

for these compounds as signals in marine trophic interactions remain to be discovered. □

## Methods

**Response of *O. marina* to acrylate gradients.** *O. marina* cell suspensions were prepared on a microscope slide without a coverslip. Neutralized acrylic acid (Aldrich) was injected by micropipette to generate spatial gradients (equilibrium concentration,  $10^{-5}$  M), and the cell response was observed for 30 s by phase-contrast microscopy and recorded on videotape using a NEC TI-23A CCD camera<sup>28</sup>. A focal plane several millimetres from the surface of the slide was chosen to minimize wall effects. Cell swimming behaviour was analysed by a computer-assisted video motion analysis system (Motion Analysis model VP 110 with ExpertVision software), and rate of change in direction (R.C.D.I.,  $\text{deg s}^{-1}$ ), an analogue for angular velocity (turning frequency), and linear speed ( $\mu\text{m s}^{-1}$ ) were calculated for 10–80 individual digitized cell paths. Control treatments were prepared with additions of seawater.

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# Effects of sea-ice extent and krill or salp dominance on the Antarctic food web

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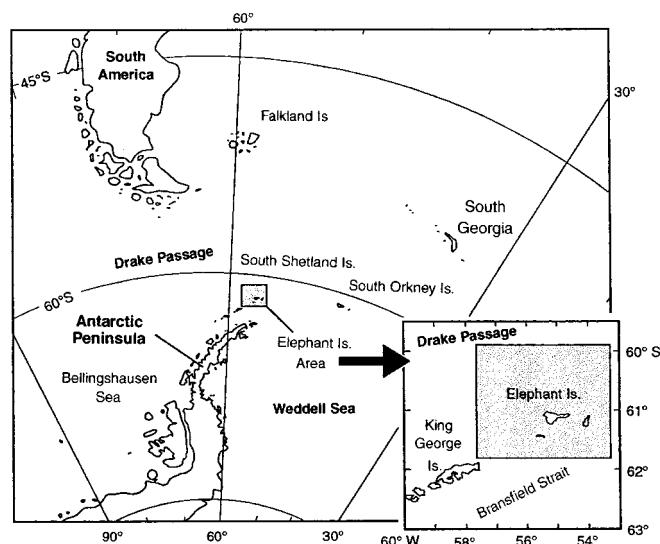
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Krill (*Euphausia superba*) provide a direct link between primary producers and higher trophic levels in the Antarctic marine food web<sup>1–6</sup>. The pelagic tunicate *Salpa thompsoni* can also be important during spring and summer through the formation of extensive and dense blooms<sup>6–9</sup>. Although salps are not a major dietary item for Antarctic vertebrate predators<sup>7,10</sup>, their blooms can affect adult krill reproduction and survival of krill larvae. Here we provide data from 1995 and 1996 that support hypothesized relationships between krill, salps and region-wide sea-ice conditions<sup>11,12</sup>. We have assessed salp consumption as a proportion of net primary production, and found correlations between herbivore densities and integrated chlorophyll-*a* that indicate that there is a degree of competition between krill and salps. Our analysis of the relationship between annual sea-ice cover and a longer time series of air temperature measurements<sup>12,13</sup> indicates a decreased frequency of winters with extensive sea-ice development over the last five decades. Our data suggest that decreased krill availability may affect the levels of their vertebrate predators. Regional warming and reduced krill abundance therefore affect the marine food web and krill resource management.

In the Elephant Island area near the Antarctic Peninsula (Fig. 1) both krill and salps exhibited large interannual abundance fluctuations between 1976 and 1996 (Table 1). In general, larger krill population densities were encountered during the earlier part of the data set; densities from 1984–85 until 1995–96 were on average an order of magnitude less than during previous years. Randomization tests on an analysis of variance<sup>14</sup> indicate that differences in abundance between these two periods are statistically significant and support lower krill abundance in recent years. In contrast, the highest salp densities occurred during three summers within the 1984–96 period.

Interannual fluctuations in krill abundance result largely from variations of year-class success: the highest population densities (for example, 1981–82) result from extremely good recruitment from the previous spawning season<sup>11</sup>. Relatively low densities in 1984–85, 1990–91 and 1994–95 followed two or three years of poor and intermediate krill recruitment. Good recruitment is positively correlated with early seasonal spawning (in December–February), and both are positively correlated with extensive sea-ice in the Antarctic Peninsula region the preceding winter ( $n = 17$ ; Kendall's  $T = 0.40$ ,  $P < 0.05$ ;  $n = 12$ ,  $T = 0.48$ ,  $P < 0.05$ ). Poor recruitment and late spawning (in March) are associated with reduced regional sea-ice formation.

In contrast to krill, salp abundance is negatively correlated with extensive sea-ice. Unlike krill, which have lifespans of more than 5 years<sup>15</sup>, *S. thompsoni* live less than one year, and their fluctuations in abundance reflect annual variability in conditions promoting

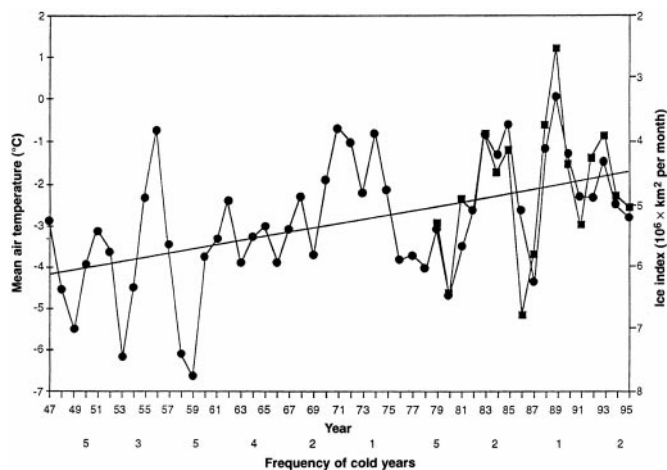


**Figure 1** Location of the Elephant Island survey area near the Antarctic Peninsula. The major Antarctic krill harvesting activities occur within the southwest Atlantic sector between the Antarctic Peninsula and 30° W. This sector also supports large populations of resident and summer migrant krill-dependent species.

explosive population growth<sup>7,16</sup>. Exceedingly high salp densities in 1983–84, 1988–89, 1989–90, 1992–93 and 1993–94 followed winters with relatively low sea-ice development. Mean salp abundance is negatively correlated with regional indices of sea-ice cover during the preceding winter ( $n = 12$ ,  $T = -0.58$ ,  $P < 0.01$ ).

The differing relationships with sea-ice may be due to the ability of krill (late larvae, juveniles and adults) to exploit available ice algae during the winter months<sup>3,17</sup>. In contrast, salps are obligate filter feeders<sup>16</sup> that may benefit from open-water conditions that promote rapid population growth in early spring. We hypothesize that: (1) winters with extensive sea-ice cover inhibit spring salp blooms and promote early seasonal krill spawning; (2) these factors ensure good survival of the larval krill and subsequent recruitment to the population at the age of one year; and (3) a second winter of extensive ice cover amplifies the effect by promoting continued early spawning of krill and ensuring good survival of larvae spawned the preceding spring and summer<sup>11–13</sup>. Conversely, we hypothesize that winters with poor sea-ice development promote extensive salp blooms and poor krill spawning. We also postulate that if the above effects are real, a long-term warming trend in the Antarctic Peninsula region could have profound effects on the dominance of krill and salp populations and, by implication, krill-dependent predators and the fate of newly fixed carbon.

Sea-ice coverage and duration in the Antarctic Peninsula region were above average during the winters of 1994 and 1995 (Table 1). As expected, salp densities were low the following summers. Krill density was low during summer 1994–95, and was dominated by large mature forms at least four years old, which is evidence of poor recruitment since the 1990–91 spawning season. However, unlike the previous three years, these krill had an early spawning season, which started in early December, and virtually all mature females were gravid or spent by mid-February 1995. Spawning success was indicated by the appearance of early-stage krill larvae in January and widespread occurrence of dense larval krill patches in February. High krill densities in 1995–96 arose mainly from the large numbers of one-year-old juveniles, and reflect exceedingly good overwintering survival and recruitment of the 1994–95 year class (Table 1). Early spawning and the presence of krill larvae during January 1996 followed above-average sea-ice conditions during winter 1995.



**Figure 2** Long-term trends in mean annual surface air temperature in the Antarctic Peninsula region 1947–1995 (circles) and the regional sea-ice index 1979–1995 (squares). Frequency of cold years reflects the number of years per respective five-year period that mean air temperature was  $\leq -2.5^\circ\text{C}$ , the temperature associated with the median sea-ice index value during 1979–1995.

Krill and salp abundance relations during summer 1994–95 and 1995–96 differ greatly from those in 1993–94, when salps dominated the macrozooplankton (Table 2). During summer 1993–94, large concentrations of salps were encountered across the survey area, and median salp biomass ( $\text{mg C m}^{-2}$ ) was an order of magnitude greater than that of krill. Using a daily consumption rate for salps of 25% of their body carbon<sup>18</sup>, the median uptake of daily primary production during January 1994 was  $100 \text{ mg C m}^{-2}$ , which was 19% of the average daily net primary production rate ( $537 \text{ mg C m}^{-2} \text{ d}^{-1}$ ). This level of consumption is probably characteristic of other major ‘salp years’ such as 1989–90 and 1992–93 (Table 1). During the less dense blooms of 1983 and 1988, salp consumption of primary production was estimated at 10% and 9%, respectively<sup>18,9</sup>. Consumption by salps during summer 1995 was negligible ( $2\text{--}3 \text{ mg C m}^{-2} \text{ d}^{-1}$ , compared with the mean primary production value of  $1,318 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and, based on the low population density, consumption by krill was probably substantially lower than in the preceding years. The high chlorophyll-*a* values observed during 1995 (Table 1) may have resulted from low consumption by both krill and salps; conversely, low chlorophyll-*a* values during 1996 may have resulted from grazing by abundant krill. Significant negative correlations (Kendall’s *T* tests,  $P \leq 0.01$ ) between individual cruise chlorophyll-*a* concentrations and krill and salp densities during 1990–1995 ( $n = 12$ ,  $T = -0.58$ , and  $n = 8$ ,  $T = -0.71$ , respectively) suggest that grazing pressure by both krill and salps may affect phytoplankton standing stock size in the area. If this is true then much of the primary production during 1995 was left to be taken up by other herbivores (such as copepods) or was lost from the photic zone by flux into deeper waters<sup>16</sup>.

Although the estimated proportion of net primary production taken up by large salp densities during the peak summer phytoplankton bloom seems to be modest (<20%), the impact of salp grazing during earlier, lower productivity spring bloom periods may be quite significant. Rapid spring population growth of *S. thompsoni* occurs in October and November; during years with extraordinarily large population growth, the grazing pressure by salps on relatively low spring phytoplankton standing stocks [primary production values  $< 50 \text{ mg C m}^{-2} \text{ d}^{-1}$  (ref. 19)] is no doubt quite significant. It has been suggested<sup>11</sup> that strong feeding competition by salps during

**Table 1 Trends in krill and salp abundance**

Field season	Krill				Salps		Chlorophyll- <i>a</i>		Sea-ice index (10 <sup>9</sup> km <sup>2</sup> -months)
	<i>N</i>	Mean (No. 1,000 m <sup>-3</sup> )	Spawning index	Recruitment index	<i>N</i>	Mean (No. 1,000 m <sup>-3</sup> )	<i>N</i>	Mean (mg m <sup>-2</sup> )	
1975-76	-	-	-	0.144	24	862.4	-	-	-
1976-77	-	-	-	0.048	-	-	-	-	-
1977-78	68	132.9	0.032	-	53	3.6	-	-	-
1978-79	-	-	-	0.069	-	-	-	-	-
1979-80	-	-	-	0.559	-	-	-	-	5.29
1980-81	33	49.5	0.896	0.757	42	24.1	-	-	6.43
1981-82	52	510.9	0.824	0.663	52	25.3	-	-	4.90
1982-83	12	90.6	-	0.119	-	-	-	-	5.12
1983-84	36	67.4	-	0.214	39	167.6	-	-	3.90
1984-85	103	12.3	0.748	0.175	115	42.1	-	-	4.48
1985-86	-	-	-	0.633	27	79.5	-	-	4.15
1986-87	-	-	-	0.291	-	-	-	-	6.77
1987-88	56	66.6	0.674	0.275	19	1.2	-	-	5.79
1988-89	50	41.7	0.144	0.063	22	200.0	-	-	3.76
1989-90	98	15.4	0.263	0.099	46	3,489.0	73	46.7	2.56
1990-91	81	4.8	0.802	0.587	-	-	85	65.2	4.35
1991-92	130	25.3	0.427	0.012	63	94.3	136	32.3	5.33
1992-93	136	26.6	0.178	0.029	137	1,399.7	144	30.1	4.27
1993-94	133	28.9	0.375	0.125	133	713.5	144	47.6	3.91
1994-95	217	14.8	0.963	0.622	217	14.9	143	60.6	4.86
1995-96	72	79.1	0.986	-	144	29.4	143	19.5	5.00

Krill and salp abundance are averaged field-season values (generally 2 or more cruises). *N* is the number of samples. Chlorophyll-*a* data are the integrated 0–100 m values. Dashes indicate that data are not available. Spawning index is proportion of the mature females in advanced reproductive stages during January–February. Recruitment index is the proportion of 1-year-old krill resulting from this spawning season to the total krill caught next field season. Sea-ice index reflects extent and duration of sea-ice across the Antarctic Peninsula region before austral spring–summer surveys.

**Table 2 Salp and krill biomass**

Biomass (mg Cm <sup>-2</sup> )	1994		1995		1996	
	Salps	Krill	Salps	Krill	Salps	Krill
Mean	570.6	314.1	7.8	242.3	20.2	337.3
s.d.	563.2	856.4	16.1	201.1	30.9	756.1
Median	400.5	25.6	1.3	43.5	10.0	72.2
Maximum	3,276.8	4,971.1	75.3	1,545.2	134.2	4,721.0
<i>N</i>	63	63	57	71	72	72
Salp : krill ratio	15.6		0.03		0.1	

Biomass in the Elephant Island area during January 1994, 1995 and 1996. *N* is number of samples. Salp : krill biomass ratios based on median values.

the spring bloom period could deprive krill of sufficient food to support their energy requirements, and therefore retard krill gonadal development and spawning, leading to poor year-class success.

Indices of the spatial and temporal extent of annual sea-ice cover in the Antarctic Peninsula region are tightly correlated with air temperature, allowing the use of the longer time series instead of sea-ice cover<sup>12</sup> (Fig. 2). A warming trend has been documented for the Antarctic Peninsula region since the 1940s (refs 20–22), and a decreased frequency of extensive winter sea-ice conditions has been associated with this trend. The observation that the frequency of cold winters with extensive sea-ice cover has decreased from four out of five years during the middle of this century to only one or two out of five years since the 1970s (refs 12, 13) is confirmed using a regional rather than a local sea-ice index (Fig. 2). Decreased frequency of strong krill year-class success and recruitment, associated with a decreased frequency of extensive winter sea-ice, may be responsible for the significantly lower population sizes of krill observed in the Antarctic Peninsula region since the mid-1980s. Reduced krill population sizes could have a profound effect on their dependent predator populations.

An example of a predator effect may be the decline in the abundance of Adelie penguins (*Pygoscelis adeliae*) among colonies in Admiralty Bay, King George Island. These penguins forage in Bransfield Strait, an area typically populated in the spring and summer months by newly recruited one-year-old krill (ref. 23). Studies since the mid-1970s indicate a significant decline in fledgling survival and a 30% reduction in population size after 1987 (ref. 24).

The large interannual fluctuations in salp and krill populations,

and related shifts in utilization of primary production, may have major implications for the food web. During years favouring strong krill recruitment success and elevated population size, a relatively large proportion of primary production is likely to be incorporated into the krill-based food web and the newly fixed carbon transferred to vertebrate predators or recycled within the upper water column with only occasional transport to deeper water<sup>6,16</sup>. During periods with massive salp blooms, poor krill recruitment, and declining krill population size, substantially less of the newly fixed carbon may be transferred through krill, with a larger proportion being incorporated into salp fecal pellets and transported to deeper waters where it may be sequestered<sup>16</sup>.

Given the current trend for periods of two to three years of above- or below-average winter sea-ice extent<sup>25</sup>, we can expect continued large variations in the relative levels of dominance by krill and salps within the Antarctic Peninsula region. Associated with increased frequency of years with dense spring–summer salp concentrations is the vastly increased importance of salps as a competitor with krill and as a link in the vertical carbon flux. Occasional years with strong krill recruitment will probably maintain diminished krill population size relative to the 1970s levels. Diminished krill supplies may have long-term negative effects on the upper trophic levels, including commercial harvest by man. These observations, in part, have prompted the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to request updated krill abundance surveys to validate or replace the 17-year-old abundance data currently used in the krill management model<sup>26</sup>. CCAMLR manages the international harvest of Antarctic krill. The current precautionary catch limit for the southwest Atlantic sector is 1.5 × 10<sup>6</sup> tons yr<sup>-1</sup>, and for the Indian Ocean sector is 77.5 × 10<sup>4</sup> tons yr<sup>-1</sup>. □

**Methods**

Krill and salp data are derived primarily from December–March net-sampling operations by German expeditions and US Antarctic Marine Living Resources (AMLR) Program surveys. The data in Table 1 generally represent averaged results from two or more cruises each field season. Details on net sampling and sample processing, and considerations of gear selectivity and sampling bias, are presented in refs 11, 14. Krill spawning index is the proportion of females in advanced reproductive stages in January–February<sup>11</sup>. Krill recruitment index is the proportion of 1-year-old individuals resulting from each spawning season of the total population sampled the next field season (*R*<sub>1</sub>); (*R*<sub>2</sub>) (the

proportion of 2-year-olds) is used when  $R_1$  is unavailable or has large variance. Recruitment indices are calculated using the maximum-likelihood method<sup>14,27</sup>. Chlorophyll-*a* data are integrated 0–100 m values. Salp biomass is derived from the internal body length: C relationship<sup>18</sup> (carbon =  $0.001336 \times \text{length}^{2.331}$ ). Krill biomass is derived from the relationships between standard length and wet weight (ref. 28) (weight =  $0.00158 \times \text{length}^{3.40}$ ) and wet weight and carbon (ref. 9) (carbon =  $72.77 \times \text{weight}^{1.0242}$ ). Sea-ice coverage is based on daily ice charts derived from passive microwave imagery by the U.S. National Snow and Ice Data Center<sup>29</sup>. Annual sea-ice indices for an area of 1,250,000 km<sup>2</sup> on the west side of the Antarctic Peninsula were determined by numerical integration of monthly estimates of ice cover for each calendar year, and expressed in units of 10<sup>6</sup> km<sup>2</sup> months<sup>30</sup>. The relationship between air temperature and the regional sea-ice index (Fig. 2) is based on mean monthly air temperatures from Palmer Station or from Faraday, adjusted as ref. 21. The regression, temperature =  $-6.514 + 0.0505$  (for years between 1947 and 1996) ( $F = 13.98$ ,  $P = 0.001$ ) is similar to that from 1944 to 1987 (ref. 12). The correlation between the regional sea-ice index and air temperature is highly significant ( $n = 17$ , Kendall's  $T = -0.66$ ,  $P < 0.001$ ).

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## Corticofugal modulation of frequency processing in bat auditory system

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Auditory signals are transmitted from the inner ear through the brainstem to the higher auditory regions of the brain. Neurons throughout the auditory system are tuned to stimulus frequency, and in many auditory regions are arranged in topographical maps with respect to their preferred frequency. These properties are assumed to arise from the interactions of convergent and divergent projections ascending from lower to higher auditory areas<sup>1</sup>; such a view, however, ignores the possible role of descending projections from cortical to subcortical regions<sup>2–10</sup>. In the bat auditory system, such corticofugal connections modulate neuronal activity to improve the processing of echo-delay information<sup>11,12</sup>, a specialized feature. Here we show that corticofugal projections are also involved in the most common type of auditory processing, frequency tuning. When cortical neurons tuned to a specific frequency are inactivated, the auditory responses of subcortical neurons tuned to the same frequency are reduced. Moreover, the responses of other subcortical neurons tuned to different frequencies are increased, and their preferred frequencies are shifted towards that of the inactivated cortical neurons. Thus the corticofugal system mediates a positive feedback which, in combination with widespread lateral inhibition, sharpens and adjusts the tuning of neurons at earlier stages in the auditory processing pathway.

The moustached bat, *Pteronotus parnellii*, emits orientation sounds (biosonar pulses) that contain a long constant-frequency component (~61 kHz) suited for velocity (Doppler) measurement. The bat uses velocity information carried by the 61-kHz component for hunting flying insects<sup>13,14</sup>. Accordingly, its auditory system, from the periphery to the cortex, contains many neurons that are sharply tuned to this frequency for fine frequency analysis<sup>15,16</sup>. The sharp frequency-tuning curves in the central auditory system are sculpted by lateral inhibition<sup>17–21</sup>. The area of the primary auditory cortex that is tuned to ~61 kHz receives input from part of the thalamus<sup>22</sup> and has a frequency axis<sup>16,17</sup> like that of the primary auditory cortex of rats, cats and monkeys<sup>23</sup>.

We studied the effect of inactivation of the corticofugal system on the auditory responses of subcortical neurons (32 thalamic and 27 collicular neurons) that are tuned to frequencies between 60.47 and 62.30 kHz. Lidocaine (a local anaesthetic) always had an effect on the subcortical neurons when applied to cortical neurons tuned to these frequencies but had no effect when applied to cortical neurons tuned to frequencies outside this range (such as 34, 57 or 84 kHz). The effect of Lidocaine when the 'best frequency' of a subcortical neuron and that of inactivated cortical neurons were 'matched' (were within  $\pm 0.20$  kHz) was different from when they were 'unmatched' (different by more than 0.20 kHz).

Cortical inactivation decreased the auditory responses of matched subcortical neurons (Fig. 1A,b) without shifting their frequency–response curves (Fig. 1A,d). In contrast, cortical inactivation increased the auditory responses of unmatched subcortical neurons and shifted the best frequency towards that of the inactivated cortical neurons. Recovery of normal tuning took 1.5–3.2 h; such an increase and recovery is shown for two unmatched thalamic neurons that had best frequencies 0.30 kHz lower (Fig. 1B) or 0.68 kHz higher (Fig. 1C) than the inactivated cortical neurons. The frequency–response curve shown in Fig. 1B,d (filled circles)