



FEATURE ARTICLE

Oceanic circumpolar habitats of Antarctic krill

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ABSTRACT: Surveys of *Euphausia superba* often target localised shelves and ice edges where their growth rates and predation losses are atypically high. Emphasis on these areas has led to the current view that krill require high food concentrations, with a distribution often linked to shelves. For a wider, circumpolar perspective, we compiled all available net-based density data on postlarvae from 8137 mainly summer stations from 1926 to 2004. Unlike Antarctic zooplankton, the distribution of *E. superba* is highly uneven, with 70% of the total stock concentrated between longitudes 0° and 90° W. Within this Atlantic sector, krill are abundant over both continental shelf and ocean. At the Antarctic Peninsula they are found mainly over the inner shelf, whereas in the Indian–Pacific sectors krill prevail in the ocean within 200 to 300 km of the shelf break. Overall, 87% of the total stock lives over deep oceanic water (>2000 m), and krill occupy regions with moderate food concentrations (0.5 to 1.0 mg chl a m⁻³). Advection models suggest some northwards loss from these regions and into the low chlorophyll belts of the Antarctic Circumpolar Current (ACC). We found possible evidence for a compensating southwards migration, with an increasing proportion of krill found south of the ACC as the season progresses. The retention of krill in moderately productive oceanic habitats is a key factor in their high total production. While growth rates are lower than over shelves, the ocean provides a refuge from shelf-based predators. The unusual circumpolar distribution of krill thus reflects a balance between advection, migration, top–down and bottom–up processes.

KEY WORDS: Euphausiid · Circumpolar · Distribution · Growth · Mortality · Predation · Risk · Bottom–up control · Top–down control

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Krill *Euphausia superba*, which grows to a size of 6.4 cm, is at the boundary between plankton and nekton, and supports a large biomass of predators as well as a commercial fishery.

Photo: Chris Gilbert

INTRODUCTION

Studying micronekton in the open ocean

In ecology, our paradigms are often governed by technical constraints on methodology. A prime example in the oceans is the issue over bottom–up or top–down control, with an emphasis on the former because it is easier to quantify than predation (Ohman & Wood 1995, Verity & Smetacek 1996). However, a basic ecological trade-off exists between occupying habitats that are risky, but rewarding, and those that are safer, but food-poor (e.g. Suhonen 1993). While this risk–reward concept is well accepted in the pelagic marine environment (e.g. for diel

vertical migration), it is rarely extended to horizontal distribution studies (e.g. Alonzo et al. 2003, Pepin et al. 2003).

Technical constraints are also behind the difficulty in classifying the mechanisms of large-scale movement in pelagic organisms. Some consider micronekton as passive drifters at large scales, even though they can be strong swimmers. Swimming behaviour is very hard to quantify in dynamic environments (Hamner & Hamner 2000), while the availability of advection models has led to much work on micronekton distribution as dictated by current flow (Fach et al. 2006, Sourisseau et al. 2006, Thorpe et al. 2007). Insects, by contrast, have a fascinating variety of behaviours that can be examined and quantified more easily (e.g. Shashar et al. 2005).

Antarctic krill *Euphausia superba*, hereafter 'krill', epitomise these problems with methodology. We have not yet fully incorporated predation into our mainly bottom-up-based view of their biology (Alonzo & Mangel 2001, Alonzo et al. 2003, Ainley et al. 2006). Growing to >6 cm and living for >5 yr, krill are at the awkward boundary between plankton and nekton. Advances have been made in understanding the advective forces governing their distribution (Hofmann & Murphy 2004, Murphy et al. 2004, Thorpe et al. 2007). However, these authors stress that it is the whole life cycle (of which advection and swimming behaviour are just 2 parts) which dictates the large-scale distribution of krill (Murphy et al. 2007). Clearly though, we need to know the position of krill along the spectra from top-down to bottom-up control (Ainley et al. 2006, Nicol et al. 2007) and from advection- to migration-dictated distribution (Nicol 2003, 2006, Murphy et al. 2007).

Polar regions are warming rapidly (Vaughan et al. 2003), and their endemic pelagic invertebrates are stenothermal, with life cycles potentially sensitive to environmental change. To predict the future, we need to understand mechanisms behind the present-day success of key species such as krill. Suggested factors for krill include its large size, longevity, flexible diet, schooling behaviour, use of winter sea ice and starvation resistance (Daly & Macaulay 1991, Quetin et al. 1994, Quetin & Ross 2003). Its asymmetrical circumpolar distribution is also extraordinary and atypical of Antarctic zooplankton. In this paper we focus on the distribution of post-larval krill during the spring to autumn (October–April) period in relation to its overall success.

Circumpolar distribution of krill

The 'Discovery' Investigations (1926 to 1939) laid the foundations for our understanding of Antarctic plankton distributions. Indeed, Marr's (1962) circumpolar map of krill (Fig. 1) remains the prime reference on their distribution today (Tynan 1998, Nicol et al. 2000a, Hofmann & Hüsrevoğlu 2003). This map, like all those following it, was based on multiple seasons of sampling with different methods. The conversion factors used by Marr (1962) were soon adjusted (Mackintosh 1973) and since then, a series of circumpolar maps of krill distribution have been created (e.g. Maslennikov 1980, Voronina 1998, Everson 2000). Without a quantitative scale, these maps are hard to interpret. Only recently have there been attempts at creating more quantitative maps using data from acoustic and net surveys (Atkinson et al. 2004, Siegel 2005).

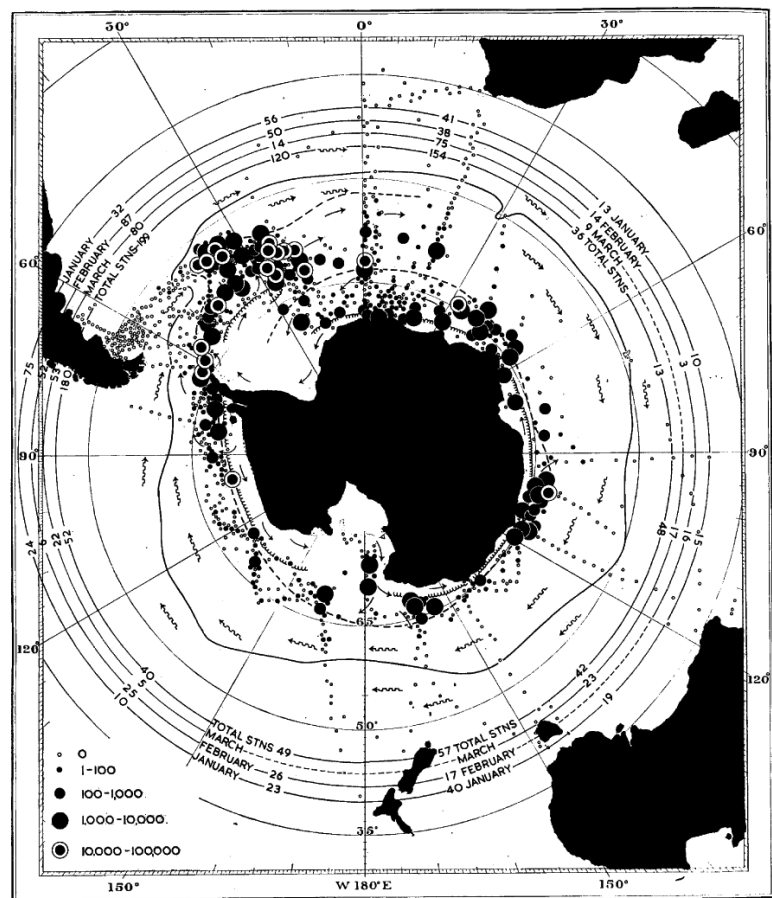


Fig. 1. *Euphausia superba*. Summer distribution of postlarvae (Fig. 135 from Marr 1962). This map was based on 970 stations sampled with both oblique and horizontal 1 m ring nets. It shows the distribution of highest recorded densities mainly between 20 and 60° W, and high catches in both near-shelf and oceanic areas, congruent with our analysis. However, because sample coverage is very uneven and the circles obscure each other, relative krill densities are not possible to quantify from this map

Several of these maps show the strongly asymmetric circumpolar distribution of krill that is atypical of other zooplankton species. Nicol et al. (2000a) estimated from acoustic measurements that biomass densities in the SW Atlantic sector were 10-fold those in the Indian sector, and Atkinson et al. (2004) calculated that 50 to 70% of the total stock were within the sector 10° to 80° W. By contrast, Fig. 2 shows much more even cir-

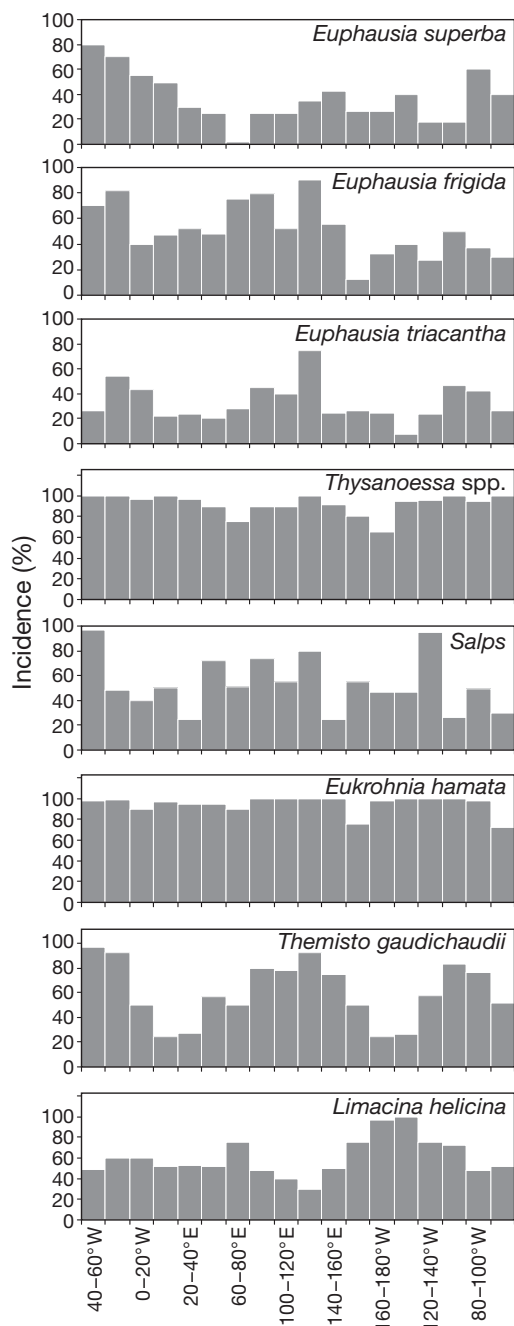


Fig. 2. *Euphausia superba*. Circumpolar distribution relative to other major zooplankton and micronekton species, plotted as percentage incidence in available hauls within each sector (redrawn from Fig. 4 of Baker 1954)

cumpolar distributions for other zooplankters, a finding since supported by specific studies on copepods (Andrews 1966) and salps (Foxton 1966, Pakhomov et al. 2002, Atkinson et al. 2004). Likewise, total mesozooplankton catch volumes differ little between sectors (Fig. 3). Has the unusual distribution of krill got a part to play in their success?

Our synthesis is based on net samples, incorporating those from Marr (1962) (excluding the horizontal hauls) and all available data since then. This database, KRILLBASE, builds on that used by Atkinson et al. (2004), with additional recent data and standardisation to a common sampling method (see Appendix 1 'Standardisation of densities within KRILLBASE', available in MEPS Supplementary Material at www.int-res.com/articles/suppl/m362p001_app.pdf). KRILLBASE is restricted to post-larval krill from non-targeted hauls executed between October and April, although most records are from the summer months (Appendix 1). This dataset yields the best available picture of the relative distribution pattern of krill (Fig 4). Based on the area of each grid cell and its krill density, 70% of the total krill stock live between 0 and 90° W. Thus, nearly three-quarters of the population are concentrated into one-quarter of the longitude.

Top-down and bottom-up controls on krill ecology

Many explanations for the circumpolar distribution of krill have been proposed, including sea ice (Mackintosh 1973, Brierley et al. 2002), gyres (Marr 1962, Pakhomov 2000, Nicol 2006), fronts (Spiridonov 1996, Witek et al. 1988, Tynan 1998), shelf edges (Siegel 2005, Nicol 2006) and high food concentrations (Constable et al. 2003, Atkinson et al. 2004). However, none of these fully accounts for the distribution patterns, as exceptions apply to each. One common factor, however, is that all are bottom-up interpretations, which relate krill to areas of enhanced food. Fig. 5 shows this modern concept that krill are a species mainly of shelf edges and their vicinity (Trathan et al. 2003, Reid et al. 2004, Nicol 2006).

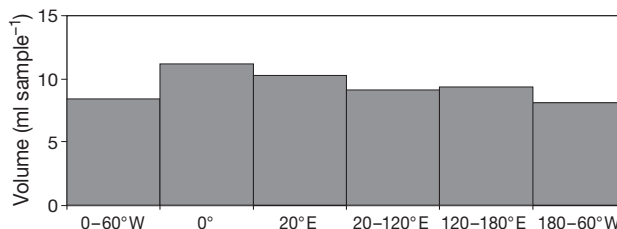


Fig. 3. Total volume of zooplankton caught with 70 cm modified Nansen net, integrated over the top 1000 m (redrawn from Fig. 17 of Foxton 1956)

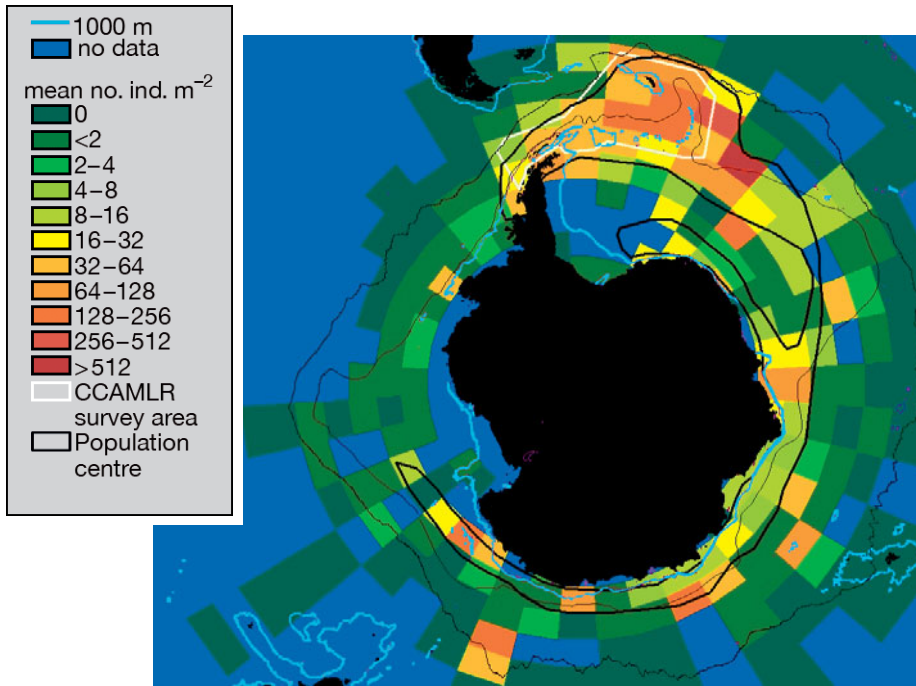


Fig. 4. *Euphausia superba*. Circumpolar distribution of krill based on standardised data from KRILLBASE (8789 stations including those north of the Antarctic Polar Front, APF). The data are plotted as arithmetic mean krill densities (ind. m^{-2}) of all stations within each 3° latitude by 9° longitude grid cell. We suspect that the isolated cells with high densities near the APF at the bottom of the map reflect a mis-identification in one particular survey. The distribution of sampling effort and the circumpolar density distribution from un-standardised data are shown in Appendix 1. Fronts shown in black lines (north to south) are the APF (Moore et al. 1999a) and the Southern Boundary of the Antarctic Circumpolar Current (Orsi et al. 1995). The population centres of krill were drawn by eye, relative to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Survey (Hewitt et al. 2004)

Few krill studies, by contrast, deal both with the ability to find food and to avoid predation. Mortality is clearly a prime force in krill population dynamics (e.g. Pakhomov 2000, Murphy & Reid 2001), with >100 million tonnes (Mt) of krill being removed annually by predators—a value similar to their total biomass (Miller & Hampton 1989, Mori & Butterworth 2006). Near islands with breeding predator colonies, predation is especially intense (Croxall et al. 1984, Fraser & Hofmann 2003). The concept of a ‘krill surplus’ following the removal of large predators through whaling during the last century reflects this top-down view of control (Mackintosh 1973, Laws 1985, Ainley et al. 2006). Ecologists studying higher krill predators often emphasise predation as a controlling factor (e.g. Reid & Croxall 2001, Fraser & Hofmann 2003, Ainley et al.

2006), whilst others highlight food resources (e.g. Atkinson et al. 2004, Siegel 2005). Clearly, these 2 approaches must be integrated (Daly & Macaulay 1991, Alonzo & Mangel 2001, Ainley et al. 2006).

Advection and migration controls on krill distribution

Are krill more like a planktonic drifter or more like a small pelagic fish? On the one hand, krill have been treated as drifters at the circumpolar scale, since advection probably plays a major part in their lives (Hofmann et al. 1998, Murphy et al. 2004, Fach et al. 2006). On the other hand, attributes more akin to those of small pelagic fish have been argued. As well as size and lifespan (Quetin et al. 1994, Quetin & Ross 2003), these attributes include cruising speeds of $\sim 20 \text{ cm s}^{-1}$ (Kils 1982), schooling (Daly & Macaulay 1991, Hamner & Hamner 2000) and horizontal migrations (Kanda et al. 1982, Siegel 1988, Sprong & Schalk 1992, Lascara et al. 1999). Despite these attributes, questions remain over the degree to which swimming controls the circumpolar distribution of krill.

Modern models emphasise both migration (Fig. 6) and advection (Fig. 7) in determining the distribution of krill. Clearly, the processes work at different scales, with the ontogenetic seasonal migration model applying to the Antarctic Peninsula area, whereas the advection model is circumpolar. However, there is need to integrate processes at both of these scales, because small differences in behaviour can have major effects on advection tracks (Hofmann et al. 1998, Murphy et al. 2004, Cresswell et al. 2007).

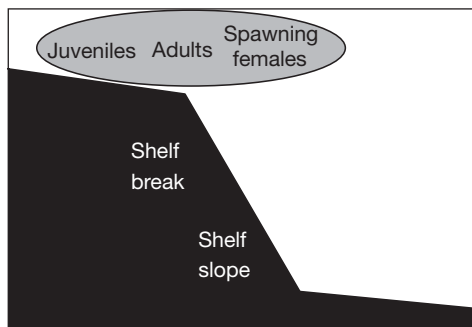


Fig. 5. *Euphausia superba*. A modern overview of summer post-larval krill distribution (redrawn from Fig. 4a of Nicol 2006) emphasising current thinking over the importance of the shelf-slope region for this species

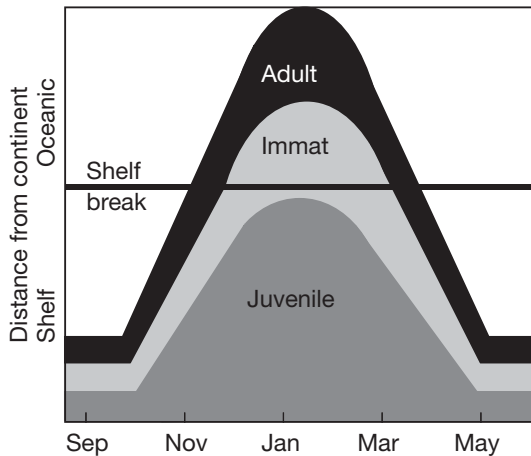


Fig. 6. *Euphausia superba*. Another modern model of krill distribution, again emphasising the role of the shelf (re-drawn from Siegel 2005). This model schematically illustrates horizontal ontogenetic spawning migrations for the Antarctic Peninsula, relative to the shelf break, depicted by a horizontal line. The abundance of adults, immature and juvenile krill is signified by the width of each respective band. The model shows an offshore spawning migration in spring followed by an onshore migration in autumn

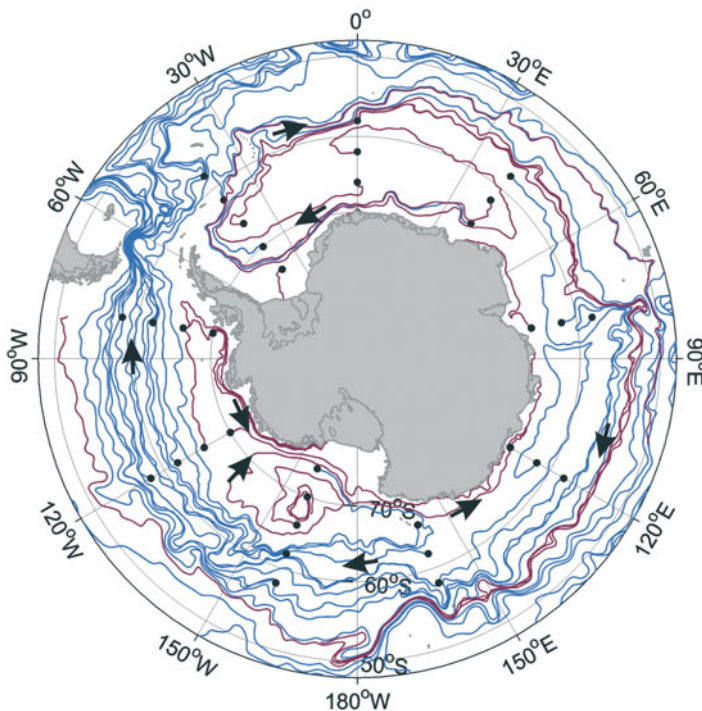


Fig. 7. Transport vectors of passively drifting particles tracked for 10 yr in the climatological velocity fields of the Ocean Circulation and Climate Advanced Modelling (OCCAM) model (reproduced from Fig. 2a of Thorpe et al. 2007 with permission). Particle release points are shown by black dots, with trajectories being depth-weighted means of the upper 182 m. Particles exiting the map area shown in blue and those remaining inside it in red. Such models have been used increasingly in the Southern Ocean to interpret krill distribution

Aim and structure of this synthesis

Many overviews of krill biology have appeared recently (Nicol 2003, 2006, Hofmann & Murphy 2004, Siegel 2005, Smetacek & Nicol 2005, Ainley et al. 2006, Murphy et al. 2007, Nicol et al. 2007). These have taken a variety of standpoints over the relative importance of top-down or bottom-up processes and the influence of advection or migration on distribution. Our meta-analysis attempts to rationalise these issues. Our central thesis is that the above controls are not mutually exclusive and that the unique distribution of krill reflects them all operating together.

This synthesis departs from a conventional review in several key features. We do not synthesise the results of past studies, but rather synthesise and re-analyse the raw data behind them. The number of such meta-analyses is increasing, following the realisation that nations must pool their datasets to address circumpolar issues (www.iced.ac.uk). KRILLBASE contains >70 times the number of stations of even the largest surveys, so circumpolar questions beyond the scope of individual campaigns can be tackled. In this synthesis, we relate krill to multiple features of their environment. After defining the potential habitats and describing the main patterns of krill distribution, we explore the concept of 'good habitat'. Do krill inhabit areas with optimal temperature-food combinations for growth? We introduce top-down controls with a simple trade-off model for occupying risky, high growth habitats vs. those that are safe, but food-poor. The next section examines the roles of advection and migration in causing the observed distribution.

Finally, we discuss the issue of net sampling methodology, which is critical to our interpretations of distribution. Methods are described fully in Appendix 1. We then rationalise the views of top-down, bottom-up, advection and migration controls of distribution, to speculate on some of the mechanisms for the success of krill. The different views are examined in the context of climate change, with some promising research avenues suggested for the future.

KRILL HABITAT

Bathymetry, fronts and the seasonal ice zone

In Fig. 8a, we delineate shelf areas as those habitats that are not covered by permanent ice and which are shallower than 1000 m. The shelf is deep, with most areas >200 m. Shelves comprise

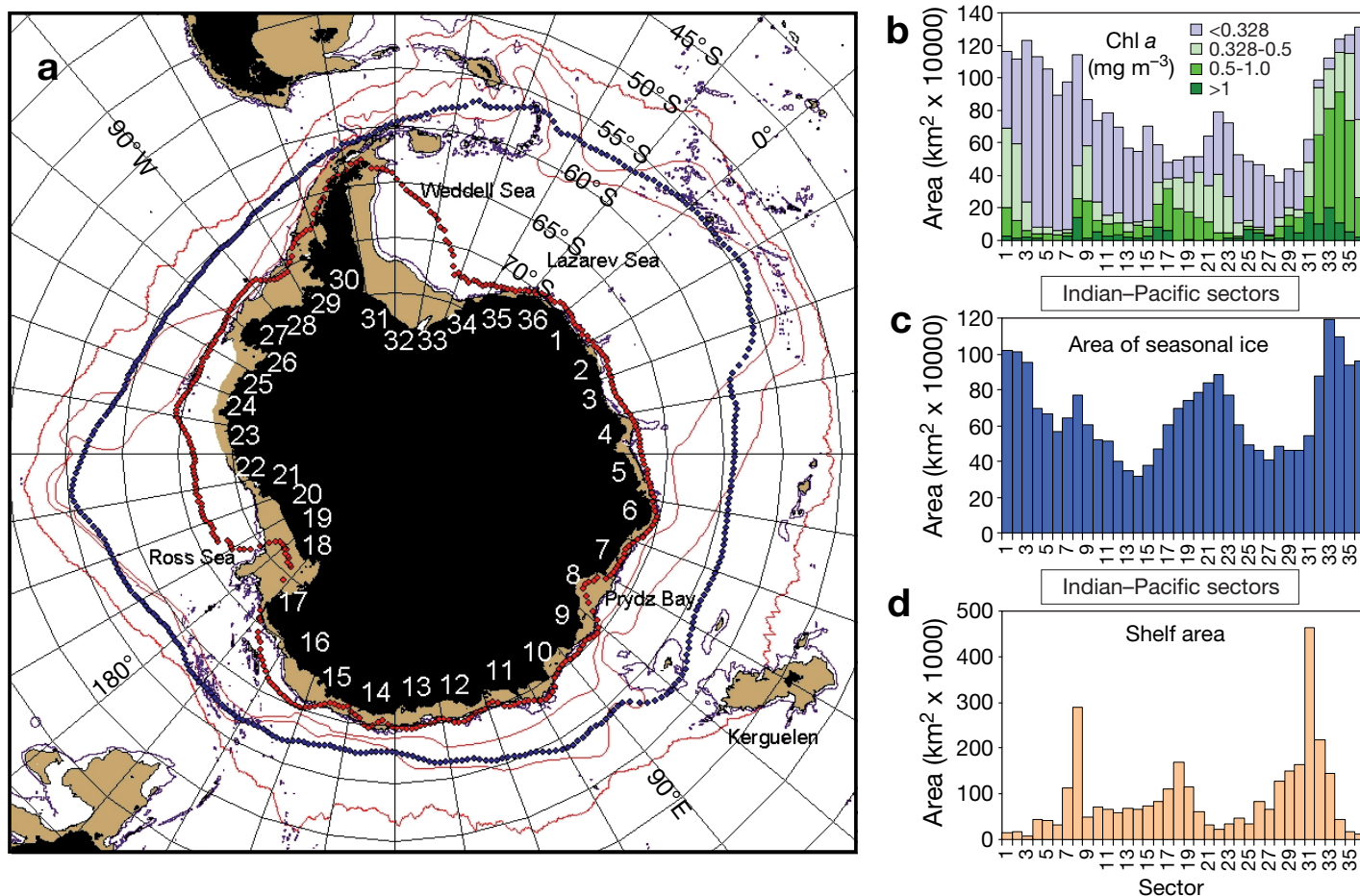


Fig. 8. *Euphausia superba*. Circumpolar habitat. (a) The 36 sectors of 10° longitude are numbered in white eastwards from the 0°, with the Atlantic sector defined as Sectors 30 to 3, Indian: Sectors 4 to 16, and Pacific: Sectors 17 to 29. Fronts (red lines) from north to south are Antarctic Polar Front (APF), Southern Antarctic Circumpolar Current Front (SACCF) (from Orsi et al. 1995, updated for the Scotia area by Thorpe et al. 2002) and the Southern Boundary of the ACC (SB-ACC). Sea ice positions are mean latitudes of 15% concentration in February (red diamonds) and September (blue diamonds). The shelf (pale brown) is demarcated by the 1000 m isobath, while the 2000 m isobath (purple line) delineates the foot of the shelf slope; (b) areas of chlorophyll *a* (chl *a*) concentrations within each 10° sector, from 7 yr (1997–1998 to 2003–2004) December to March SeaWiFS averages. Green shades (i.e. >0.328 mg chl *a* m⁻³) correspond to those above the half saturation constant calculated for krill growth (Atkinson et al. 2006); (c) areas of sea ice zone (SIZ) per sector (data from Nicol et al. 2004); (d) Area of shelf (<1000 m water depth) per sector (data from Nicol et al. 2004)

only one-tenth of the total area south of the Antarctic Polar Front (APF), but their extent varies greatly between sectors. Although isolated island shelves are important for krill in the SW Atlantic (defined here as 30 to 70° W), most of this habitat comprises the shelves of Antarctica itself.

Both the Southern Boundary of the Antarctic Circumpolar Current (SB-ACC) and the northern sea ice extent lie far from the continent in the Weddell-Lazarev sectors and progressively converge with the continent in the Indian sector. Within the Atlantic sector, there is a dramatic transition between the Antarctic Peninsula, where the northern ice edge and fronts are near to the coast, and the Lazarev sector, where they are far apart.

Chlorophyll *a* distribution

The highest chlorophyll *a* (chl *a*) concentrations south of the APF tend to be in shelf areas or in plumes downstream of them (Fig. 9). However, major exceptions exist, as for example the massive and remote ocean blooms south of New Zealand and in the Lazarev Sea. There is also a clear asymmetry in chl *a* distribution, with the Atlantic sector having a large area of elevated chl *a* (Fig. 8b), an effect amplified by the great width of the Antarctic Circumpolar Current (ACC) in this region. While chl *a* concentrations generally tend to decrease throughout the productive season, especially at lower latitudes, the locations with enhanced chl *a* remain basically similar throughout this period (Fig. 9).

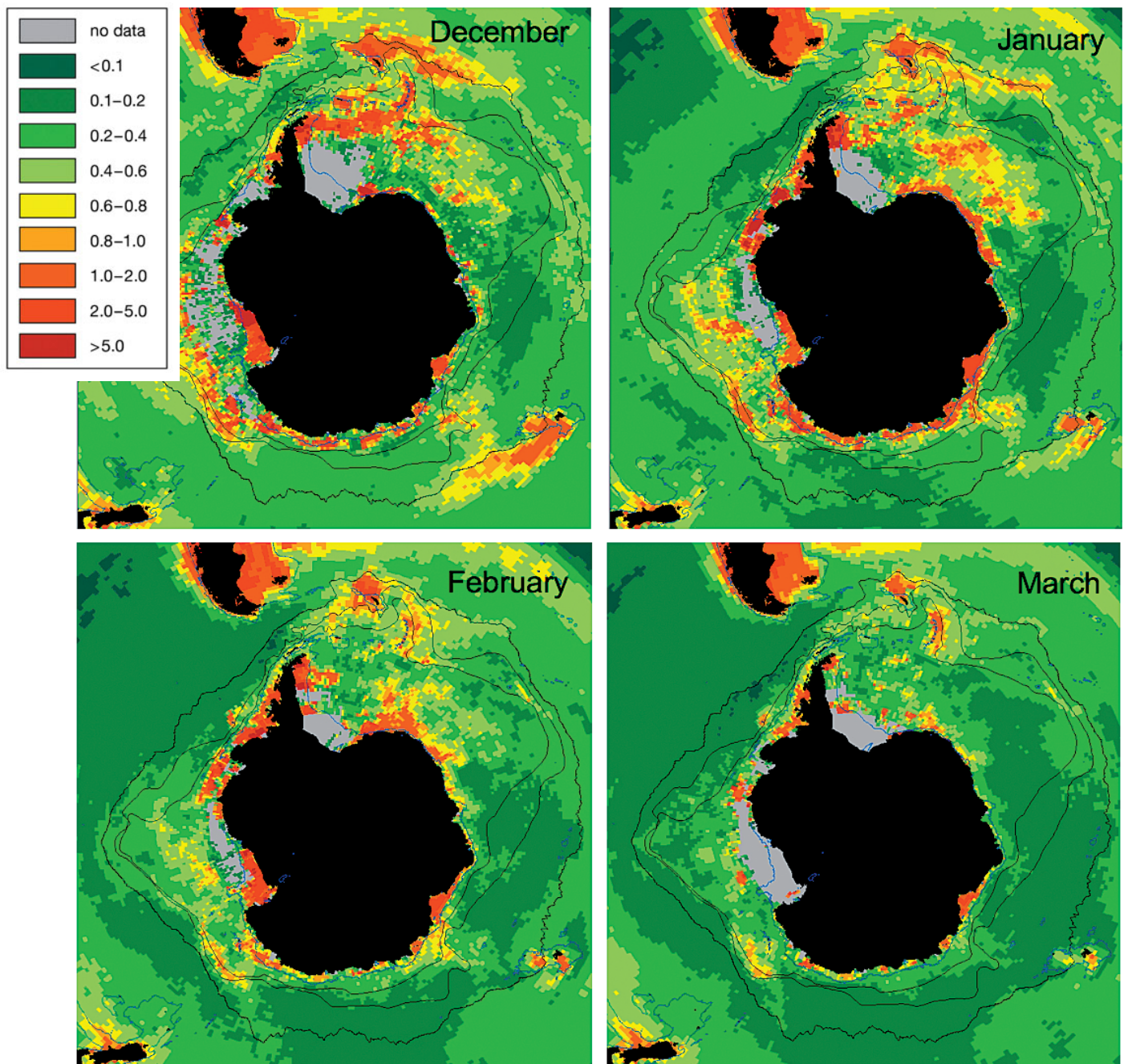


Fig. 9. Monthly mean chl *a* values ($\text{mg chl } a \text{ m}^{-3}$) for the main open water season, based on 7 seasons of SeaWiFS data (summers of 1997–1998 to 2003–2004). Values are plotted on a 0.5° latitude by 1° longitude grid, with the multi-season mean for each grid cell weighted according to the number of data pixels available from each season. Grey grid cells thus had no pixels for any of the 7 seasons. Fronts (black lines) as in Fig. 8. The 1000 m isobath is denoted by the blue line

CIRCUMPOLAR KRILL DISTRIBUTION

Overview

Although only non-targeted scientific net hauls were used for KRILLBASE, the data were derived from a composite of surveys that differ in sampling depth,

gear used, proportion of day vs. night hauls, and time of year of sampling. Since all of these factors could bias the distribution map, their effects were removed as far as possible by standardising to a common method (see Appendix 1). This approach is a refinement of that used by Marr (1962) and Mackintosh (1973) for their maps.

Our standardised data (Fig. 4) show a concentration of krill in the SW Atlantic sector and a tail extending around Antarctica, closer to the continent. As shown previously (Marr 1962, Mackintosh 1973, Nicol et al. 2000a, Siegel 2005), this tail is of much lower density than in the SW Atlantic. We have tentatively marked the core of the distribution in Fig. 4 to highlight 2 further features:

Within the SW Atlantic, the highest mean densities are not at the Antarctic Peninsula but further east and north, in Sectors 32 to 35 (marked in Fig. 8). Indeed, the Antarctic Peninsula-Scotia Sea system does not contain most of the krill, even within the Atlantic sector. Based on the areas and krill densities within each grid cell in Fig. 4, the CCAMLR Synoptic Survey area (Hewitt et al. 2004) contains only 26% of the total circumpolar stock (this value is 28% if the densities are stratified on a finer-scale 2° by 6° grid, A. Atkinson et al. unpubl.). By comparison, the whole 0° to 90° W sector contains 70% of the total stock. These calculations assume conservatively that the unsampled (blue) grid cells in Fig. 4 contain no krill.

The data suggest 2 population centres between Sectors 34 and 4 (see Fig. 8 for sectors). One aligns with the ACC stream and the other is in the counter-current near the continent. This result also holds for individual surveys in the area, for example those in 1934 and 2004. Like so many aspects of krill biology, this pattern has already been proposed many years ago (Mackintosh 1973, Makarov & Spiridonov 1993). KRILLBASE suggests a connection between the northern population (the main 'stock' in the Atlantic sector) and the remaining 30% of the stock. This connection is made tentatively, given the paucity of sampling here—the region clearly demands a more focussed survey effort.

Long-term change in density and distribution

The standardised data in Fig. 4 are a composite of data spanning 80 yr, during which krill density within the SW Atlantic sector has declined over the period 1976 to 2003. This observation was based on subsets of un-standardised data, causing concerns over possible sampling artefacts (Quetin et al. 2007). However, Fig. 10 shows that, even after applying our standardisation procedure, the decline persists.

This decline in krill within the SW Atlantic sector is accompanied by a regional increase in water temperature (Meredith & King 2005) and decrease in sea ice (Parkinson 2002) and follows larger-scale and longer-term changes (de la Mare 1997, Gille 2002, Cotté & Guinette 2007, Whitehouse et al. in press). Consequently, an overall change in krill abundance is plausible within a 30 yr period, taking into account that the

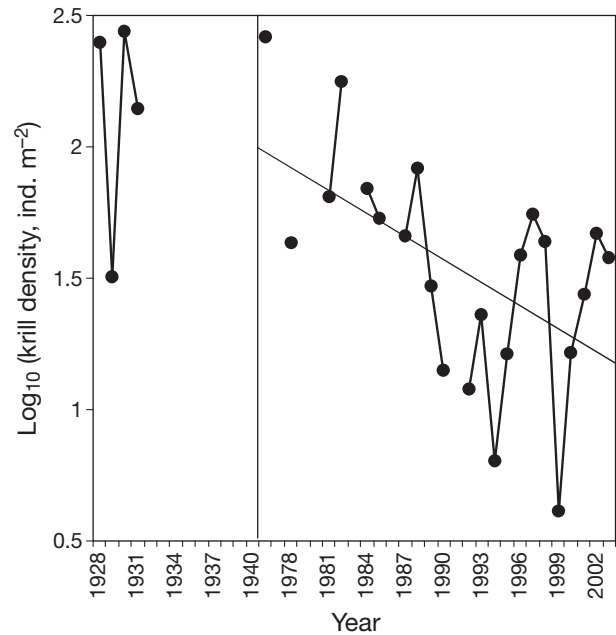


Fig. 10. *Euphausia superba*. Change in mean density (ind. m⁻²) within the SW Atlantic sector (30 to 70° W), based on standardised densities, for comparison with Fig. 2a of Atkinson et al. (2004) based on un-standardised values. Only years with >50 stations are plotted. The vertical line separates the 1926 to 1939 and post-1976 eras. Based on the post-1976 dataset there is a significant decline: $\log_{10}(\text{krill density}) = 60.07 - 0.0294(\text{yr})$; $R^2 = 31\%$, $p = 0.007$, $n = 22$ yr

population can fluctuate greatly from year to year. However, in the context of this synthesis, the question is: Has this been accompanied by a re-distribution? Within the limits of the available data, we found no convincing evidence for any change in krill distribution between the 'Discovery' expeditions and recent years, so the 'climatology' in Fig. 4 is a reasonable overall picture.

Seasonal change in distribution

Our standardisation procedure (see Appendix 1) revealed that krill density peaks in the middle of summer (January) and declines thereafter. This reflects the pulse of recruitment from larvae during spring–summer and subsequent mortality. However, there is a latitudinal difference in this simple picture. We illustrate this with a plot of density anomalies (Fig. 11), calculated from standardised densities, and comparing seasonal trends in density between the northern and southern parts of the krill distribution range. In our analysis, we have divided the 8137 sampling stations into a standard sample size, a nominal $n = 36$ groups of stations, to make it compatible to a recent circumpolar habitat-based analysis (Nicol et al.

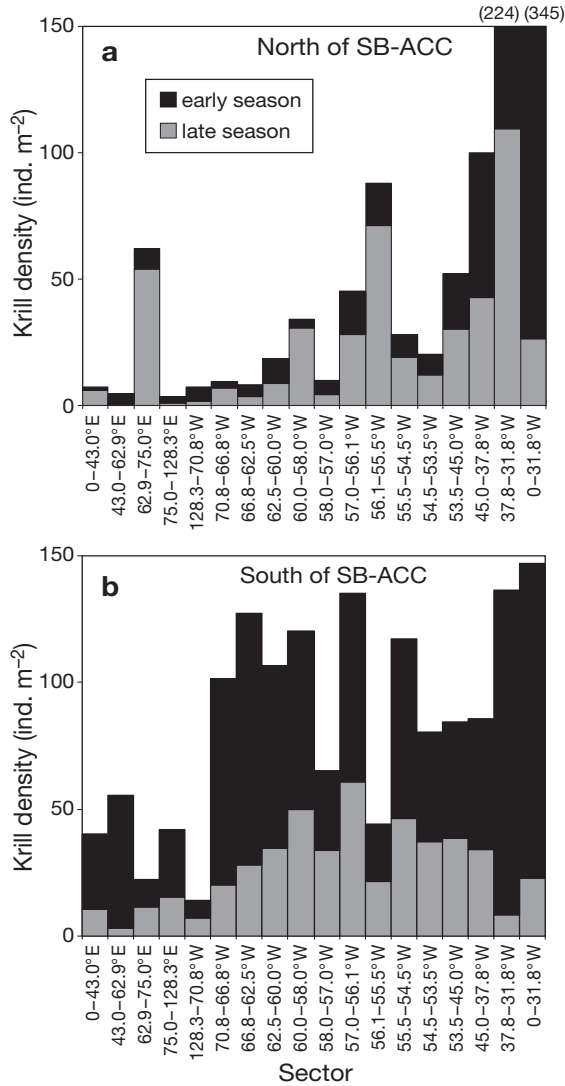


Fig. 11. *Euphausia superba*. Seasonal change in standardised mean krill density within the (a) northern and (b) southern portions of the circumpolar habitat of krill. The Southern Ocean is divided here into 18 sectors of variable width but with equal numbers of stations in each, to enable more robust statistical comparison (Table 1). Mean densities within each sector are compared for the early season (before 1 Feb) and the late season (after 1 Feb), to show the different seasonal trajectories between the northern and southern regions. SB-ACC: See Fig. 8

2004). Fig. 11 shows that, overall, the population to the north and south follow different seasonal trajectories, with a seasonal increase in krill density in the south relative to the north. This trend remains significant in raw, un-standardised density data (Table 1), so it is not an artefact of our standardisation.

Several factors may contribute to this pattern. Throughout the northern region, and within the main ACC flow, the decrease in density could be related to mortality throughout the season. It could also reflect vertical migration out of the 0 to 200 m layer (Siegel 2005, Taki et al. 2005), even to the seabed (Gutt & Siegel 1994). Alternatively, it could reflect migration or advection of krill southwards across the SB-ACC.

The seasonal increase in krill in the southern zone is harder to explain. Mortality would decrease density rather than increase it, and the late season sampling efforts took place after the main pulse of recruitment—the new recruits enter the sampled population in December to January (Quetin et al. 1994). It is possible that the increase reflects a redistribution from the southern, ice-covered regions, or from the seabed. Another explanation is a transport (or migration) of krill southwards as the season progresses. This topic is revisited below under ‘Roles of advection and migration’.

Distribution in relation to shelves

Continental shelves and slopes are increasingly considered to be key habitats for summer postlarval krill (Trathan et al. 2003, Reid et al. 2004, Nicol 2006), with animals advected into the open ocean being disadvantaged by food shortage (Fach et al. 2002, 2006). Shelves and slopes are indeed more predictable places to find krill than the vast expanses of ocean, due to their higher mean density there. These hotspots are also foci for krill fishery (Ichii 2000, Kawaguchi & Nicol 2007), for most research efforts, and for locally intense energy fluxes within the food web (Atkinson et al. 2001, Murphy et al. 2007). This has led naturally to the concept of krill being reliant on these hotspots. Cur-

Table 1. *Euphausia superba*. Comparison of early and late season krill density (ind. m⁻²) within each of the 18 sectors in Fig. 11. SB-ACC is defined in Fig. 4, with ACC defined as between the SB-ACC and the APF (for definitions see Fig. 8). Individual density values are standardised (see Appendix 1), and paired *t*-tests for the sectors support a late-season decrease in density in the ACC and an increase to its south

Degree of standardisation	Mean of [log (density pre-1 Feb) – log(density post-1 Feb)] South of SB-ACC	ACC	<i>t</i>	<i>p</i>
Unadjusted data	-0.176	0.139	-2.71	0.015
Adjusted, but not for season	-0.138	0.208	-2.67	0.016
Fully adjusted (including for season)	-0.335	0.0439	-3.12	0.006

rent models of their seasonal distribution (Siegel 2005, Nicol 2006) infer shelves to be a key part of the summer habitat for postlarvae (Figs. 5 & 6).

Our circumpolar scale view, however, provides a radically different picture. Based on all net sampling stations south of the APF, mean krill density over shelf-slope areas (water depth <2000 m) is only 1.65 times that over deep ocean. This relatively slight difference in krill density from the shallowest to deepest water can also be seen from acoustic data taken from Reid et al. (2004) and re-plotted in Fig. 12. By stratifying the density estimates by area, we calculate (see Appendix 1) that 87% of the total krill population live over water depths >2000 m. This reflects the rather small density gradient and the 10-fold greater habitat area.

Plotting krill density in relation to distance from the shelf break also shows the same basic picture. At a circumpolar scale (Fig. 13a), there is a decline in krill density from onshore to offshore, but the relatively small density difference and 10-fold greater area of ocean mean that most of the population are oceanic. Based on both types of analysis, the finding that only 13% of the global krill stock live in the shelf-slope habitat shows that krill are mainly an oceanic species.

This overall pattern, however, obscures major differences between sectors. Prior analysis revealed 3 broad patterns of distribution found in the Antarctic Peninsula area, the main Atlantic sector, and the Indian-Pacific sector. These sub-areas (Fig. 13b–d) are plotted on the same scale to show the much lower density in the Indian-Pacific sector and the scarcity over its

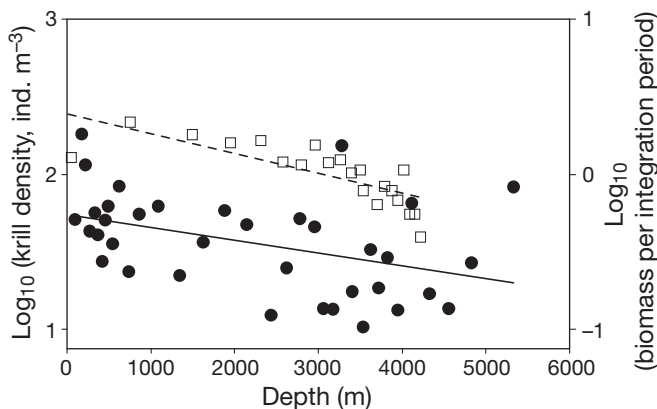


Fig. 12. *Euphausia superba*. Krill density (left axis, filled circles, solid regression line) in relation to water depth. Data from all 8137 net stations south of the APF were first ranked in order of increasing water depth and then divided into 36 groups of 226 stations. The mean krill density for each group is plotted here against the respective mean water depth. Regression statistics (but with both predictor and response variables logged) are presented in Table 2. Also plotted is relative acoustically derived biomass vs. water depth (right axis, open squares, broken regression line) with data recalculated from Reid et al. (2004)

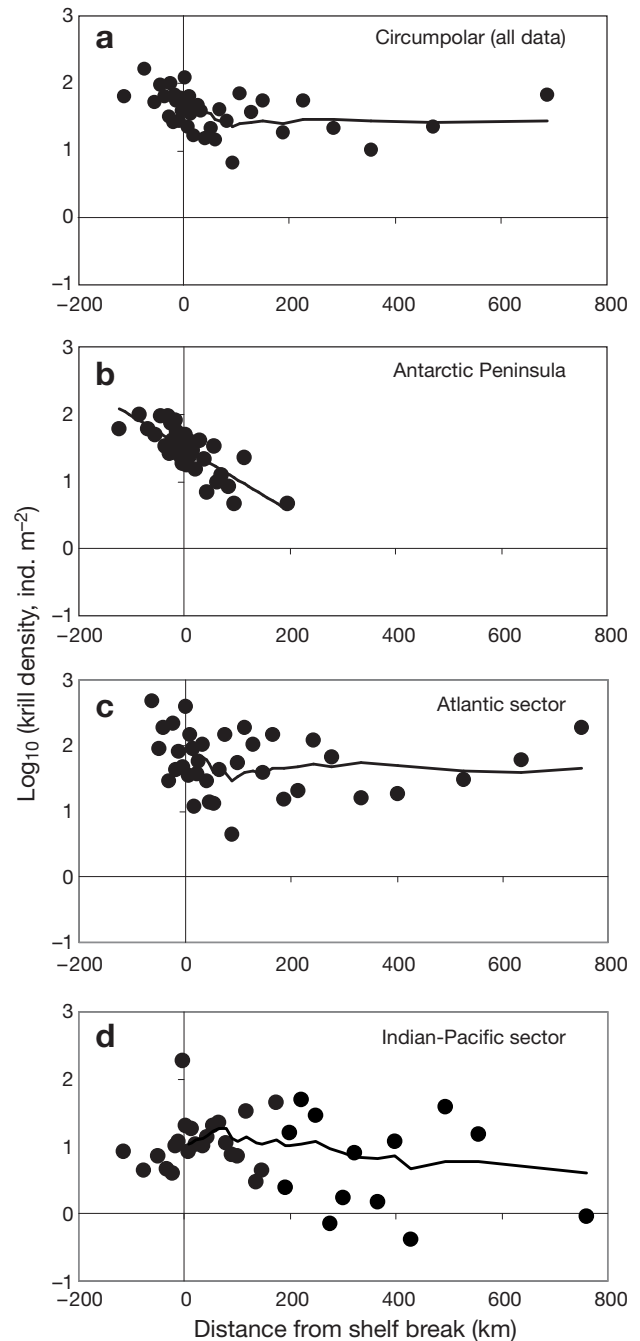


Fig. 13. *Euphausia superba*. Distribution in relation to the shelf break; (a) Circumpolar density data (8137 stations south of APF) in relation to distance from the nearest shelf break (defined as any 1000 m isobath occurring south of the APF). Shelf stations are assigned with negative distances; (b) Antarctic Peninsula data only (3992 stations from 50 to 70° W; Sectors 30 to 31) $\text{Log}_{10}(\text{krill density}) = 1.5 - 0.0047(\text{distance from shelf break, km})$, $R^2 = 0.628$, $p < 0.01$, $n = 36$; (c) Atlantic sector only (2142 stations from 50° W to 30° E; Sectors 32 to 3; (d) Indian-Pacific sector only (2003 stations from 30° E to 70° W; Sectors 4 to 29). Trend lines in Panels (a,c,d) represent 10-sample running means. We used our standard protocol of dividing each subset of data into 36 groups with equalised samples sizes

shelves (Fig. 13d). Here, krill density is often maximal within a few hundred kilometres of the shelf break, with a general decline further offshore. This pattern, with maximum densities south of the SB-ACC, has been observed in detailed surveys within this sector (Hosie 1994, Nicol et al. 2000b,c).

The Antarctic Peninsula, by contrast, shows a completely different pattern with highest densities often close inshore near the islands and the convoluted coastline (Fig. 13b). Clearly, the shelf here is better krill habitat than its high latitude counterpart around the main continent. The latter, with heavier ice cover, is inhabited by its congener *Euphausia crystallorophias* (Hosie 1994).

While the oceanic habitat near the Antarctic Peninsula is narrow, unproductive and contains few krill, the oceanic Atlantic sector is productive and much more extensive, and high krill densities occur within the ACC remote from land (Fig. 13c). In this sector, there is also a concentration close to and over shelves, but the shelf–ocean difference in density is not great. Because krill abundance is highest in this main Atlantic sector it dominates the overall circumpolar pattern.

These differences are illustrated for 3 well-studied areas in Fig. 14. Krill are confined to the inner shelf at the southern Antarctic Peninsula, and only further into the Atlantic sector are they abundant in the open ocean (Fig. 14a). Within this sector, South Georgia shows a well-known concentration of krill over its northern shelf (Marr 1962, Watkins et al. 1999) and high densities patchily distributed across the oceanic area, mainly south of the Southern ACC Front (SACCF, Fig. 14b). By contrast, Prydz Bay (Fig. 14c) illustrates the third pattern—a concentration just offshore of the shelf break.

This is not a rigid attempt to classify 3 types of shelf–oceanic distribution of krill, since Fig. 14a shows transitions. The key point is that the sectors differ greatly—a factor that needs to be taken into account before any attempt is made to generalise from one area. Over the entire habitat, the mainly oceanic distribution of krill has fundamental implications for their ecology, which is described in the following sections.

BOTTOM-UP CONTROL FACTORS

Distribution in relation to food and environmental variables

The circumpolar distribution of krill has been described in relation to areas of high productivity, namely productive shelf breaks, fronts, sea ice zone (SIZ) and gyres. The effects of these bottom-up vari-

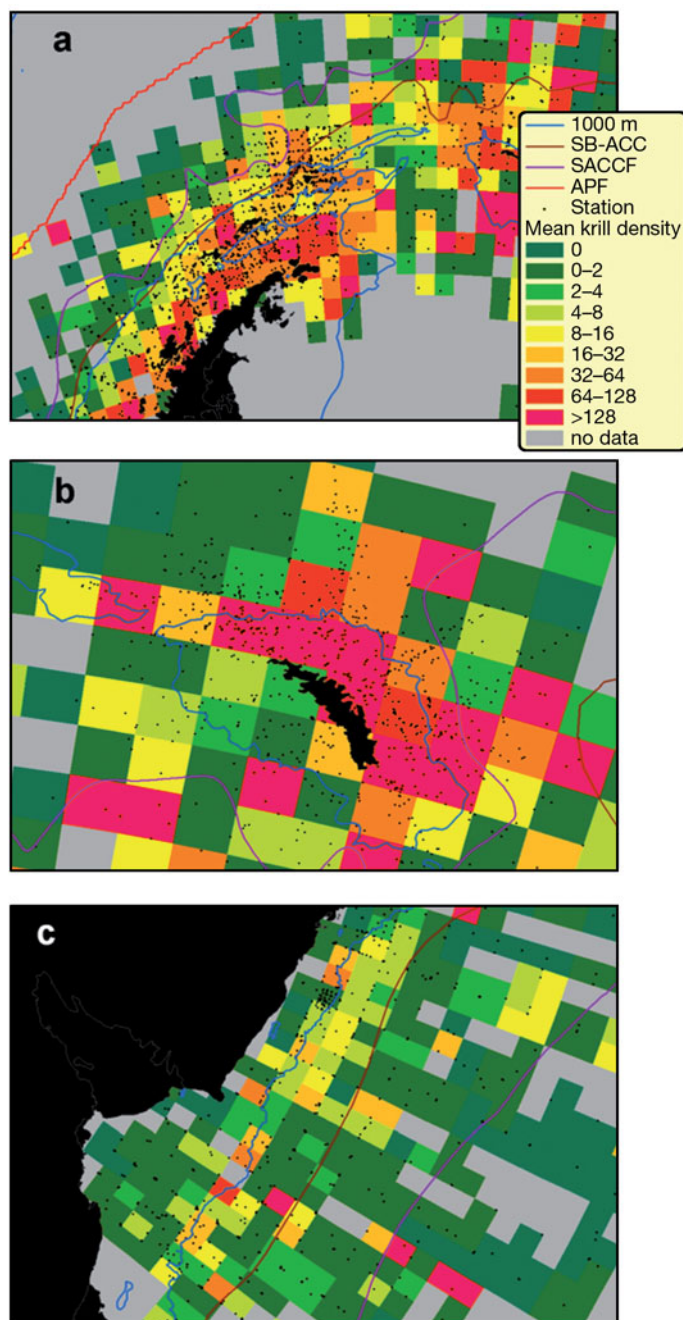


Fig. 14. *Euphausia superba*. Distribution near (a) the Antarctic Peninsula, (b) South Georgia, (c) Prydz Bay to illustrate the varying types of association with shelf areas. The plots are of arithmetic mean (standardised) density (ind. m⁻²) on a 0.5° latitude by 1° longitude grid

ables are compared in Table 2. We stress that all of these relationships are between ‘climatologies’ (averages over multiple seasons)—not between concurrently measured variables. This methodology preserves the large sample sizes needed for such analysis, since KRILLBASE includes data from before the satel-

Table 2. *Euphausia superba*. Circumpolar-scale relationships between \log_{10} of krill density (ind. m^{-2}) and physical–biological environment and Gross Growth Potential (GGP). For definitions of APF, SIZ and SB-ACC see Fig. 8. $N = 36$ for all regressions, which use all available data (>8000 stations) pooled into 36 groups either of equal sample size or into sectors of 10° longitude. ns: not significant ($p > 0.05$)

Relationship	Predictor (x) variable (All logged)	Regression (of logged predictor and response variables)	R ² (%)
Food	Mean chl <i>a</i> (mg m^{-3}) (chl <i>a</i> data in Fig. 17a, regression shown in Fig. 15a) ^a	$y = 1.76 + 0.304x / (1 + 0.991x)$	48
	Area of chl <i>a</i> > 0.5 mg m^{-3} in 10° sector (1000 km^2) (chl <i>a</i> data in Fig. 8b, regression in Fig. 15b)	$y = -1.96 + 1.11x$	30
	Mean chl <i>a</i> in 10° sector (mg m^{-3})	ns	–
Water depth	Mean water depth (m) (data derived from Fig. 12)	$y = 2.54 - 0.31x$	23
	Area from coast to 1000 m isobath in 10° sector (1000 km^2) (data from Nicol et al. 2004, presented in Fig. 8d)	ns	–
Distance from shelf break	Distance (km) from any 1000 m isobath south of APF (km) (data in Fig. 13a)	ns	–
Food and Water depth	Mean chl <i>a</i> , <i>C</i> mean depth, <i>Z</i>	$y = 2.39 - 0.135 C + 0.201 Z - 1.75 C^2$ (C^2 is the only significant term: $p = 0.004$)	58
GGP	GGP (data from Fig. 16a)	$y = 0.513 + 0.382x - 0.0300x^2$	28
Area of SIZ	Maximum minus minimum sea ice extent in 10° sector (1000 km^2) (data from Nicol et al. 2004, presented in Fig. 8c)	ns	–
Area south of SB-ACC	Area from coast to SB-ACC in 10° sector (km^2) (data from Nicol et al. 2004)	ns	–

^aA hyperbolic relationship provides a statistically better fit ($F_{1,33} = 14.36$, $p = 0.001$) than a straight line. A quadratic relationship provides an even better fit ($R^2 = 61\%$), but the effects at highest chl *a* concentrations are uncertain

lite era, and the records do not include concurrently measured environmental data.

After dividing the Southern Ocean south of the APF into 36 sectors of 10° longitude, no relationship was found between mean krill density per sector and its area of shelf, the SIZ, or area south of the SB-ACC. Some of these relationships (for example between krill density and area south of the SB-ACC) hold for parts of the circumpolar habitat (Nicol et al. 2000b,c), but not for all of it. Krill density and recruitment are linked to sea ice extent, but this is a temporal relationship for the SW Atlantic (Kawaguchi & Sataki 1994, Siegel & Loeb 1995, Loeb et al. 1997, Atkinson et al. 2004) and is not seen at circumpolar scales (Constable et al. 2003, Table 2, this paper).

However, krill density relates significantly both to food and to water depth. These co-vary, but multiple

regression (Table 2) teases apart the 2 effects—we find no significant effect of water depth after allowing for the effect of food. Indeed, the relationship with food concentration (Fig. 15a) is non-linear and much stronger than that with water depth (Table 2). Thus, variation in krill density between sectors is more influenced by their areas of enhanced food than by shelf areas within the sectors (Table 2, Fig. 13b).

Our reappraisal of what constitutes good krill habitat helps interpret their concentration in the SW Atlantic. Factors invoked previously include its larger shelf area, retention by the Weddell Gyre and convergence of currents (Reid et al. 2004, Nicol 2006, Thorpe et al. 2007). However, Fig. 4 suggests a scarcity of krill around the Weddell Sea (see also Siegel 2005), and krill density per sector does not relate to its area of shelf. Fig. 15b shows the SW Atlantic simply as part of

the circumpolar relationship between krill density and the area of suitable feeding grounds. Clearly, this area must also support the whole life cycle. For example, its lower latitudes may receive enough winter light to promote pelagic- and ice-derived food for overwintering, larval growth and early spawning (Murphy et al. 2007, Quetin et al. 2007).

The issue of scale is central to these analyses. Given the complex interactions between predator and prey, the sign and type of relationship observed between them depends on the scale of analysis (Rose & Leggett 1990). We therefore repeated the krill–food analysis, but at a smaller scale, by pairing each krill record with SeaWiFS data for the same year and month of sampling and extracting the mean chl *a* value from within 50 km of the station ($n = 1943$ stations). Like the clima-

tology analysis, this also produced a dome-shaped relationship, with highest krill densities at moderate chl *a* values. However, the explanations might not be the same. For example, the larger scale relationship reflects the high-chl *a* Antarctic shelf being south of the main range of krill, while at the smaller scale high densities of krill could have grazed down their food.

Distribution in relation to growth potential

A circumpolar prediction of successful spawning habitats exists (Hofmann & Hüsrevoğlu 2003), but none for predicting habitats ideal for growth. An empirical model of summer growth rates now allows this (Atkinson et al. 2006), being designed for large-scale, satellite-derivable food and temperature indices. While there are caveats to any predictive model, Fig. 16 is a first numerical attempt to explore how food and temperature interact to dictate the circumpolar growth habitats for krill.

We defined different growth habitats by their Gross Growth Potential (GGP), which is the body mass of a krill at the end of March divided by that at the beginning of December (see Appendix 1 for calculation method). The growth rate decreases as krill get longer, so the GGP is higher for smaller starting sizes of krill (Fig. 16a,b). Each season varies in its conditions, and thus in its ability to support high growth rates. This is illustrated in Fig. 16c,d—a high chl *a* season (summer 1999–2000) supports much higher growth rates than one with low chl *a* (2002–2003).

To check these predictions, we obtained an overall mean GGP for the Southern Ocean by weighting the cell-specific GGPs (Fig. 16a) with their respective krill densities. This provides a GGP of 3.7. For comparison, a quadrupling of krill mass from December to March (i.e. a GGP of 4) equates to a 30 mm krill growing at 0.1 mm d^{-1} . This is close to respective values of 0.11 mm d^{-1} and 0.06 to 1.2 mm d^{-1} from studies using the Instantaneous Growth Rate (IGR) method in the Indian-Atlantic sectors (Kawaguchi et al. 2006) and the Antarctic Peninsula (Ross et al. 2000), and to growth rates of field populations (Rosenberg et al. 1986, Siegel & Nicol 2000).

All of these model outputs show starvation (shrinkage) north of the APF, while rapid growth follows the availability of chl *a* in habitats south of the APF. The interaction of food and temperature in dictating growth is illustrated in Fig. 17. The shrinkage north of the APF is probably due to adverse effects of high temperature. The upper temperature limit for krill survival is $\sim 8^\circ\text{C}$ (Naumov & Chekunova 1980) and their normal northern limit is the APF. The model on which the GGP values are based (Atkinson et al. 2006) yields maximal

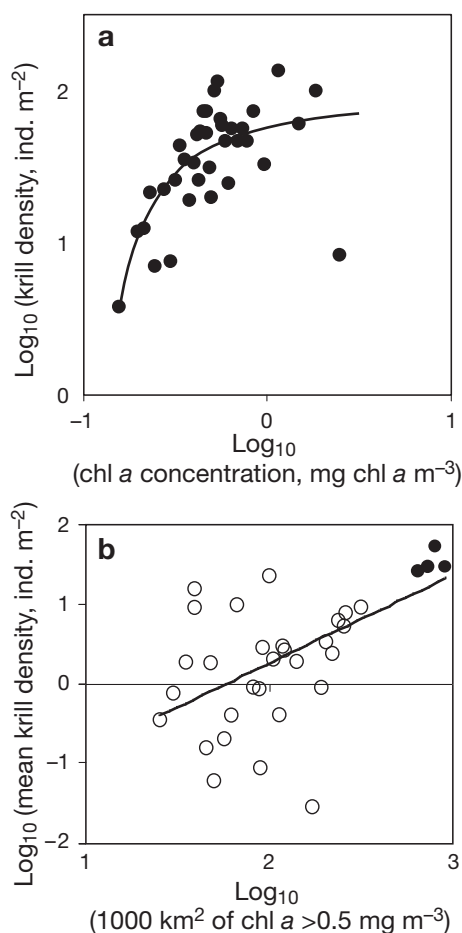


Fig. 15. *Euphausia superba*. Log–log relationships between climatologies (i.e. multi-season means) of krill density and simple indices of their food availability. (a) Krill density vs. food concentration, based on our standard division of all 8137 sampling stations into 36 groups of equal size; (b) krill density within each of the 36 sectors vs. its area of elevated chl *a* (arbitrarily defined as $>0.5 \text{ mg chl } a \text{ m}^{-2}$). The SW Atlantic-Peninsula sectors (here defined as 10 to 80°W) are shown with filled symbols. Regressions are in Table 2

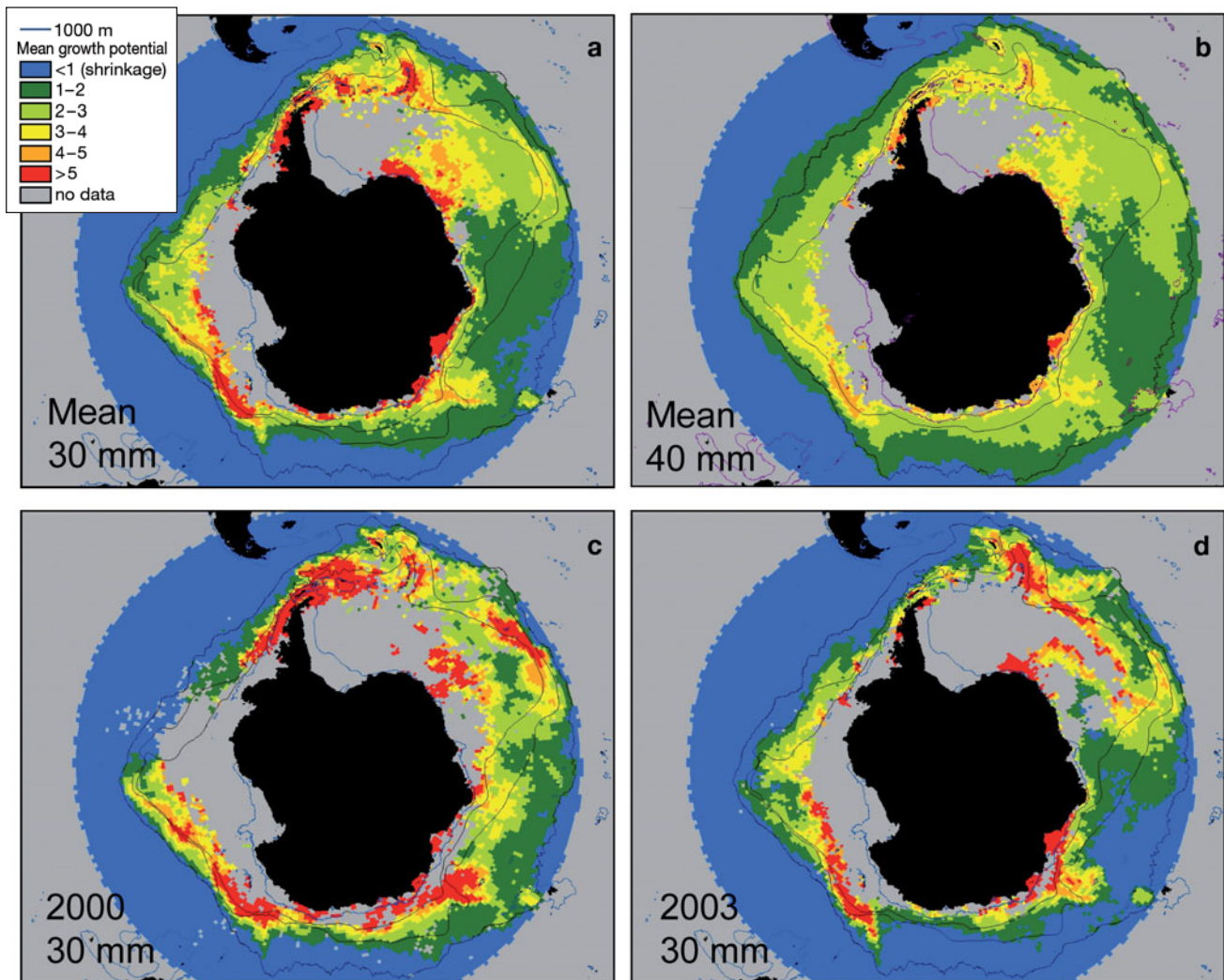


Fig. 16. *Euphausia superba*. Distribution of habitats supportive of elevated summer growth, based on Gross Growth Potential GGP (unitless). (a) GGP for a krill 30 mm long at the start of the model run on 1 Dec. The values in (a) and (b) are averaged across the 7 SeaWiFS summers used to drive the growth model; (b) equivalent mean GGP for a Model run with a 40 mm krill (see Appendix 1); (c) GGP for a Model run with a 30 mm krill in a high chl *a* summer, 1999–2000, for comparison with that in (d) a lower chl *a* summer, 2002–2003. Note that these are predictions of growth potential, not the actual distribution of production, since some of the potentially high growth habitats have few krill. Fronts (black lines) from north to south are the APF, the SACCF and the SB-ACC (see Fig. 8)

growth at 0.5 to 1°C and a progressive decline at higher temperatures. It is possible that the warm waters near the APF in the SW Atlantic are viable krill habitat because the costs from high water temperatures are offset by the rewards from abundant food (Fig. 15).

Overall, krill density relates significantly to GGP (Figs. 4 & 17, Table 2), but the relationship is non-linear, with highest density where the GGP is moderate. Some of the habitats offering the highest growth potential (namely cold, highly productive waters of the Antarctic continental shelf) have only moderate or low krill concentrations, being south of their main range of distribution (Fig. 14c). However, the key point about

this relationship is that krill are rare where growth potential is poor; in other words, they do not inhabit the large belts of high nutrient-low chlorophyll (HNLC) water.

To show the implication of this, we calculated total krill production based on their GGP and distribution (i.e. summing all GGP values in Fig. 17c, having first weighted them in proportion to their mean krill density in Fig. 4). This provides a total gross production of 353 Mt (based on conservative 4-fold conversion of dry mass to wet mass). However, if the same total number of krill was redistributed with the same density (ind. m⁻²) across all cells, their production would be only 281 Mt. Thus, whatever the mechanism, the con-

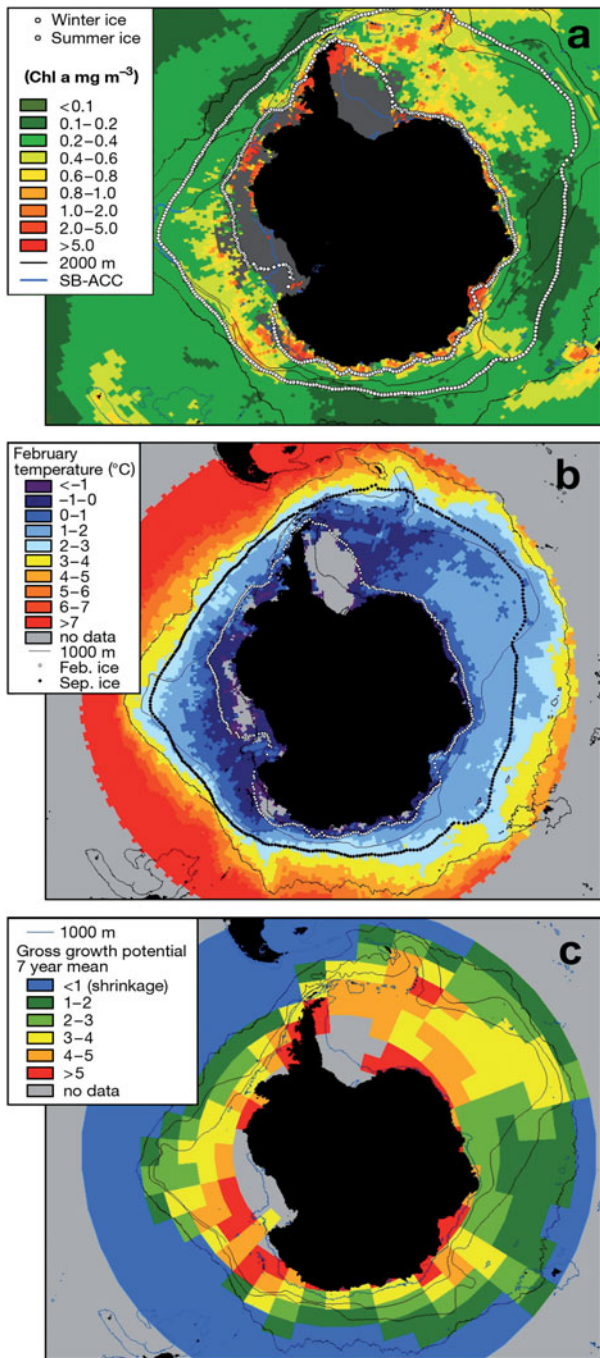


Fig. 17. *Euphausia superba*. Combinations of food and temperature that allow krill growth. (a) December to March, 7 yr mean (1997–1998 to 2003–2004) chl a concentration in relation to mean February and September winter ice extents (northern 15 % concentration) and 2000 m isobath, which marks the base of shelf slope, plateau and seamounts conducive of blooms. Data are SeaWiFS pixel averages plotted on a 0.5° latitude by 1° longitude grid; (b) maximum summer sea surface temperature (mean from February 2002 to 2004) (c) GGP (unitless) based on a 30 mm krill, with values from Fig. 14a averaged onto the same 3° by 9° grid as used for krill density (Fig. 3) to allow comparison. Fronts (black lines) from north to south are the APF, the SACC and the SB-ACC (see Fig. 8)

centration of krill in enhanced growth habitats boosts their production by 72 Mt.

To sum up, the distribution of summer post-larval krill does indeed relate to bottom-up factors. However, the highest krill densities coincide with intermediate food concentrations and growth potential, rather than with the highest values for both factors. We suggest that this is due to reduced predation risk in such areas.

TOP-DOWN CONTROL FACTORS

Risk-reward model of habitat suitability

The productive growth habitats for krill near islands, shelves, fronts and ice edges also host abundant predators (Ainley et al. 1991, 2006), so living here is a trade-off between eating and being eaten (Fig. 18). This basic trade-off exists partly because several key predator species need solid substrates (ice or land) to breed on, and because this same property promotes iron fertilisation (de Baar et al. 1995, Smetacek et al.

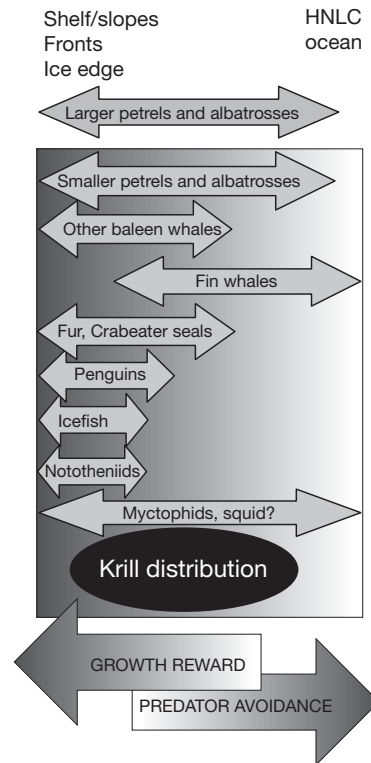


Fig. 18. *Euphausia superba*. Conceptual model of the trade-off between predation risk and growth reward. This shows the opposing gradients from productive but risky habitats to the safer but low growth high nutrient-low chlorophyll (HNLC) areas, with schematic distribution of krill relative to food and its major predators. The model pertains to the summer period only, when most data are available on predators and krill

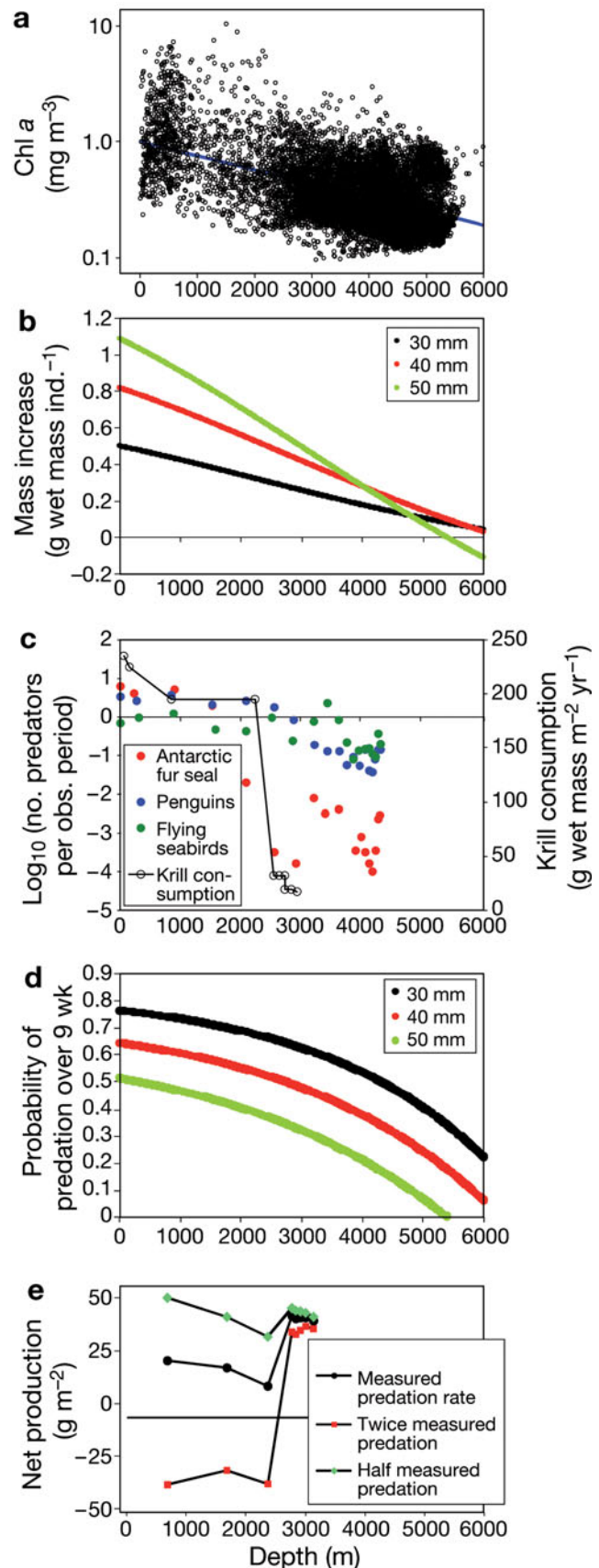
2004). Many non-land breeders such as icefish (Koch et al. 1994) and whales (Reilly et al. 2004, Friedlaender et al. 2006) also concentrate in chl *a*-rich habitats, while the distribution of others relative to chl *a* is unknown (e.g. squid or myctophid fish).

The best approach to explore this trade-off numerically would be to relate growth potential and predation risk to chl *a*, but we are unaware of predation data expressed in this form. Instead, we related both growth and predation risk to water depth, since this is a reasonable proxy for chl *a* concentration (Fig. 19a) and is a tractable means of describing trends in predator distributions. The environmental data (Fig. 19a), combined with the growth model, generate an onshore–offshore gradient in growth potential for an individual krill (Fig. 19b). This quantifies the potential benefit in the extreme scenario of optimising individual growth and ignoring mortality risk.

However, krill predators also track these hotspots. This is shown in Fig. 19c for the land-breeding component in relation to water depth. Predation risk is depicted here both by predator densities (Reid et al. 2004) and by estimates of krill consumption (Murphy 1995). The changes in predator densities and consumption estimates with water depth are substantial, and certainly in line with the differences in predation risk that are calculated to balance growth (Fig. 19d).

These opposing gradients in growth potential and predation risk have a cancelling effect in calculations of net production. The krill consumption estimates in Fig. 19c provide a more specific illustration of this

Fig. 19. *Euphausia superba*. Risks and benefits for krill calculated for January–February, all in relation to water depth. (a) Overall average relationships are food concentration C ($\text{mg chl } a \text{ m}^{-3}$) vs. depth Z (m): $\text{Log}_{10} C = -0.00268 - 0.00012 Z$ ($R^2 = 28\%$, $p < 0.001$, $n = 10338$ grid cells of 0.5° by 1° south of the APF). Temperature T ($^\circ\text{C}$): $T = 0.496 + 0.000344 Z$ ($R^2 = 8\%$, $p < 0.001$, $n = 10338$); (b) predicted mass gains of 3 sizes of krill over 9 wk, from the relationships above and the growth model (Eq. 9 in Appendix 1); (c) left axis, logarithmic scale: relative densities of major krill predators across the SW Atlantic sector (data recalculated from Reid et al. 2004); right axis: calculated krill consumption by seabirds at Bird Island, South Georgia (data from Murphy 1995); (d) predation calculated to balance exactly the mass increase from growth predicted in Panel (b) (i.e. to yield 0 net growth). This simple calculation shows the ‘balance point’ for the counteracting risk–reward trade-off for comparison with predator observations in Panel (c) (see Appendix 1); (e) predicted net production (g wet mass m^{-2}) after 9 wk, based on an evenly distributed starting population of 40 mm krill on 1 Jan with growth in Panel (b) and mortality based on Murphy’s (1995) values in Panel (c). Model sensitivity to mortality is examined by doubling and halving the predation rates of Murphy (1995); negative net production (values below the horizontal line) equates to greater consumption rates than can be supported by growth



trade-off for the South Georgia area. The predation estimates are conservative for this region, comprising only the seabird fraction of the total predators, and being calculated pro-rata from annual rates. Nevertheless, a simple sensitivity analysis (Fig. 19e) shows that net krill production is very sensitive to predation loss, implying the importance of top-down control.

The period for which krill data is available, from 1926 to 2004, follows a major perturbation of their predators, with a large proportion of fur seals, southern right, humpback and blue whales removed before 1926 (Laws 1985, Moore et al. 1999b). These comprise both shelf-based and pelagic foragers, so it is hard to predict how their removal might affect krill distribution. While krill density relates significantly ($p < 0.05$) and negatively to water depth in both eras of sampling efforts included in KRILLBASE (1926 to 1939 and 1976 to 2004, see Appendix 1) with a substantial shelf-ocean difference for the 1926 to 1939 era, no significant difference in the slopes of the regressions was detected.

In summary, our risk-reward analysis shows that the best feeding grounds for krill may not be best for net population growth. The exercise is not to infer that krill have necessarily evolved a risk-balancing strategy—the krill we observe are those remaining after predation has operated. In other words, a reduced predation risk may be the implication of the observed distribution and not its cause. Notwithstanding this caveat, the concept of risk and reward allows us to rationalise the surprising finding that 87% of the krill population live over deep ocean. Here, krill are growing at sub-maximal rates, but they are sheltered from the most intense predation.

Efficient growth in low-risk areas

The penalty for reduced predation risk is less food, but 2 features of krill decrease the impact of this effect. First, they are rare in the great HNLC belts. Second, they can grow fairly well at moderate chl *a* concentrations. Krill have a classic hyperbolic functional growth response, and this non-linearity means near maximal growth at chl *a* concentrations of $\sim 1 \text{ mg chl } a \text{ m}^{-3}$ and substantial growth at half of this value (Ross et al. 2000, Atkinson et al. 2006). We have illustrated this in Fig. 20. Clearly, reproduction incurs high energy costs (Nicol et al. 1995, Virtue et al. 1996), so the risk-reward trade-off will vary with ontogeny. Our point is that postlarval krill do not need blooms to grow.

Krill are adapted to cope with food scarcity, whether in summer or winter. During a survey of the eastern Scotia Sea in summer 2002–2003, for example, chl *a* values were unusually low, with only 0.2 to 0.3 mg

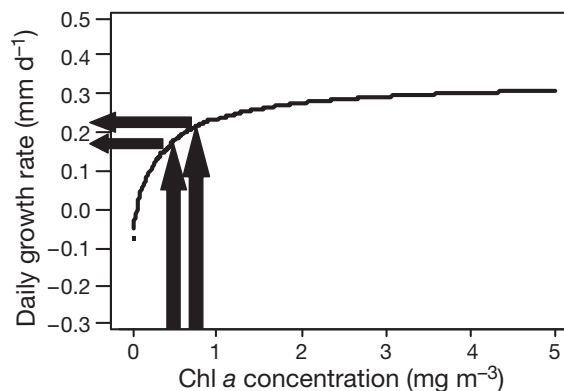


Fig. 20. *Euphausia superba*. Functional relationship between krill growth and chl *a* concentration (Atkinson et al. 2006), showing the relative benefits of shelf (<1000 m water depth) and oceanic habitats for growth, based on their mean chl *a* concentrations from Fig. 19a. The difference is illustrated here for a 25 mm krill, but the relatively small amount of growth sacrificed in a presumably safer oceanic habitat is also shown by the other sizes of krill

chl *a* m^{-3} (Atkinson et al. 2006). Even so, krill were able to grow by exploiting the microbial food web instead (Schmidt et al. 2006). By contrast, the copepods *Calanoides acutus* and *Rhincalanus gigas*, normally found in surface layers at this time of year (Andrews 1966, Atkinson 1991), were still in diapause at depth, as phytoplankton was presumably insufficient that summer (Ward et al. 2006). Thus 'efficient' feeding may be a key to the oceanic life of krill, whether by locating patches of food, assimilating it efficiently or exploiting alternative prey (Schmidt et al. 2006). Models of their energy budget also point to this (Fach et al. 2002, 2006), although the mechanisms need further clarification.

ROLES OF ADVECTION AND MIGRATION

There is general consensus that advection plays a major part in distributing krill, both at mesoscales (Everson & Murphy 1987) and over larger scales (Hofmann & Murphy 2004). Indeed, Fig. 4 shows a general alignment of krill populations along the major flows of the ACC and the continental counter-current. The extent to which krill actually behave as drifters is unknown, since the direct evidence either for drifting or migrating is limited by the logistical difficulty of such studies.

It is not easy to reconcile the circulation pattern (e.g. Fig. 21a) with our krill distribution map (Fig. 21b). Juxtaposed, these 2 maps pose a conundrum. The drift, both with currents and with sea ice (Thorpe et al. 2007), carries krill northwards towards the APF or east-

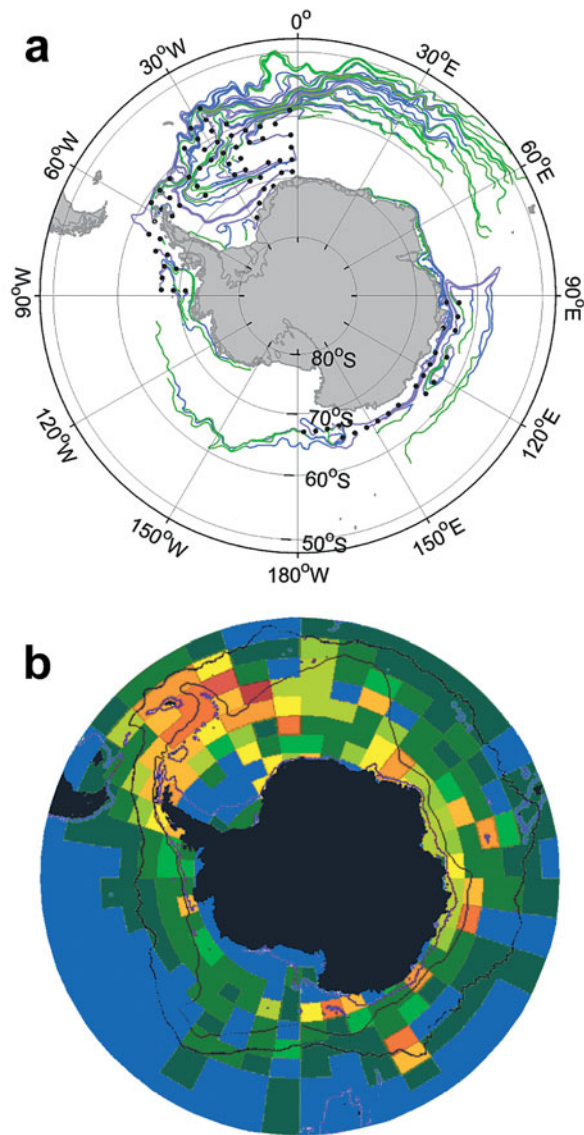


Fig. 21. *Euphausia superba*. The distribution of krill in relation to large scale advection. (a) 3 yr drift trajectories for particles released at the black spots and transported with OCCAM model-derived flow fields in the surface layer. The 3 colours represent the 3 successive years of transport (Fig. 4a of Thorpe et al. 2007, with permission); (b) krill distribution from standardised data showing that the particles released in Panel (a) would be transported away from the main distribution centres of krill, signified by the brighter colours (legend as in Fig. 4)

wards into HNLC areas, neither of which have high abundances of krill. A scenario of major expatriation and great losses from starvation or predation may exist, but postlarvae can withstand >200 d without food (Ikeda & Dixon 1982), and krill predators are scarce in HNLC regions.

A tendency for expatriation could be remedied by a southwards migration in summer and autumn, to return krill towards the SIJZ. That would connect the

opposing conveyors of the ACC and continental counter-current, providing the gyre-type trajectories proposed by Nicol (2006). Such a southwards migration has been described by Siegel (1988) at the Antarctic Peninsula and is supported by observations elsewhere (Kanda et al. 1982, Sprong & Schalk 1992). It also seems to be supported by our observation of a seasonal decrease in krill density in the ACC and an increase to its south (Fig. 11 & Table 1), although other explanations for this are possible (see 'Seasonal change in distribution' above).

Clearly, the extent to which advection and migration dictate krill distribution must be resolved (Murphy et al. 2007). This migration issue has several facets; for example, we need to show whether or not krill have the sensory abilities to allow 'navigation', whether they can sustain the necessary swimming speeds within schools (Ritz 2000, Swadling et al. 2005) and whether schools do actually migrate. For the latter, the krill fishery offers some future possibilities for tracking schools (Kawaguchi & Nicol 2007).

DISCUSSION AND CONCLUSIONS

Interpreting krill distribution from net-based data

Certain net sampling methods may lead to underestimates of krill density by orders of magnitude due to a serious degree of escapement (Watkins et al. 2000). The extreme view is that data from net tows simply cannot be trusted for a picture of krill distribution (see Everson 2000). Here we showed that, if we standardise to a single method (an 8 m² mouth area net fished from 0 to 200 m at night), KRILLBASE provides a valid map of the relative distribution of krill.

We used this database to estimate total krill biomass values of between 117 and 379 Mt, based on unstandardised and standardised data, respectively (A. Atkinson et al. unpubl. data). These are high values that lie within the 60 to 500 Mt range of recent estimates from acoustic data composites (Nicol et al. 2000a, Siegel 2005). This surprising level of agreement between nets and acoustics is also shown for the CCAMLR 2000 Synoptic Survey. The latest acoustic estimate for this area is 37 Mt (Demer et al. 2007), similar to the RMT 8-based value of 18.7 g wet mass m⁻² or 38.6 Mt (Siegel et al. 2004).

Of course, a circumstantial agreement between 2 methods is no guarantee that they are correct, and the suspicion is that both are underestimating biomass. However, gross (by an order of magnitude) underestimation is implausible. If this was the case, total krill biomass would average several billion tonnes, which is unsupported by primary production (Voronina 1984,

1998, Tseitlin 1989, Priddle et al. 1998). To sum up, we have combated a variable degree of underestimation of krill density within KRILLBASE by standardising to a single, relatively efficient method. Energy flow considerations suggest that the residual under-estimation cannot be too serious, and this is reassurance that our maps capture real trends in krill distribution.

Facets to the success of *Euphausia superba*

Clearly, a variety of factors involving the complete seasonal life cycle must be involved in the success of krill (Spiridonov 1996). Nevertheless, our focus on summer postlarvae sheds light on one part of the life cycle involving high energy fluxes. That postlarvae are mainly oceanic, that 'source regions' at the Antarctic Peninsula do not have the highest densities, and that krill can grow without blooms are surprising assessments, but they can be rationalised in our habitat-based approach.

The unusual asymmetrical distribution of krill reflects their concentration in specific regions that enhance their growth. This finding is non-trivial, as they could theoretically circumnavigate Antarctica if carried passively (Hofman & Murphy 2004), spreading them across HNLC as well as productive sectors (Fig. 19). While their concentration in habitats of enhanced growth boosts total production, the mainly oceanic distribution would reduce mortality loss. How this remarkable distribution is achieved appears to be a blend of top-down, bottom-up, migration and advection controls. Krill have meshed their life cycle intricately with the Southern Ocean circulation, and now we need to learn exactly how this is achieved (Hofmann & Murphy 2004, Murphy et al. 2007).

Krill are often described as a species of extremes, for instance in their size, biomass, lifespan, school size, food requirements or predation loss. While this is true for some of these traits, our analysis suggests that they are not simply a 'boom or bust' species with high food requirements and high mortality. On the contrary, the main habitat of krill is in lower-risk environments with moderate food levels. By analogy with investment, their high production (i.e. 'overall profit') is based on a high biomass (high 'capital') because most of their population inhabit low-risk oceanic areas with little erosion of this capital. They are also rare in the unprofitable HNLC belts or the physiologically costly zone north of the APF. Nevertheless, their large distributional range spans a wide spectrum of risk and reward, thus spreading risk. This presents a more subtle picture than one simply of 'risky stocks' with high gains and high potential losses.

Implications of climate change

While krill are successful at present, the fact that they are stenothermal and have a life cycle keyed to sea ice makes them potentially sensitive to climatic change. At the Antarctic Peninsula, for example, recent rapid loss of sea ice and a warming ocean coincided with a decline in krill (Loeb et al. 1997, Atkinson et al. 2004). However, such studies provide only a limited capacity to predict the future—we also need to examine the mechanisms for the present day success of krill, and to relate these to longer-term environmental changes.

Krill have survived for millennia in much warmer and colder conditions than today (Spiridonov 1996, Jarman et al. 2000). The great temperature oscillations over the last 20 millennia produced a periodic shrinkage and expansion of suitable krill habitat (Spiridonov 1996). In cold eras, when ice closed off Antarctica's shelves, the only shallow water would have been near just a few isolated islands—very different to today. In contrast, the basic ACC circulation is bathymetrically constrained (Orsi et al. 1995) and appears to have persisted.

In such a changeable climate, adapting to flows linking specific shelves is too narrow a repertoire for a successful circumpolar euphausiid. More logical is a life cycle keyed to the wider ACC circulation (Spiridonov 1996), with deep sinking eggs (Marr 1962, Quetin & Ross 1984, Hofmann & Hüsrevoğlu 2003), mainly oceanic larvae (Marr 1962, Brinton 1985, Hosie 1991) and mainly oceanic summer postlarvae, able to grow in moderate food concentrations. This may provide some of the context for the present-day oceanic distribution of krill. Their flexibility, for example in feeding, overwintering and use of sea ice, is often stated as another key to their success (see Quetin et al. 1994). To predict how resilient their populations are to rapid, regional climate change, we now need to progress towards learning some of the mechanisms involved.

Perspectives

This millennium has seen a renaissance in krill biology, with rejuvenated interest for example in larvae (e.g. Meyer et al. 2003, Pakhomov et al. 2004), growth (Ross et al. 2000, Atkinson et al. 2006, Kawaguchi et al. 2006) and overwintering strategies (Daly 2004, Ashjian et al. 2008, Lawson et al. 2008). Likewise, our analysis follows several recent studies of large-scale distribution (e.g. Siegel 2005, Thorpe et al. 2007), all of which raise questions over the degree of connection between krill stocks, the role of migration and advection or, more broadly: how krill are maintained within a suit-

able habitat. These all converge on a central issue: the trajectories of individual krill over periods of >1 wk.

Tackling this issue of 'krill flux' requires a diversity of approaches (Nicol 2003, Hofmann & Murphy 2004, Murphy et al. 2007). Genetic analyses are being refined (Zane et al. 1998), but even if no genetic isolation of 'stocks' is found, the connection between subpopulations is still germane to fisheries management (Constable et al. 2000, Nicol 2003). Length-frequency distributions can act as population tracers (Watkins et al. 1999), and fishery data can provide time series (Kawaguchi & Nicol 2007). The contrasting onshelf-offshelf distributions of krill between the Antarctic Peninsula, Atlantic and Indian sectors are tantalising in this respect—are they separate stocks that evolved with different solutions to their environment, and how else do they differ?

These issues must be resolved before we can model a realistic circumpolar distribution of krill. Such models, in turn, are a precursor to further models that embed the whole life cycle of krill in oceanic circulation patterns, similar to that for *Calanus finmarchicus* in the north Atlantic (Spiers et al. 2006). While the development of such a model can realistically be expected within the next decade, observational data will always be a key element in validation. KRILLBASE has shown the value of multinational collaboration to pool datasets, but this sort of approach needs to be expanded to validate whole life cycle models.

A further benefit of such data composites is that they tell us where to sample in future. For example, the sector between 20° W and 50° E has been neglected, despite containing a large part of the krill stock and representing a potential connection between the 2 postulated subpopulations. New programmes, for example during the International Polar Year, are sampling some of these areas. This is indeed an exciting time in krill biology.

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