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Report

Adult Antarctic Krill Feeding at Abyssal Depths

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Summary

Antarctic krill (*Euphausia superba*) is a large euphausiid, widely distributed within the Southern Ocean [1], and a key species in the Antarctic food web [2]. The *Discovery* Investigations in the early 20th century, coupled with subsequent work with both nets and echosounders, indicated that the bulk of the population of postlarval krill is typically confined to the top 150 m of the water column [1, 3, 4]. Here, we report for the first time the existence of significant numbers of Antarctic krill feeding actively at abyssal depths in the Southern Ocean. Biological observations from the deep-water remotely operated vehicle *Isis* in the austral summer of 2006/07 have revealed the presence of adult krill (*Euphausia superba* Dana), including gravid females, at unprecedented depths in Marguerite Bay, western Antarctic Peninsula. Adult krill were found close to the seabed at all depths but were absent from fjords close inshore. At all locations where krill were detected they were seen to be actively feeding, and at many locations there were exuviae (cast molts). These observations revise significantly our understanding of the depth distribution and ecology of Antarctic krill, a central organism in the Southern Ocean ecosystem.

Results and Discussion

We used the inaugural science dives of the deep-water remotely operated vehicle (RoV) *Isis* to obtain imagery from the seabed of Marguerite Bay, western Antarctic Peninsula, from depths of 200 m on the continental shelf to 3500 m on the abyssal plain (Figure 1). Temperature traces obtained from an expendable bathythermograph deployment taken close to the location for *Isis* dive 7 on January 26, 2007, revealed a warm surface layer and a slightly deeper thin layer of markedly colder water, below which were warmer waters all the way to the bottom (Figure 2). This water column structure was found across the Marguerite Bay shelf and is typical of the area in that the warmer waters of the Upper Circumpolar Deep Water extend to the seabed but are capped by a combination of colder remnant Winter Water and the seasonally varying surface waters [5].

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Fresh phytodetritus was observed on all dives, with the exception of those close inshore (see the Supplemental Data available online). In many areas, there were signs of active reworking of sediments by infauna and surface macrofauna, presumably in response to the recent arrival of phytodetritus at the seabed. The seasonal cycle of primary production in the surface waters of Marguerite Bay has been described from weekly observations taken in Ryder Bay since January 1997 [6]. The annual cycle shows the typical high-latitude pattern of a well-defined summer phytoplankton bloom combined with a long winter period of very low chlorophyll levels (Figure 3). The bloom typically reaches peak values in December and January, with the suggestion of a secondary late summer bloom in March. The bloom is shallow, with peak chlorophyll *a* levels above 20 m, though the bloom does extend to approximately 60 m. This averaged picture exhibits a relatively simple structure that masks considerable interannual variability in the timing, intensity, and depth of the bloom; the 2006/07 season was, however, fairly typical and is well described by the long-term climatology shown in Figure 3. Phytodetrital flux is not measured routinely in Marguerite Bay, but the timing of the main period of phytodetrital sedimentation established for the WAP continental shelf for the period 1993 to 2005 shows a sharp annual pattern, with flux lasting 50–100 days and a peak typically in January [7], though, as with the timing of the bloom, there is significant interannual variability [8]. A single nearshore sediment trap recovered from Ryder Bay, northern Marguerite Bay, in December 2006, just weeks before the start of the RoV work, was full of phytodritus. We are therefore confident that our RoV observations were made at a time immediately following the main pulse of phytodetrital flux to the seabed for 2006/07 austral summer season.

Details of the RoV dives with biological observations are given in Table 1. With the exception of the nearshore fjord areas (dives 12 and 15), where the water column was exceptionally cloudy with glacial debris and no krill were observed, there was a loose correlation between the amount of phytodetritus on the seabed and the abundance of krill observed there. Adult Antarctic krill can be recognized easily from their size, and gravid females can be distinguished by the markedly swollen thorax (Figure 4A) and the red thelycum. They could be distinguished from the large deep-water mysid *Antarctomysis maxima* by their different shape, swimming activity, and posture in the water column. The Antarctic krill observed at the seabed from *Isis* were of adult size, and many were obviously gravid (Figure 4B). On one dive, an adult Antarctic krill was caught in the camera mounting of *Isis*, and although this was most likely trapped at depth (which is where the cameras and manipulators were used and sometimes trapped fish), it is also possible that this individual was caught in the surface waters.

A glacial gully in the midshelf region at 550 m contained relatively little phytodetritus, and only small numbers of krill were observed, though some were gravid females (dive 10). At 850 m, around a well-marked drumlin (a glacially formed ridge), we encountered extensive phytodetritus and large numbers of krill (dive 2). At the bottom of the continental slope (2100 m), there were large amounts of phytodetritus and

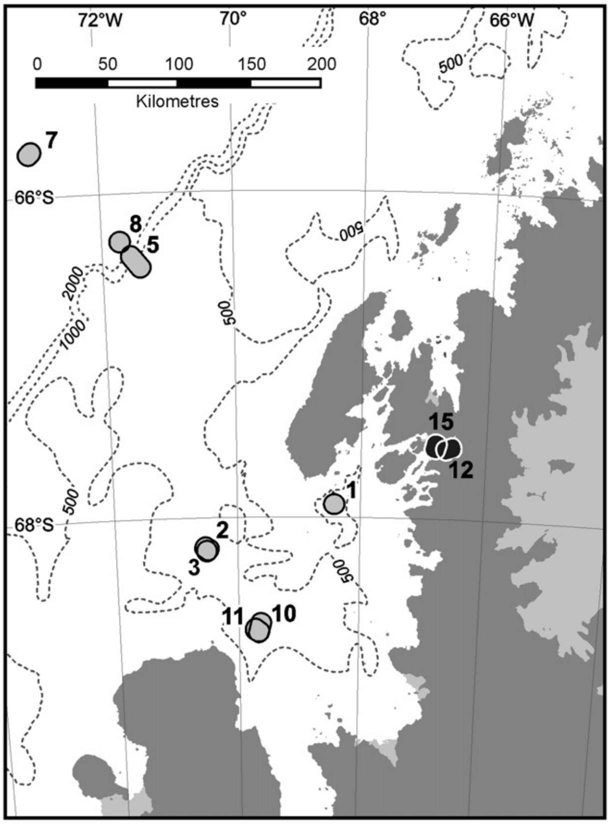

Figure 1. Map of Marguerite Bay Showing the Biological Transects Undertaken by *Isis*

The numbers refer to individual dives, distinguishing dives where krill were found (gray symbols) from those where they were not (black symbols). Isobaths indicate cross-shelf glacially carved canyons (500 m), the edge of the continental shelf (1000 m), and the bottom of the slope (2000 m). Note that dives where no biological data were collected are not shown; details of dives with biological data are given in Table 1.

abundant krill. Many of these krill were mature females, and there were also large numbers of exuviae (cast exoskeletons) in the water column. On the continental slope at 1350–1200 m, phytodetritus was less in evidence and there were only small numbers of krill. At the shelf break (around 900 m at this location), there was again dense phytodetritus and some krill (all observations from dive 5).

The most surprising observations came from the deep water of the abyssal plain (dives 7 and 8). At the very foot of the continental slope (3000 m), we encountered abundant phytodetritus on smooth mud and abundant krill. Again, many were gravid females (Figure 4B), and there were many exuviae in the water column. At 3500 m, phytodetritus was notably less abundant, but some krill were still encountered.

At all sites where krill were encountered, they were moving rapidly and feeding, and some gravid females were observed. We frequently observed a characteristic behavior whereby the krill would nosedive into the sediment and then rise up and feed actively on the resuspended sediment. Typically, the krill would dive head first from a height of less than 1 m above the seabed and at a fairly steep angle of 30°–50°. This would raise a small volume of sediment into the water column, and the krill would then swim rapidly upward and filter the resuspended material with characteristic movements of its feeding basket. It would seem that these individuals were resuspending

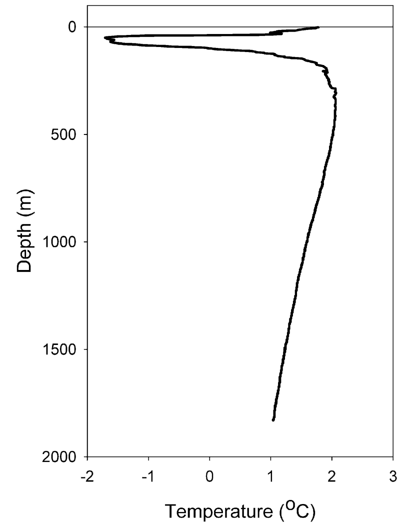

Figure 2. XBT Trace Showing the Thermal Structure of the Water Column throughout Marguerite Bay

Note the warm Upper Circumpolar Deep Water (>1°C) extending to the seabed, capped by the cold remnant Winter Water, above which is the seasonally warmed Antarctic Surface Water.

sediment in order to extract phytodetritus or other food material. Similar behavior was noted in krill feeding at approximately 200 m depth over soft sediments in northern Marguerite Bay (A.C., unpublished data, Julian Gutt, personal communication [joint UK-German work from cruise JR17 in December 2000]).

The traditional techniques for estimating krill abundance, echosounders and nets, really sample only the top 250 m of water, leaving open the questions of how many krill are found below these depths, especially if they are dispersed rather than in swarms. Previous work in Marguerite Bay, particularly that associated with the Southern Ocean Global Ocean Ecosystemas Dynamics (GLOBEC) program [9], has established that this is an important area for Antarctic krill. Although the bulk of the population appears to be found in the surface waters, in early winter a significant fraction descends to deeper water (150–450 m). It is not possible to estimate the population of Antarctic krill close to the seabed from our observations, partly because the lights of *Isis* might have

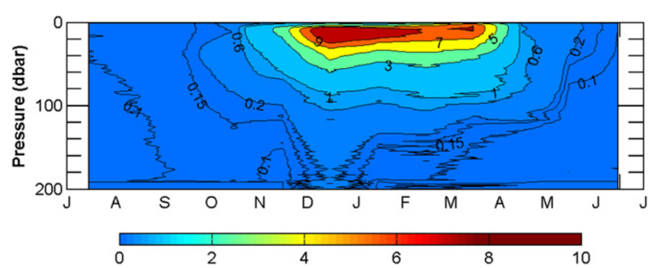

Figure 3. The Seasonal Cycle of Chlorophyll in Marguerite Bay

Mean progression of the phytoplankton bloom in surface waters, 1997 to 2006, calibrated with extracted chlorophyll. Contours are scaled for the emphasis of detail at low chlorophyll levels; peak concentrations typically exceed 20 mg m^{-3}. Note that data are plotted from midwinter (July) to midwinter (June) so that the austral summer season lies in the center of the plot, and the indication of vertical flux shown by the deepening of the concentration contours from late November to late January. Reproduced with permission from [6].

Table 1. Details of *Isis* Dives from which Biological Observations Were Made

Dive	Date	Lat (S)	Long (W)	Depth (m)	Duration (hr)	Phytodetritus	Krill
2	Jan 21	68.18	70.52	800–850	20.2	High	Moderate
5	Jan 24	66.39	71.55	800–2100	21.3	Moderate or High	Low or Moderate
7	Jan 26	65.73	72.99	3500	9.0	Low	Low
8	Jan 27	66.30	71.71	3000	8.6	Moderate	High
10	Jan 29	66.65	69.62	550	20.7	Moderate	Low
12	Feb 2	67.58	66.66	240	6.9	High	None
15	Feb 3	67.57	66.81	20–600	8.4	High	None

The date (2007) and latitude and longitude (decimal degrees) are for the start of the dive; duration (hr) is time on the bottom. Note that no biological imagery was taken from dives 1 (RoV trial), 3, 6 (collections only), 4, 9, 11, 13, 16 (geological dives for swath bathymetry), or 14 (technical failure). The classification scheme used for phytodetritus and krill is described in the Experimental Procedures; where concentrations of phytodetritus or krill varied along the transect, the range of values is indicated.

concentrated local krill, although there was no overt indication that the krill were attracted strongly. The number of individuals was, however, often large, and in places there were substantial numbers of exuviae. Krill molt regularly in summer, with the frequency dependent on size and state of reproductive maturity [10]. In particular, adult female krill molt immediately after spawning [11]. Krill larvae have been found in the upper waters of the Marguerite Bay area [12], suggesting active reproduction in the area, and it is thus possible that these exuviae represent postspawning molts. Female krill, however, are believed to spawn in surface waters, because the released eggs require descent below the surface mixed layer into deeper waters where the warmer water allows more rapid development, and the newly hatched larvae then undergo a developmental ascent [13]. It would therefore seem more likely that the concentrations of exuviae found close to the seabed at several locations represent the accumulation of cast exoskeletons from molting activity higher in the water column.

Because the RoV descended to depth fairly rapidly, often without lights, and no formal biological watch was undertaken during ascent or descent, it is not possible for us to estimate the extent to which either adult krill or their exuviae were present in the bulk of the water column below the mixed layer. Our observations do establish, however, that significant numbers of krill can be found at the seabed in Marguerite Bay, both on the continental shelf and the abyssal plain. These include reproductively active krill, which current knowledge suggest would need to return to surface waters to spawn. We therefore suggest (but clearly cannot demonstrate) that at least some adult krill are descending to great depths and that they feed actively at these depths. It is possible that some krill follow sedimenting phytoplankton to the seabed, either by active swimming or passive sinking. Returning to the surface obviously requires active migration, but krill are strong swimmers and ascent from 3000 m at 20 cm s^{-1} would only take approximately 4 hr. Previous work has established that some physiological activities in krill are very sensitive to temperature, particularly at subzero temperatures [10]. Adult krill are, however, clearly physiologically capable of migrating through the cold remnant Winter Water that lies below the mixed layer and above the uniformly warm water that characterizes the deeper shelf, slope, and abyssal plain of Marguerite Bay. The presence of Upper Circumpolar Deep Water on the western Antarctic continental shelf [5, 6] means that the thermal environment of the Marguerite Bay shelf is, however, distinctly warmer than that of the Weddell and Ross Sea embayments (where Bottom Water typically keeps seabed temperatures below zero).

Our work has thus revealed two striking and previously quite unknown aspects of its biology, namely the enormous depths to which krill will descend and the significant numbers of mature females observed there. Previous RoV work in Antarctica [14] demonstrated significant numbers of Antarctic krill in January at approximately 450 m on the continental shelf of the eastern Weddell Sea. The observations we report here are the first demonstration that adult krill will descend to the seabed

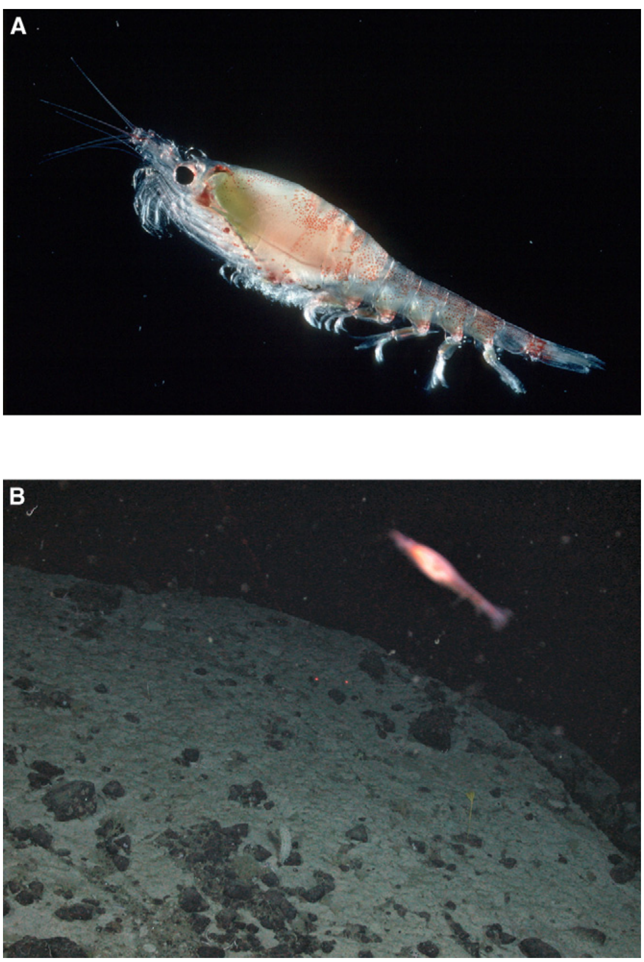

Figure 4. Antarctic Krill, *Euphausia superba*

(A) Gravid female *Euphausia superba* showing the markedly swollen thorax caused by the maturing ovary (image copyright British Antarctic Survey).
(B) Image taken from *Isis* at 3000 m (dive 8), showing adult Antarctic krill just above the seabed (image copyright Paul Tyler, National Oceanography Centre, Southampton).

on the continental slope or abyssal plain. A single RoV cruise has thus changed significantly our understanding of a key organism of the Southern Ocean, indicating also that there is still an important role for exploration in our attempts to understand our world.

Experimental Procedures

The United Kingdom deep-water RoV *Isis* was deployed from the research ship RRS *James Clark Ross* in Marguerite Bay, western Antarctic Peninsula, in January and February 2007. RoV transects were designed to cover major geomorphological structures on the continental shelf (level shelf and glacial canyons), the continental slope (glacial gullies), and the abyssal plain (sediment fans). Biological imagery was taken from the RoV flown at approximately 0.6 m above the seabed with a Pegasus video camera. In addition still images (3.5 megapixel) were taken of the seabed and specific organisms. The observations reported in this paper were noted in the biological log recorded at the time by watch-keeping biologists.

Krill could be recognized easily in video imagery from their large size and swimming behavior, together with the red thelycum and markedly swollen thorax in gravid females. In many areas, we also encountered the large mysid *Antarctomysis maxima*, but this species was easily distinguished by its very different shape, its quite different swimming behavior, and its very characteristic posture in the water column. Phytodetritus level was scored in real time from the video imagery as follows: high (large amounts of fresh-looking green phytodetritus, with coverage greater than 50% of the sediment surface and frequently extensive signs of active reworking by infauna or surface megafauna), moderate (approximately 20% to 50% coverage), or low (0% to 20% coverage). Krill abundance was scored in real time as high (thousands of individuals), moderate (hundreds of individuals), or low (tens of individuals).

Supplemental Data

Two figures are available at http://www.current-biology.com/cgi/content/full/18/4/282/DC1/.

Acknowledgments

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References

1. Marr, J.W.S. (1962). The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Reports *32*, 33–464.
2. Murphy, E.J., Morris, D.J., Watkins, J.L., and Priddle, J.H. (1988). Scales of interaction between Antarctic krill and the environment. In Antarctic Ocean and Resources Variability, D. Sahrhage, ed. (Berlin: Springer-Verlag), pp. 120–130.
3. Godlewska, G. (2005). Vertical migrations of Antarctic krill (*Euphausia superba* Dana). Pol. Arch. Hydrobiol. *43*, 9–63.
4. Siegel, V. (2005). Distribution and population dynamics of *Euphausia superba*: Summary of recent findings. Polar Biol. *29*, 1–22.
5. Meredith, M.P., Renfrew, I.A., Clarke, A., King, J.C., and Brandon, M.A. (2004). Impact of the 1997/98 ENSO on upper ocean characteristics in Marguerite Bay, western Antarctic Peninsula. J. Geophys. Res. *109*, C09013.
6. Clarke, A., Meredith, M.P., Wallace, M.I., Brandon, M.A., and Thomas, D.N. (2008). Seasonal and interannual variability in temperature, chlorophyll and macronutrients in Ryder Bay, northern Marguerite Bay, Antarctica. Deep Sea Res. (*Part II*), in press.
7. Ducklow, H.W., Fraser, W., Karl, D.M., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M., and Daniels, R.M. (2006). Water column processes in the west Antarctic Peninsula and the Ross Sea: Interannual variations and foodweb structure. Deep Sea Res. *53* (*Part II*), 834–852.
8. Smith, C.R., Mincks, S., and DeMaster, D.J. (2006). A synthesis of bentho-pelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change. Deep Sea Res. *53* (*Part II*), 875–891.
9. Lawson, G.L., Wiebe, P.H., Ashjian, C.J., Gallager, S.M., Davis, C.S., and Warren, J.D. (1994). Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. Deep Sea Res. *51* (*Part II*), 2041–2071.
10. Quetin, L.B., Ross, R.M., and Clarke, A. (1994). Krill energetics: Seasonal and environmental aspects of the physiology of Antarctic krill, *Euphausia superba*. In Southern Ocean Ecology: the BIOMASS Perspective, S.Z. El-Sayed, ed. (Cambridge: Cambridge University Press), pp. 165–184.
11. Cuzin-Roudy, J. (2000). Seasonal reproduction, multiple spawning, and fecundity in northern krill, *Meganyctiphanes norvegica*, and Antarctic krill, *Euphausia superba*. Canadian Journal of Fisheries and Aquatic Sciences *57*, 6–15.
12. Pakhomov, E.A., Atkinson, A., Meyer, B., Oettl, B., and Bathmann, U. (2004). Daily rations and growth of larval krill *Euphausia superba* in the Eastern Bellingshausen Sea during austral summer. Deep Sea Res. *51*, 2185–2198.
13. Ross, R.M., and Quetin, L. (2000). Reproduction in Euphausiacea. In Krill: Biology, Ecology and Fisheries, I. Everson, ed. (Oxford: Blackwell Science), pp. 150–181.
14. Gutt, J., and Siegel, V. (1994). Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctic). Deep Sea Res. *41*(*Part I*), 169–178.