Antarctic Ecosystem: Are Deep Krill Ecological Outliers or Portents of a Paradigm Shift?

Serendipitous observations of Antarctic krill feeding at abyssal depths may revolutionise our view of the ecology of this supposed surface-dwelling animal that is key to the function of the Southern Ocean ecosystem.

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In his poem 'Thirteen Ways of Looking at a Blackbird' [1] Wallace Stevens' description of a *Turdus* in a snowy autumn landscape alludes to the Cubist practice of observing subjects simultaneously from numerous viewpoints to present a novel perspective. There is little direct interaction between Cubism and biology, but when biologists look at systems in new ways, or with new techniques, we often discover something new, and data from multiple perspectives can reveal a view to which conventional observations have been blind. Observations from a remotely operated vehicle (ROV) of apparently healthy Antarctic krill, an animal thought to live its adult life in the near-surface zone, in the abyssal depths of the Southern Ocean [2] provide a vivid illustration of this. These observations may require us to reappraise fundamentally our notion of the biology of this key Southern Ocean species, and affirm that there are still discoveries to be made by basic exploratory research.

Antarctic krill (*Euphausia superba*) play a central role in the Southern Ocean ecosystem. These diminutive crustaceans, which reach a maximum length of about 6 cm and wet mass of about 2 g, consume phytoplankton at the base of the food chain and, so doing, make the carbon that phytoplankton have fixed available to the suite of higher predators, including whales, penguins and fish, that feed upon krill [3]. Without krill, many of Antarctica's iconic megafauna would be absent. Adult krill have been considered traditionally as occupants of the upper ocean [4,5]. They feed at the near-surface, where photosynthesis occurs, and migrate to depths of not much more than 250 m by day to darker waters that provide some refuge from predators that hunt by sight. Krill mate and spawn in this epipelagic zone. Although fertilized krill eggs may sink to more than 1000 m [6], adults have not previously been thought to descend to the depths from which some larvae emerge during their ontogenetic ascent. Surveys of krill distribution for fishery- and ecosystem-management purposes have been conducted on this premise [7] and estimates of circumpolar krill biomass — some in excess of 500 million tonnes, more than the global human biomass — have been calculated on the presumption of a near-surface distribution [8]. The observations by Clark and Tyler [2] of mature krill feeding at depths as great as 3500 m may necessitate a rethink of this and many other aspects of the biology and ecology of krill. In fact, if these point observations turn out to be representative of a wider geographic or temporal phenomenon, they may trigger a paradigm shift for our understanding of the function of the entire Southern Ocean ecosystem.

Stevens [1] observed his blackbird among 'twenty snowy mountains'. Clark and Tyler [2] discovered krill in the abyssal waters that are fringed by the snowy mountains of Adelaide and Alexander Islands to the west of the Antarctic Peninsula. Their unexpected observations were made off Marguerite Bay during surveys in the austral summer of 2006/07 with the ROV *Isis* (Figure 1). The biologists were piggybacking on a cruise run primarily to look at deep sea geological processes, and were hoping to use video footage of the seabed taken by the ROV to study large benthic invertebrates such as sea cucumbers and sponges. Krill were unexpected in this abyssal environment: the phytoplankton and smaller zooplankton that are the mainstays of krill diet are concentrated in the photic zone near the sea surface several thousand meters above. In the short-lived Antarctic spring and summer krill must eat large quantities of food if they are to reproduce successfully. The pronounced seasonal nature of this high-latitude location is characterised by a sharp pulse of primary production as phytoplankton proliferate in the nutrient-rich surface waters that become illuminated and warmed following the passing of the long polar night and the melting of the sea ice. Grazers such as krill tune their lifecycles to capitalize on this brief period of feast and, whilst the summer months are favourable for ship-based deep sea research, conventional oceanographic wisdom has it that grazers should be near surface at this time.

The rate of phytoplankton production during spring and summer blooms can, however, sometimes be so great that it exceeds the rate of consumption by grazers in the shallows of the watercolumn. Observations elsewhere in the global ocean have shown that heavy falls of 'marine snow' — dead and decaying plankton remains sinking from the surface — coincident with the surface phytoplankton bloom provide an important pulse of food to the otherwise impoverished deep sea environment [9]. The 'snow' particles can accumulate to depths of several mm on the seabed before biodegrading. Clark and Tyler [2] observed krill nose-diving into the seabed in a behaviour that resuspended particulate matter, which the krill then ate. The authors suggest

Figure 1. The *Isis* ROV being deployed from RRS *James Clark Ross* (photograph by Julian Dowdeswell).

that the krill they observed may have migrated to the deep sea to exploit this accumulated phytodetritus resource, but lack the time series of observations necessary to test this hypothesis. In fact their paper is as stimulating for the questions it tacitly poses as for the truly fascinating observations it reports. The observed krill might well have migrated recently from the surface: krill complete their twice-daily vertical migrations of about 250 m in less than 2 hours around dawn and dusk and, at that rate, could achieve a 3500 m descent in about a day. Krill could have swum downwards, feeding on the falling 'snow' on the way [10], and might remain near the seabed feeding on the accumulated drifts before returning to the surface once the table has emptied.

There have been reports of size segregation of krill off the western Antarctic Peninsula [11], with larger animals being more abundant off shore in summertime. Perhaps some component of the adult population migrates routinely down the shelf slope — Clark and Tyler [2] observed krill at all sampled depths between 550 m to 3500 m — and eventually returns directly to the surface from the abyss such that the post-bloom surface distribution [11] is a consequence of a deep sea foraging migration. This raises the possibility of a previously unrecognised carbon transport pathway mediated by krill. Daily krill migrations may play an important role in transport of surface-fixed carbon to the ocean interior [12]. If it turns out that krill feed routinely on phytodetritus in the deep sea and then return to the surface, the carbon they re-import to the surface could diminish the extent to which carbon is naturally sequestered to the deep sea by the 'biological pump'. It has been suggested that physical processes have now rendered the Southern Ocean less of a carbon sink than it has been historically [13]: the potential deep sea foraging behaviour of krill could have additional consequences for the global carbon cycle and hence for the climate.

An alternative interpretation of the observations of krill in deep water [2], however, is that these animals are members of a distinct and hitherto unrecognised permanent deep sea population that live out their life in the deep sea. Given what we believe about the dependence of krill on sea ice for reproduction [14] this seems unlikely, but then again it seemed unlikely 18 months ago that krill would be found feeding at 3500 m. The only previously published report of krill at the seabed in deep water [15], observed by an ROV at c. 400 m in the Weddell Sea, was made in summer. The lack of observations of krill in deep water in winter so far may simply be a function of zero sampling effort in winter. Year-round sampling in the upper water column has revealed previously unknown patterns of variation in krill abundance [16], and deep sea biology has benefited from data gathered remotely by long-term instrument deployments [17]. The Global Ocean Observing System (www.ioc-goos.org) strives to collect data from ocean environments at time and space scales not practicable using standard ship-borne sampling, and the deep waters off Marguerite Bay are just one of many global ocean environments worthy of year-round monitoring.

In the shorter term, genetic studies could provide insight to the degree of exchange of animals between putative surface and deep populations, and an additional challenge for future ROV deployments there would be to collect large numbers of samples as well as images. A deep sea population of krill decoupled reproductively from sea ice could be more resilient to the environmental change manifesting to the west of the Antarctic Peninsula than surface cousins, since deep sea temperatures are more stable than surface temperatures. Krill in deep water may literally and metaphorically be out of hot water but, at this stage, this remains little more than speculation.

Yet another alternative explanation for the deep-water krill [2] is that they are unhealthy individuals that have experienced difficulty in maintaining depth by swimming and have sunk out from the surface. Net caught krill can appear to be swimming actively in the bottom of buckets after removal from the net, but sometimes lack the ability to swim up into the water column, perhaps due to injuries sustained during capture. Clarke and Tyler [2] noted cast-off exoskeletons at the seabed that are indicative of moulting. Crustaceans moult to grow and animals that are growing are generally healthy. However, intriguingly, for krill, there are reports of stressed or starved individuals moulting to attain a smaller size with subsequently reduced metabolic demands [18]: moulting might be an act of desperation for an animal struggling out of its depth or, as Clarke and Tyler [2] suggest, the moults might simply have accumulated at the seabed following cast-off from healthy animals near the surface.

Whilst our knowledge of temporal variation in abundance of krill in the deep sea is effectively nil, our knowledge of spatial extent is not much greater. There have been concerted efforts to map the distribution of krill abundance throughout various sectors of the Southern Ocean [7] but, frustratingly, the ROV observations [2,15] have been off the grids of these large scale surveys (Figure 2), and no contemporaneous water column data are available. Thus, we do not know how seabed concentrations of krill are related, if at all, to distributions in the near surface. Clarke and Tyler [2] were unable to estimate abundance of krill on the seabed because their data, collected with surveys of immobile or slowly moving megabenthos in mind, are not amenable to quantitative appraisals of krill. We remain largely ignorant of the biomass of krill in the deep sea. All that we can say is that the locations sampled so far by ROVs are not considered centres of pelagic krill concentration (Figure 2), raising the possibility that elsewhere deep sea abundances might be higher.

Given that krill play such a central role in the Southern Ocean ecosystem, efforts to determine circumpolar abundance in the deep sea as well as in the open ocean and under sea ice should perhaps be encouraged. Observations by SCUBA divers and shallow-water ROVs first revealed the importance to krill of feeding under ice, and subsequent observations by an Autonomous Underwater Vehicle (a free-running vehicle not constrained by an umbilical) have revealed something of the extent to which krill are distributed under ice [19]. The ROV *Isis* is a powerful research tool with full-ocean-depth capabilities, and has provided another leap forward in knowledge of krill: widespread use of this and the arsenal of sampling devices available to the modern-day marine scientist will likely reveal additional fascinating insights to the private lives of krill and other ocean inhabitants.

The 2007 fieldwork by Clark and Tyler [2] was part of the inaugural science deployment of the *Isis* ROV. Their startling and unexpected observations make it clear that there is still a need for

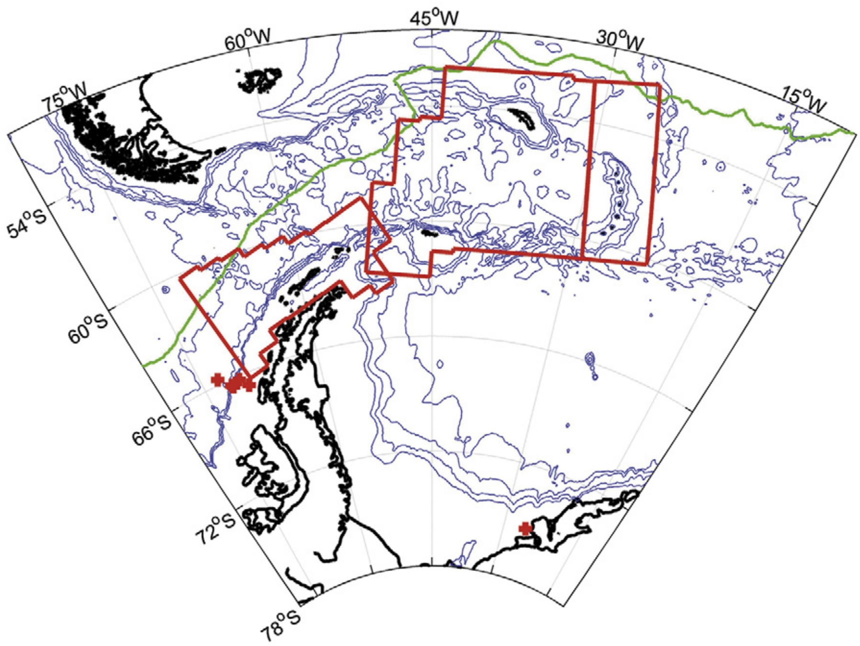

Figure 2. How much krill is out there?

Deep water seabed observations of krill (red crosses) are at locations off the grid of the most extensive recent water column survey (bounded by red polygons). That survey [7] was designed to cover the regions where fisheries and historic scientific sampling have suggested the bulk of krill biomass is distributed. Depth contours in 1000 m increments to 4000 m are shown in blue, and the mean position of the Polar Front, which demarks the northern extent of krill distribution, is shown in green.

the type of basic exploration of the planet's inner space that remote and autonomous technologies excel at [2,19]. It can, however, be difficult to persuade funders to support basic exploratory research because, in the absence of knowledge, it is difficult to erect the kinds of credible null hypotheses that grant review panels are often directed to favour, and 'fishing expeditions' with no defined endpoint can loose out in the competition for finances. The *Isis* ROV was delivered in 2003 and the joke for too long was that *Isis* was Irretrievably Stuck In Southampton (the city on the south coast of the UK where the National Oceanography Centre is located). Whilst Cubists can create in the studio, students of the deep sea must embark to their natural laboratory, and the difficulties in getting *Isis* to sea were for several years a source of major frustration. Fortunately the research community is learning to frame its proposals in terms that make them competitive and this, together with the attention to *Isis* that has been drawn by the influential House of Commons Science and Technology Committee [20], will hopefully ensure that the vehicle can be exploited increasingly in the coming years. As Apsley Cherry-Garrard and companions learnt during their 'Worst Journey in the World' to gather penguin eggs in the winter of 1911, the quest for knowledge in far-flung locations can be fraught with risk. In the grand scheme of things, however, 21st century deep ocean exploration is likely to deliver far greater reward than the financial 'risk' it presents. Hopefully in the coming years biologists will match Cubists in their ability to portray their subjects from multiple spatial and temporal perspectives, and progress towards the holistic view required for fuller understanding of ecosystem function.

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DOI: 10.1016/j.cub.2008.01.022