1981, 1990, 1991, 1992, 1994, 1996 and 1997). For these data matches, the gradients in density estimates between successive data were derived. The first derivative of the EI krill-density model provides a model of this krill-density gradient.

In an attempt to demonstrate formally any link between changes in krill densities at South Georgia and Elephant Island, the Spearman rank-correlation coefficient r_s was calculated for the observed gradients of the mean density estimates from each area for matching years.

Results

Densities of *Euphausia superba* at South Georgia and Elephant Island have fluctuated markedly between years over the past two decades. Fig. 2a plots all available yearly mean-density data for both sites. Density estimates for years in which data are available from both the SG and EI locations are given in Table 2. This table also highlights the gradient in krill density (changes in krill density per year) within a site from the previous common year (magnitude and direction), and shows that in all instances there was concordance in the gradient at both sites. The gradients between successive common years ($\text{g m}^{-2} \text{yr}^{-1}$) are plotted in Fig. 2b.

The observed variations in krill density may have links to cyclical changes in environmental factors such as those apparent from the power spectral analysis of the EI ice index (Fig. 3a), of the air temperature at Palmer Station (Fig. 3b), and of the SST at SG (Fig. 3c). Collectively, the spectral analyses of these series show energy in 8, 5, 4, 3 and 2 yr cycles. A Gauss–Newton

they may impart on relative (*rel*) density estimates [$\Delta MVBS$ difference in mean volume backscattering-strength at 38 and 120 kHz (see Madureira et al. 1993)]

method (Deuflhard and Apostolescu 1980) was employed to fit Eq. (1) to the EI krill density estimates and to estimate the model parameters. The resultant model of temporal variability in krill density at EI (Eq. 2) is plotted over the time series of observed density estimates for each site in Fig. 2a.

$$d(t) = 46.7 + 23.9 \cos\left(\frac{2\pi t}{8} + 5.5\right) - 15.5 \cos\left(\frac{2\pi t}{5} + 0.5\right) + 11.0 \cos\left(\frac{2\pi t}{4} + 4.3\right) + 12.1 \cos\left(\frac{2\pi t}{3} + 1.3\right) + 4.2 \cos\left(\frac{2\pi t}{2} + 1.8\right) \quad (2)$$

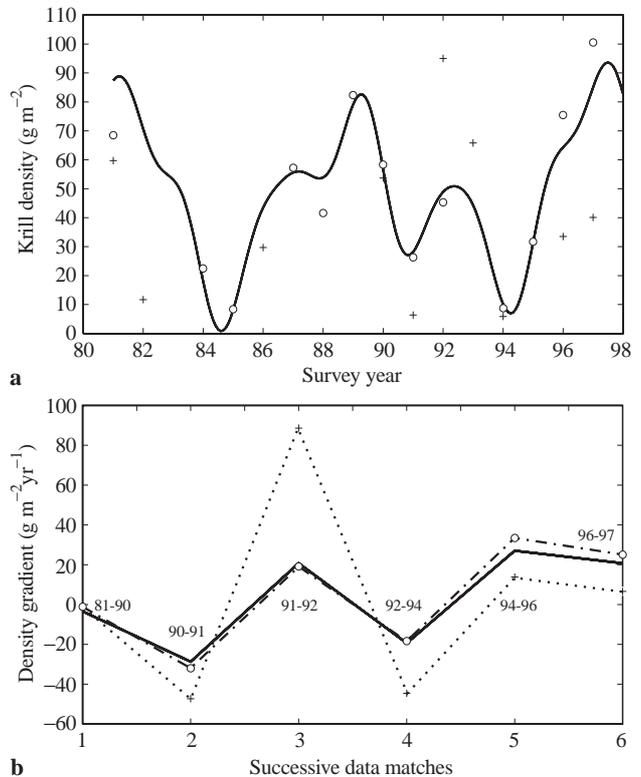


Fig. 2 *Euphausia superba*. Acoustic estimates of krill density at South Georgia (+) and Elephant Island (O) from 1981 to 1997 (a), and observed between-year gradients of change in krill density at each site where data were available for both areas (b) (dotted line South Georgia; dashed line Elephant Island), and first derivative of the model (continuous line) which also describes predicted gradients of the series between the years

Table 2 *Euphausia superba*. Krill-density estimates for South Georgia (SG) and Elephant Island (EI) for years in which data were available for both regions, and gradient of change in density between subsequent years. In all instances there is concordance between sites (agreement between signs of gradients)

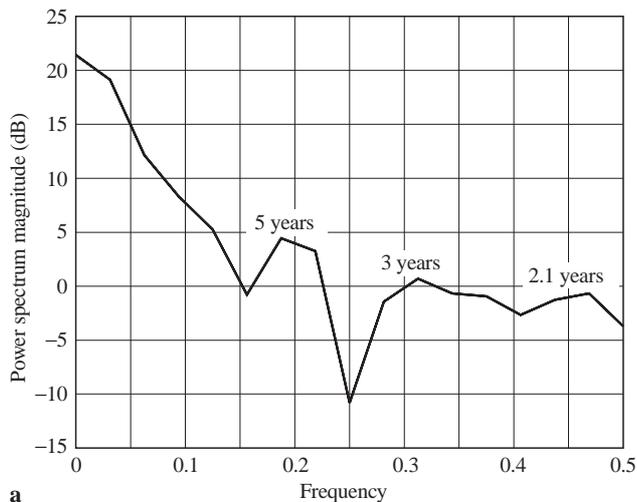
Year	SG		EI	
	Density (g m ⁻²)	Gradient (g m ⁻² yr ⁻¹)	Density (g m ⁻²)	Gradient (g m ⁻² yr ⁻¹)
1981	59.7	–	68.5	–
1990	53.7	–0.7	58.3	–1.1
1991	6.4	–47.3	26.3	–32.0
1992	95.0	88.6	45.4	19.1
1994	5.9	–44.5	8.7	–18.4
1996	33.5	13.8	75.5	33.4
1997	40.1	6.6	100.5	25.0

Interestingly, the model coefficients with the largest absolute values are associated with the 8 yr (23.9 g m⁻²) and 5 yr (15.5 g m⁻²) cycles, which also had the highest power spectral densities in the air temperature at Palmer Station, and both the EI ice index and SG SST, respectively.

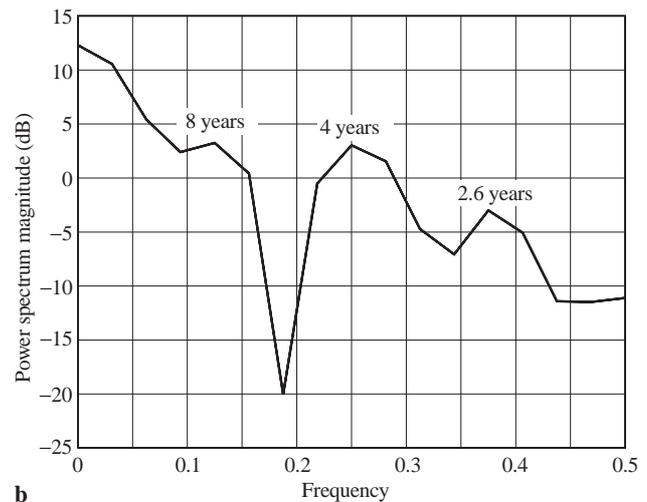
The Spearman rank-correlation indicated that ranked gradients in the time series of observed krill densities from each area were closely correlated ($r_s = 0.83$, $p < 0.10$). Furthermore, the binomial probability of obtaining 6 out of 6 agreements in concordance is very low (0.02). The gradient in modelled krill abundance at Elephant Island, or the discrete first derivative of (2), is plotted in Fig. 2b for those years where observed data were available for both SG and EI.

Discussion

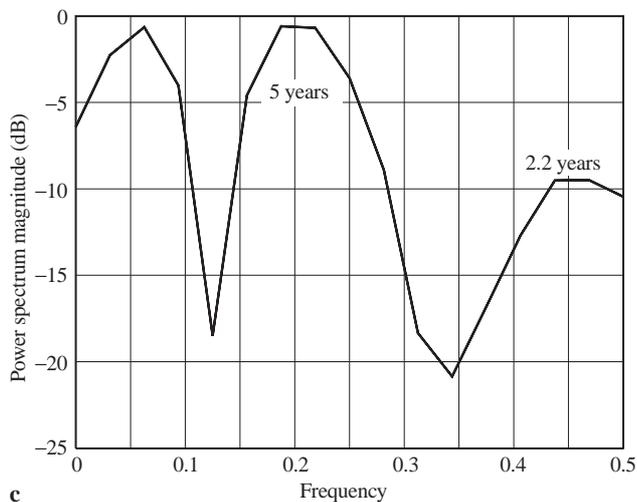
Acoustic estimates of *Euphausia superba* density at both South Georgia and Elephant Island have varied considerably between years over the past two decades. Within the framework of this variability, however, abundance at EI has most often been higher than at SG (Table 2). The estimate for the only year in which abundance at SG appeared to be higher than at EI (1992) is a year when the biomass estimate at SG was based upon a survey conducted only on shelf. Because



a



b



c

Fig. 3 *Euphausia superba*. Power spectral analyses (32-point fast Fourier transform) of annual ice index at Elephant Island, **a** (Hewitt 1997); air temperature at Palmer Station, **b** (Loeb et al. 1997); and sea-surface temperature from west South Georgia area, **c** (Trathan and Murphy 1998) during periods 1981 to 1997, 1981 to 1995, and 1982 to 1996, respectively (*Frequency* is cycles yr⁻¹)

krill abundance is frequently higher on the shelf or near the shelf-break (Miller and Hampton 1989), there is sufficient reason to suspect that this estimate may be disproportionately high compared to other estimates at SG which include areas both on and off the shelf.

There are several possible explanations for the observation that abundance at EI is higher than at SG; two are expanded below.

Firstly, systematic differences in the density estimates for the South Georgia and Elephant Island areas may simply be due to the differences in the survey and data-analysis techniques employed at each site. Although the surveys in both areas are now conducted with the same narrow-band echo-sounder frequency (120 kHz) and interpreted using the same target strength-to-krill length relationship (Greene et al. 1991), the approaches to survey timing (day/night) and the apportionment of the acoustic backscatter to krill versus other scatterers are fundamentally different (Table 1). These differences could induce bias although, as indicated in Table 1, if differences in survey method constituted the major source of apparent differences in density between areas, then one might expect krill density at EI to be lower than at SG. It is clear from Table 2 that this is not the case, and that density at EI (mean of all years = 54.7 g m^{-2}) is consistently higher than at SG (mean 42.0 g m^{-2}). The potential for differences in survey execution and analysis to induce bias does, however, highlight the need for adopting provisional standards for all facets of data collection and analysis of acoustic data if comparisons between areas are to be effected in a fully quantitative manner. Clearly, adherence to such protocols will be requisite for integration and analysis of data arising from the proposed quasi-synoptic survey of krill density in CCAMLR Area 48 (SC-CAMLR 1996). Surveys at SG and EI may also cover differing proportions of on- and off-shelf waters, and the differential association of krill to one or other of these or to the intermediary shelf break region may further bias relative abundance estimates.

Secondly, the differences in krill density between South Georgia and Elephant Island may in fact be real, and be the result of krill dispersal mechanisms operating over the entire Scotia Sea (reviewed, for example, by Lubimova et al. 1985; Sahrhage 1988; and by Murphy et al. 1998; Watkins et al. 1999). A common and central tenet of the literature on krill distribution is that krill spawned at the Antarctic Peninsula, or in Weddell Sea waters, may become entrained within the north-easterly flowing Antarctic Circumpolar Current and be carried toward SG, possibly via EI. If the Peninsula or Weddell Sea are indeed sources of krill throughout much of the Scotia Sea (this has yet to be confirmed or refuted; genetic studies to date have been inconclusive, e.g. Fevolden and Schneppenheim 1989), then one might expect fewer krill at SG than at EI since SG is more distant from these sources. Predation at South Georgia (Trathan et al. 1995) would compound the reductions in abundance due to dispersal effects, although mecha-

nisms restricting krill to the south of the Antarctic polar front may prevent dispersal mechanisms from simply reducing abundance as a function of distance. Notwithstanding the possible systematic differences in krill density between South Georgia and Elephant Island, it is apparent from Fig. 2a and b that concordance exists in data sets from both areas. In each of the six years for which the comparison can be made, increases or decreases in krill densities at one site relative to the previous survey were accompanied by changes in the same direction at the other location. Analysis of these trends is likely to provide clearer insight into patterns of variation in krill density throughout the Scotia Sea than are comparisons of absolute biomass between sites; within-site trends are not subject to the method-related problems associated with comparisons between sites outlined in the third paragraph of the "Discussion". If krill densities at SG and EI were both influenced by environmental processes at the Peninsula (e.g. ice extent; see Loeb et al. 1997) then in years when krill density at EI was low, low density should also be expected at SG. Conversely, following strong recruitment at the Peninsula, increased numbers of krill might be expected at EI, and larger numbers might also be propagated across the Scotia Sea to SG. Inspection of the two time series of observed krill density, and of the predictions of the model developed here, suggest that this could indeed be the case.

In an early review of a time series of data on breeding success of krill predators at South Georgia and Signy Island (South Orkneys), Croxall et al. (1988) noted that patterns of variability at the two locations did not resemble each other. More recently, however, Boyd (1998) has shown that inter-annual variability in the foraging trip duration of Antarctic fur seals (a species with a documented dependence upon krill; Reid and Arnould 1996) can be linked to processes of environmental variability at the Antarctic Peninsula. This suggests that the effects of processes likely to impact upon krill populations near the Peninsula may also pervade areas further afield and influence, either directly or indirectly, populations at least as far away as South Georgia.

It appears that krill population processes at South Georgia and Elephant Island are not independent. Known ocean currents and their dispersive effects can be used to explain both systematic differences in absolute biomass and similarities in trends of krill densities at the two locations, and support the existence of teleconnection processes across the Scotia Sea, transmitting possible environmental-mediated change in density across this basin. Krill-density phenomena apparent at EI in any particular year also seem to be manifested at SG in the same season, with no apparent lag in propagation between locations. In terms of krill density therefore, both SG and EI appear to be directly coupled. In ecosystem- and fishery-management terms, this suggests that in a year characterised by low krill abundance in one location, abundance will be low throughout the

Scotia Sea. In such years, krill-dependent predators throughout the region are likely to fare worse than usual, and fishermen failing to catch krill in one location are unlikely to fare better by moving to other grounds within the Scotia Sea.

The finding here that krill density at EI fluctuates according to a cyclical pattern that can be described broadly by fluctuations in environmental parameters is in agreement with previous work reporting interannual variability in krill abundance (e.g. Loeb et al. 1997). What is more, assuming that the observed periodicity in environmental variability persists into the near future, it is possible to use the density model in a predictive fashion. So doing, it would appear that the next slump in krill abundance will occur in the 1999/2000 austral summer. This is the season for which the forthcoming multinational synoptic survey of krill abundance is planned (Trathan et al. 1995; cf. SC-CAMLR 1996). Those hoping to use the krill abundance data from that survey for management purposes should be aware that it is possible that the abundance observed during that survey may be at a cyclical low.

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