Krill, Currents, and Sea Ice: *Euphausia superba* and Its Changing Environment

STEPHEN NICOL

Investigations of Antarctic krill (Euphausia superba) *over the last 40 years have examined almost every aspect of the biology of these ecologically important animals. Various elements of krill biology have been brought together to provide concepts of how this species interacts with its environment, but there have been few recent attempts to generate a generalized conceptual model of its life history. In this article I present such a model, based on previous descriptions, observations, and recent data from the scientific literature. This model takes into account a range of findings on krill biology and on the relationships between Antarctic krill and its biotic and abiotic environment. Krill life history is thus viewed as an evolved product of interactions between the species and its environment. The model places particular emphasis on the different forces that act on the larval and adult stages, and on the interaction between krill behavior, systems of ocean currents, and sea ice.*

Keywords: Antarctic krill, Southern Ocean, sea ice, currents

Antarctic krill (*Euphausia superba;* **figure 1) is one** of the best-studied species of pelagic animal, yet there are still considerable uncertainties about key elements of its biology and of the forces that determine its distribution and abundance (Nicol 2003). Early accounts of the life history of krill provided a large amount of detail on its distribution and basic biology, based largely on the results of collections made with plankton nets, and many of the accepted concepts of krill ecology stem from these studies (Marr 1962, Mackintosh 1972). More recently, a number of attempts have been made to review information on krill biology (Ikeda 1985, Miller and Hampton 1989, Siegel 2000), and conceptual models have been put forward to account for the observed patterns of distribution and abundance of krill's various life history stages (Siegel 1988, 2000, Smetacek et al. 1990, Daly and Macaulay 1991). Over the last 25 years, a large research effort has been devoted to better understanding the ecology of krill and its distribution, and this has resulted in some changes in perspective. This period has been characterized by concerted activity on two fronts: experimental krill biology (Mangel and Nicol 2000, Kawaguchi and Nicol 2003) and biology relevant to management of the krill fishery (Nicol 2000, Watkins et al. 2004). At the same time, attention has been devoted to understanding the ecology of the Southern Ocean in relation to the prospect of rapid climate change, and this too has featured krill research (Hofmann et al. 2004). Climate change research has also vastly improved scientists' understanding of the physical environment of the Southern Ocean and its links to global processes (Busalacchi 2004). These research efforts have produced a wealth of information on krill distribution, ecology, and biology, which is yet to be synthesized. This article attempts such a synthesis, focusing on recent information that provides a perspective on krill ecology; it builds on the findings of early research and brings in results from a wide range of studies.

Despite findings that krill are active schooling animals (Hamner and Hamner 2000) and evidence suggesting active migrations (Siegel 1988), a predominant view among Southern Ocean ecologists is that krill are planktonic organisms largely at the mercy of their physical environment (Hofmann and Murphy 2004). An alternative perspective, that the distribution and abundance of krill can be explained by the interaction between the animal's evolved life cycle and the physical environment, has not been articulated. This article represents a conceptual model of how krill pursue their lives in their challenging physical environment, and further develops ideas put forward by other authors. It is presented as a generalized case, accepting that there are exceptions and, as in all models, oversimplifications. The purpose of this model is to stimulate discussion and to provide a framework for future research and Southern Ocean ecosystem modeling.

Stephen Nicol (e-mail: steve.nicol@aad.gov.au) is the program leader for Southern Ocean Ecosystems, Australian Antarctic Division, Department of Environment and Heritage, Kingston, Tasmania 7050, Australia. © 2006 American Institute of Biological Sciences.
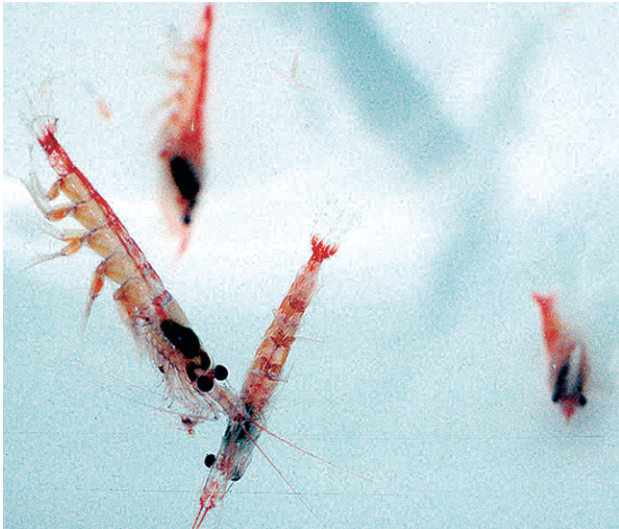
Figure 1. "The 'krill' is a creature of delicate and feathery beauty, reddish brown and glassily transparent. It swims with that curiously intent purposefulness peculiar to shrimps, all its feelers alert for a touch, tremulously sensitive, its protruding black eyes set forward like lamps. It moves forward slowly, deliberately, with its feathery limbs working in rhythm and, at a touch of its feelers, shoots backwards with stupefying rapidity to begin its cautious forward progress once again" (Marr 1962, p. 156, quoting Ommanney 1938).

The historical perspective

The traditional view of krill life history is that they are relatively short-lived, with a life span between 2 and 3 years. They reproduce in their second and third years; eggs are laid in the surface layer, and the embryos sink, then hatch; the developing larvae actively swim upward, reaching the surface in autumn. The larvae develop under the ice during the winter and emerge as juveniles in the spring (Marr 1962). Krill have a circumpolar range, although they have an uneven distribution both latitudinally and meridionally. Generally, all stages of krill are found in higher numbers near the Antarctic or island coasts, and they are also found in greater abundance in certain regions where putative stocks have been described (Mackintosh 1972).

There were some suggestions that krill stocks could be associated with oceanographic features such as the Weddell gyre, and the relationship between the distribution of krill and the area annually covered by sea ice was acknowledged, but the exact role of sea ice in krill life history remained unexplored because of the difficulties of sampling this habitat in winter (Marr 1962, Mackintosh 1972). Adult and larval krill were viewed as being largely at the mercy of the ocean currents, although the ability of krill to form dense and highly localized swarms was noted as something of a paradox. In his monumental monograph on the species, Marr (1962) observed, "Clearly then, by the time it is half grown, if not before, *E.*

superba far from remaining a passive drifter, has on the contrary become a creature of great agility, powers of locomotion, purposeful intent and not a little awareness" (p. 156). How such animals cope with a dynamic, fluid, and periodically ice-covered environment is a critical area for study, but such research is fraught with difficulties (Hamner and Hamner 2000). The ecological role of krill, in the traditional view, was to consume phytoplankton, mainly diatoms, and to serve as the critical food source for fish, squid, and large air-breathing mammals and birds (Miller and Hampton 1989).

Over the last 25 years, a number of findings have improved researchers' knowledge of krill life history, and various events, described in table 1, have altered our perspective on Antarctic krill. These findings include a far better understanding of the distribution patterns of krill on all scales (Everson 2000), of the importance of the link between krill and sea ice, and of the role of sea ice communities in the annual cycle of krill (Smetacek et al. 1990, Daly and Macaulay 1991). Experimental investigations on living krill have also improved scientists' knowledge of the diet, physiology, behavior, and growth rate of krill (Nicol 2003). We now know that krill are long-lived, schooling animals with high energy demands that are met through a varied diet, and with a complicated life cycle that utilizes, in different phases, pelagic, benthic, and sea ice environments. An updated view of krill life history, therefore, has to take into account this wealth of information and present it in a form that is biologically realistic.

Distribution, abundance, and ocean currents

Early accounts of krill distribution and abundance relied on the results of sampling surveys using plankton nets, although such nets were acknowledged early on to be far from ideal for capturing krill (Marr 1962). More recently, echo sounders have been used to determine krill distribution and abundance, which has greatly improved researchers' understanding of detailed patterns of abundance at all scales (Macaulay 2000). Information from scientific nets has also been used to examine questions of long-term change in krill populations (Atkinson et al. 2004) and to provide critical data on krill demographics (Siegel 2000). Krill distribution patterns have been intensively investigated on large scales (100,000 to 1,000,000 square kilometers [km^2]) (Nicol 2000, Watkins et al. 2004), on smaller scales (1000 to 10,000 km^2) (Brierley et al. 2000), and at the level of the swarm (< 100 km^2) (Hamner and Hamner 2000).

The overall concept of krill distribution has changed little since the early studies; krill are still viewed as a circumpolar species, with their main centers of concentration around island groups and along the continental shelf break and slope. Oceanic populations of adult krill are known to exist, particularly in the Southeast Atlantic, but have been little studied. Regionally, the South Atlantic has been confirmed as the area where both the largest concentrations and the highest densities are found (Atkinson et al. 2004), though the conditions that allow this high abundance are not well defined

Table 1. Events that have resulted in significant changes in scientists' views of the life history of Antarctic krill.

Date	Event	Significance	Reference
1936	First experimental study on living Antarctic krill	First reported attempt to work with living krill	Fraser 1936
1962	Publication of Marr's monograph on krill	Laid the foundation for later studies on krill: described krill distribution; laid out theory of developmental ascent of larvae; and proposed a 2-year life cycle	Marr 1962
1964	First physiological experiments	Demonstrated the feasibility and usefulness of experimental research on living krill	McWhinnie and Marciniak 1964
1972	Publication of account of krill distribution in relation to sea ice	Linked the overall distribution of krill to the physical environment	Mackintosh 1972
	Commercial krill fishery commences	Led to concerns for the Southern Ocean ecosystem and spurred international scientific and diplomatic efforts to understand and manage krill	Nicol and Endo 1999
1981	First international BIOMASS (Biological Investigations on Marine Antarctic System and stocks) expedition	International multiship survey of Southern Ocean to determine krill abundance using scientific echo sounders	El-Sayed 1994
	Signing of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR)	CCAMLR has been called the "krill convention" because it was designed to ensure the sustainable harvesting of krill in the Southern Ocean	Nicol and Endo 1999
1982	Demonstration that krill shrink and sexually regress when starved	Questioned all previous studies on krill age and growth	Ikeda and Dixon 1982
1983	Report of krill feeding on ice algae	Reopened the question of how krill overwinter	Hamner et al. 1983
	Evidence that krill can lay several batches of eggs	Increased estimates of production, which had been based on single lifetime spawning episode	Ross and Quetin 1983
	First acoustically detected "superswarm"	Krill can be found in massive aggregations (1 million metric tons) that can affect the biological and chemical environment	Macaulay et al. 1984
1986	Evidence of benthic swarms of krill	Krill can utilize the entire water column and can seasonally migrate	Kawaguchi et al. 1986 Gutt and Siegel 1994
1987	Demonstration that krill longevity could exceed 9 years	Changed perception of krill from short lived and fast growing to long lived and slow growing	Ikeda and Thomas 1987
1988	Suggestion of ontogenetic spawning migrations	Provided evidence that krill behavior can affect their location	Siegel 1988
1992	First quantitative life history models for krill	Formalized the life history of krill	Hofmann et al. 1992
1995	Recruitment of krill is linked to annual variation in sea ice	Recruitment to the krill population is highly variable, and the variability is related to the physical environment	Siegel and Loeb 1995

(Constable et al. 2003). Judging from comparable surveys, using both nets and acoustics, it would appear that average krill densities in the South Atlantic may be 10 times higher than in East Antarctica (Nicol et al. 2000a). Also, because of the more convoluted coastline and the proliferation of island groups in the South Atlantic, the available habitat for krill in this region is much greater.

Along most of the Antarctic coastline, the center of distribution of the adult krill population is near the continental shelf break, where current flows are complex (Ichii et al. 1998, Lascara et al. 1999, Nicol et al. 2000b, Klinck et al. 2004). Juveniles are found in inshore waters with a general westward drift (Trathan et al. 1993, Siegel 2000), and the eggs and larvae are found offshore in waters with an eastward drift (Siegel 2000). Modeling studies of the relationship between krill and currents have assumed that krill are passive particles in the geostrophic flow field, and that the dominant current system in their life cycle is the Antarctic Circumpolar Current (ACC; Hofmann and Murphy 2004). Other studies have suggested that advection by the ACC may play a lesser role and that smaller-scale circulation patterns on the shelf-slope regions, coupled with active vertical and horizontal migrations by the krill population, may better explain regional krill dis-

tribution and abundance (Ichii et al. 1998, Lascara et al. 1999, Nicol et al. 2000c).

The systems of ocean currents around Antarctica are not simple. Although the Southern Ocean is dominated by the eastward flow of the ACC, the environment within the range of krill is far more complex, with the ACC interacting with the Antarctic Coastal Current in a series of fronts and eddies. Around the Antarctic continent, a series of gyres link the westward-flowing Coastal Current and the ACC (Amos 1984, Pakhomov 2000). Over the years, a number of studies have indicated that there are areas around the perimeter of the continent where krill are more abundant and other areas where they are scarce, and these variations in abundance have been linked to the gyral circulation patterns (Mackintosh 1972, Amos 1984). Krill concentrations appear to track gyral systems off East Antarctica, where they have recently been mapped in the regions between 30 degrees (°) and 90° east (E) (Pakhomov 2000) and between 80° and 115° E (Nicol et al. 2000c), and this association may well hold for other areas too (Klinck et al. 2004). There are very few large-scale studies in which direct measurements of current systems have been combined with *in situ* observations of krill distribution, but historical krill distributions overlaid on maps of known cur-
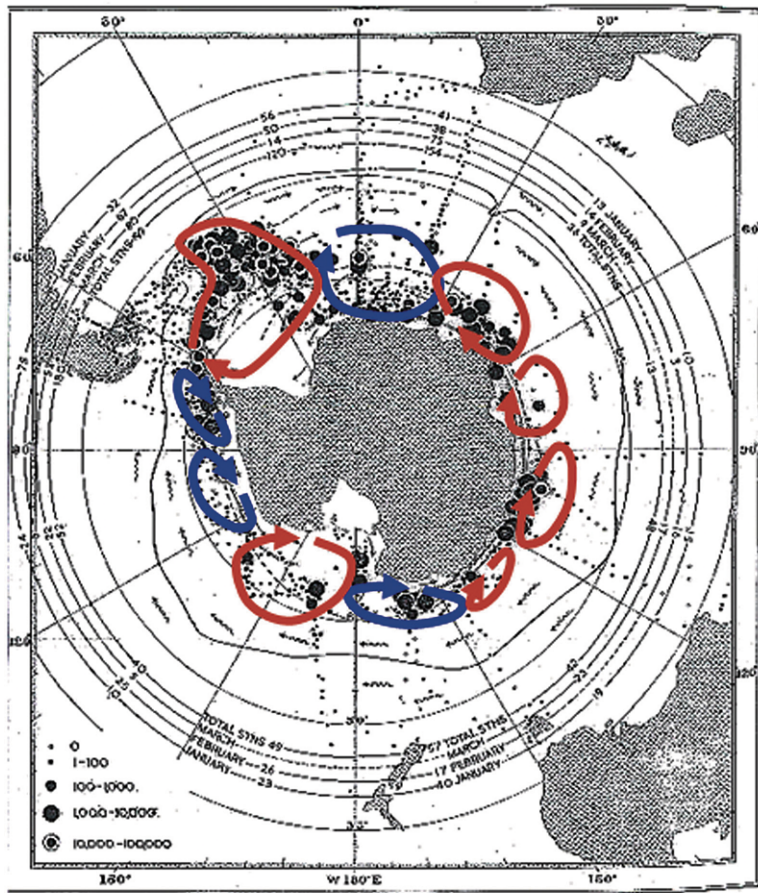
Fig. 135. Distribution of the staple whale food in summer. Ice-edge February mean.

Figure 2. The overall distribution of krill from Marr (1962), overlaid with surface ocean circulation patterns. Red gyres are well documented; blue ones are more speculative.

rent features suggest that krill concentrations may be related to surface circulation (figure 2). Whether these concentrations constitute genetically distinct stocks is uncertain, because no study to date has used sensitive enough methods with an appropriate sampling regime to discriminate between populations (Jarman and Nicol 2002).

The vertical ocean circulation also plays an important role in the successful maintenance of krill populations (Hofmann and Husrevoglu 2003). Intrusions of the relatively warm Upper Circumpolar Deep Water (UCDW) onto the continental shelf provide not only nutrients for phytoplankton growth, and hence improved feeding conditions, but also warmer water, which accelerates embryonic development, and a transport path for larvae from deep water to the continental shelf. Such intrusions of UCDW occur unevenly around the continent; they are related to bathymetry and horizontal circulation, and thus may play a critical role in the development of regional krill populations (Hofmann and Husrevoglu 2003).

Antarctic krill thus have a habitat that encompasses a number of physical features, but the boundaries to this habitat are a product of the interactions between the biology of this species and its physical and biological environment. The distribution pattern of each life history stage is a product of evolution, behavior (e.g., vertical migration, ontogenetic migrations), water currents, and ice drift; it is not merely a product of immediate physical forcing.

Sea ice and krill

Early studies noted that the overall distribution of krill matched the distribution of winter sea ice quite well (Mackintosh 1972), but not until the 1990s were conceptual models developed, based on winter studies, that viewed the seasonal presence of ice as being vital in the life history of krill (Smetacek et al. 1990). Investigating the processes that link krill distribution to sea ice cover required not only technological advances but also time-series data. The advent of satellite remote sensing in the late 1970s allowed a much clearer examination of annual sea ice extents and properties, and their variability with time and space (Parkinson 2004). Since the 1980s, mesoscale (approximately 10,000 km^2) acoustic krill surveys have been carried out regularly in the South Atlantic, and these have stimulated the examination of time series of regional krill abundance along with sea ice records (Hewitt et al. 2003). The picture that has emerged for the South Atlantic is that regional krill abundance in summer is positively related to the extent of sea ice the previous winter (Brierley et al. 2000, Hewitt et al. 2003), and that historically there is a relationship between the extent of winter sea ice and overall krill abundance in the South Atlantic (Atkinson et al. 2004). The mechanism proposed for this relationship is twofold: The community of microorganisms growing on the underside of the ice provides food for overwintering adult and larval krill, and this under-ice community seeds the surface waters with algae in spring when the sea ice melts. Thus, larger extents of sea ice result in more extensive sea ice communities and, consequently, in more favorable grazing conditions both in winter and in spring, when more algal biomass is released into the surface waters (Smetacek et al. 1990). It should be noted, however, that the relationship between sea ice extent and the biomass of the sea ice community, though logical, has not yet been empirically verified (Brierley and Thomas 2002).

There is now considerable evidence that krill, both adults and larvae, feed on under-ice communities, particularly during late winter (Hamner et al. 1983, Marschall 1988), and experimental studies have indicated that they do so efficiently (Stretch et al. 1988). Krill are also known to be capable of omnivory, prolonged starvation, metabolic reduction, and benthic detritivory, all of which can support the adult population through the winter (Atkinson et al. 2002). Krill most likely use different overwintering strategies, depending on their biological condition and on the local environmental conditions.

Furthermore, adult krill are robust and can withstand considerable deprivation, whereas larvae require food to grow and develop during their first winter (Quetin et al. 1996). Because the requirements of adults and larvae differ, it is likely that they will behave quite differently, and exhibit different distribution patterns, when food is most scarce. There is increasing information to suggest that populations of adult krill may overwinter in deep water, often close to the Antarctic coast (Gutt and Siegel 1994, Lawson et al. 2004), while larvae are closely associated with sea ice. Autumn and winter are undersampled seasons in the Antarctic, and it is uncertain how krill adults or larvae survive the period between autumn and late winter, when sea ice communities are poorly developed and unable to sustain large populations of grazers.

The strong association between larval krill and sea ice means that the larvae would drift with the sea ice during winter, and it has become apparent that the movements of sea ice are complex and variable (figure 3). The primary factor driving the drift of sea ice is the wind field, but underlying this is the surface ocean circulation; the resultant drift pattern can be highly dynamic, but it does have some general features that reflect the dominant circulation patterns of the region. The ice, which is formed inshore, tends to drift in a series of cyclonic gyres as it is moved offshore by the winds and is transported from the coastal current regime to the oceanic environment dominated by the ACC (Heil and Allison 1999).

On an oceanwide scale, there are some inconsistencies if sea ice alone is seen as the dominant factor in determining krill distribution and abundance. Krill abundance is highest in the area where sea ice extent is minimal (off the western Antarctic Peninsula) or nonexistent (South Georgia; Atkinson et al. 2004), and is thought to be relatively low in areas where sea ice extent is at its greatest (Nicol et al. 2000a). At South Georgia, the large krill population in the shelf-slope area is thought to be a product of transport in the ACC, although direct observations of krill transport are rare (Nicol 2003, Hofmann and Murphy 2004). There are also suggestions that perhaps sea ice and krill abundance are both reacting to either regional or temporal variations in circulation patterns, rather than being in a simple cause-and-effect relationship (Nicol et al. 2000c). It may well be that in areas where winter sea ice cover is minimal, such as off the Antarctic Peninsula, small year-to-year changes in ice cover may have an amplified effect on productivity, whereas in areas with considerable ice cover, the effect of small changes is proportionally less.

The trophic role of krill

The traditional view of krill as mainly diatom feeders has changed in light of research showing that all life history stages can adapt to locally available food. Larvae are probably highly dependent on ice algae and on the under-ice microbial community (Quetin and Ross 2001). Adults may consume detritus and heterotrophic material in winter (Perissonotto et al. 2000), and are less associated with the underside of the ice than are the younger stages (Quetin et al. 1996). All stages utilize pelagic food sources throughout the
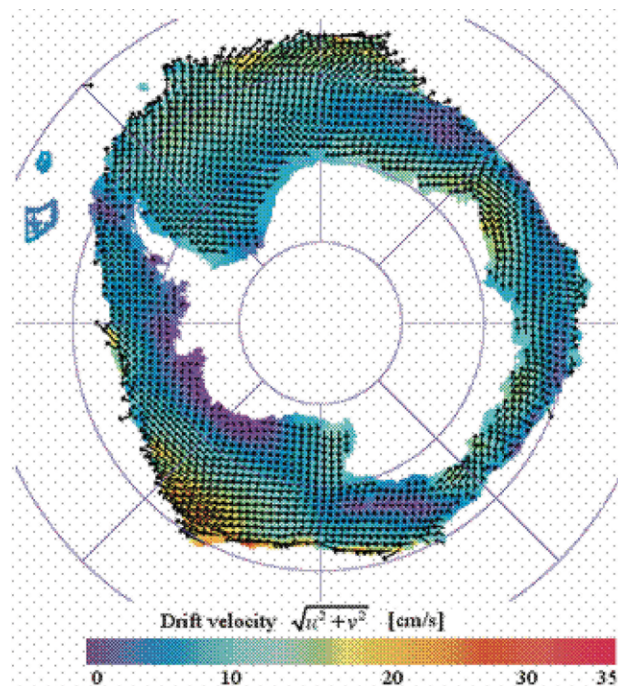

Figure 3. *1979–1997 Antarctic sea ice drift velocities recorded by special sensor microwave/imager (SSMI) for the month of July (winter). Gridded fields are interpolated from SSMI point data, with arrows showing drift. Source: Schmitt and colleagues (2004).*

year; adults are probably less discriminating than the smaller stages, but adults are probably inefficient at consuming items smaller than 5 micrometers (Quetin and Ross 1985).

Krill swarms can extend over kilometers and can contain many billions of individuals, each with a considerable requirement for food (Nicol 2003). Individual krill may be selective feeders, but it is difficult to see how an individual embedded within a large swarm can afford to be anything but an indiscriminate consumer of whatever particulate matter it encounters. Other pelagic organisms are often absent in the surface layer when krill are dense (Atkinson et al. 1999, Perissonotto et al. 2000), which may be because krill in large swarms are capable of sweeping the water clean. Most experiments on krill feeding have been conducted on individuals or on small groups, and so have been unable to simulate the effect of high densities and large numbers of krill. The powerful effect of krill in the pelagic zone comes about because they have a very large biomass concentrated in a limited area, and they have a high requirement for food in a restricted time period (Perissonotto et al. 2000). Within their range, which has been estimated to be only one-quarter of the Southern Ocean (Nicol et al. 2000c), krill are undoubtedly the dominant species of macroherbivore. Although there is evidence that krill are most abundant in those areas within their range where production is highest (Atkinson et al. 2004), there is no simple correlation between productivity in the Southern Ocean and krill abundance (Constable et al. 2003). The coastal zone is highly productive and yet supports pop-

ulations of another species of krill (*Euphausia crystallorophias*), so factors other than food concentration must combine to determine the extent of krill habitat.

Reproduction and development

Krill reproduction is an energetically demanding process, but under the right environmental conditions female krill can produce continuous batches of eggs throughout the four-month summer period (Ross and Quetin 1983). This is far in excess of earlier estimates, which assumed only a single spawning in a 2-year life span (Clarke 1980). Female krill have been observed to lay up to 3588 eggs in a single batch and may be capable of producing nine batches in a season (Ross and Quetin 2000). There is now considerable information on the importance of where krill would have to lay their eggs for the greatest hatching success (Hofmann and Husrevoglu 2003, Hofmann and Murphy 2004) and on the conditions that must be present for the success of the larvae once they have hatched (Ross et al. 1988). Generally, gravid krill are found offshore of the rest of the adult population, in deeper water (Trathan et al. 1993, Nicol et al. 2000b), and this would place the embryos in suitable waters for their development (Siegel 1988).

Antarctic krill eggs sink, which is probably a key feature in their life history. The eggs of some other euphausiid species float, and some species brood eggs (Ross and Quetin 2000), so sinking eggs are an adaptation that allows this species of krill to produce successful offspring in its natural environment. The general assumption, though not empirically verified, is that if krill embryos reach the sea floor, their survival will be impaired. Thus eggs laid on the continental shelf are unlikely to develop, and those laid in deep water are more likely to survive (Hofmann and Murphy 2004). Female krill seem to undertake spawning migrations to deeper waters, which would enhance the survival chances of their larvae (Siegel 1988, Trathan et al. 1993, Nicol et al. 2000b, Quetin and Ross 2001). The requirement for access to deep water for spawning may separate Antarctic krill, with a deep-sinking egg, from the coastal species of krill, *E. crystallorophias,* which produces a neutrally buoyant egg. If krill have evolved a sinking egg and a spawning migration, then what advantage accrues to the population from having the eggs and developing larvae laid offshore from the main body of the krill population? Krill swarms are the dominant consumers of suspended particulate material within their habitat, so separating the small, food-sized eggs and larvae from the juveniles and adults must enhance their chances of survival (Siegel 1988, Quetin and Ross 2001).

Eggs (or, more correctly, embryos) are laid in December–March, and larvae develop from these eggs in offshore waters, performing a "developmental ascent" (Marr 1962). The embryos hatch into free-swimming larvae at depths of 700 to 1000 meters. The larvae swim upward, developing as they swim, and reach the surface some 30 days after the eggs were laid. The first feeding stage (the first calyptopis) is reached after 30 days, and it is critical for survival that the larvae find food within 6 days. Temperature and pressure affect larval growth and development, and the location of spawning and the temperature of the underlying water masses and their movements play a large part in determining the rate of development (Ross et al. 1988, Hofmann and Lascara 2000). In late winter through early spring, the larvae metamorphose into juveniles, and they grow through the summer and the following autumn and winter to emerge the following spring as adults.

Eggs laid offshore in deep water result in the embryos and larvae developing in the eastward-flowing waters of the ACC and in the warmer water layers of the UCDW (Hofmann and Husrevoglu 2003). In winter, the larval habitat becomes covered with pack ice, and the larvae, which have risen to the surface, drift with the movement of the pack. As the pack ice drifts in a series of cyclonic gyres (Heil and Allison 1999), larvae associated with the pack ice can be transported from the offshore waters, where they are spawned to the inshore waters where the juveniles are found.

Toward a holistic view of Antarctic krill in its environment

Krill have evolved a life history that is obviously highly successful at exploiting their seasonally variable environment. In viewing the life history of krill, various elements, such as feeding behavior, distribution, and reproductive activity, have often been treated separately. In the model presented below, the various life history traits outlined in the previous sections are part of an overall system that allows Antarctic krill to survive in a highly seasonal fluid environment. For the purposes of this model, krill are divided into developmental stages: larvae, juveniles, and adults. A secondary division separates the gravid females from the rest of the adult population. These groupings are thought to remain geographically separate (Siegel 2000). A simple seasonal representation of these life history stages is shown in figures 4 and 5. In summer, the adult krill population is centered close to the shelf break, which allows access to pelagic food supplies but also places the populations within a counter-current circulation system with the ACC to the north and the Coastal Current to the south. Small movements within this region can have major effects on the horizontal distribution of individuals and populations. Krill females that move offshore to spawn place their young into the eastward-flowing waters of the ACC, but the developing young are not lost to the system, because of the gyral circulation patterns that link the ACC to the Coastal Current and because of the vertical circulation patterns near the shelf break (figure 4a). These currents will also bring the larvae back inshore to the shelf regions where juveniles are encountered the following summer. Sea ice communities are essential for larval krill in winter, and their movement is linked to that of the ice (figure 4b). Adult krill are robust and can utilize food resources other than the under-ice community, or they can starve and shrink; in either case, they would not need to compete with the larvae that must feed, develop, and grow over the winter months. Adult krill thus can be found deeper in winter, and may also move inshore in deep troughs or

canyons. In spring, the adults feed on the phytoplankton bloom at the ice edge (Brierley et al. 2002), but may remain vertically or horizontally separated from the larvae in the decaying sea ice zone, which retreats onto the shelf (figure 4c). In summer, the juvenile krill are found inshore of the adults, which again make their ontogenetic migration to the shelf break. The effect of these differential distribution patterns is that the krill in younger stages are separated from the adults. This reduces competition for food resources and also reduces the risk of the adults' predation on the younger stages (Siegel 1988).

Around the Antarctic, krill populations are likely to persist where the females can find enough food to reproduce and then can reach deep water for spawning. These conditions may not occur uniformly. To grow and survive, the larvae resulting from this spawning must be able to find sufficient food when they reach the surface, and they must be where a sea ice community is available for their use as an overwinter food source. The circulation pattern of the area must also be such that, by spring, the newly developed juveniles are in their preferred habitat, inshore of the shelf break (figure 5).

Alternative views of krill life history

Other descriptions of krill life history have included some of the elements described here. Siegel (1988) laid out the concept of ontogenetic migrations of krill to explain the observed distribution of life history stages, which was confirmed in subsequent studies (Trathan et al. 1993). The role of sea ice in the life cycle of krill has been explored (Smetacek et al. 1990, Daly and Macaulay 1991). Quetin and colleagues (1996) introduced the concept of a krill population that is much more reactive to its physical and biological environment than had previously been assumed, and brought together year-round observations to assemble an overall picture of the krill life cycle. The relationship between local krill populations and gyres has been suggested before (Mackintosh 1972, Amos 1984, Pakhomov 2000). The conceptual model outlined here has incorporated many diverse findings from the published literature and has developed a framework built around the concept of krill being more than passive players in their environment. Krill are a species with a long and complex life cycle that has evolved to exploit a highly seasonal environment; hence the complete life history of krill and its distribution cannot be explained without invoking known behaviors and observed adaptations to its environment.

The life history of krill remains unresolved because of the uncertainties surrounding the forces that determine the distribution of the species at all scales. Krill have been viewed as particles in a generally eastward-flowing current field, which means that the clues to determining the success of any particular life history stage most likely lie in waters to the west, not in local events (Hofmann and Murphy 2004).
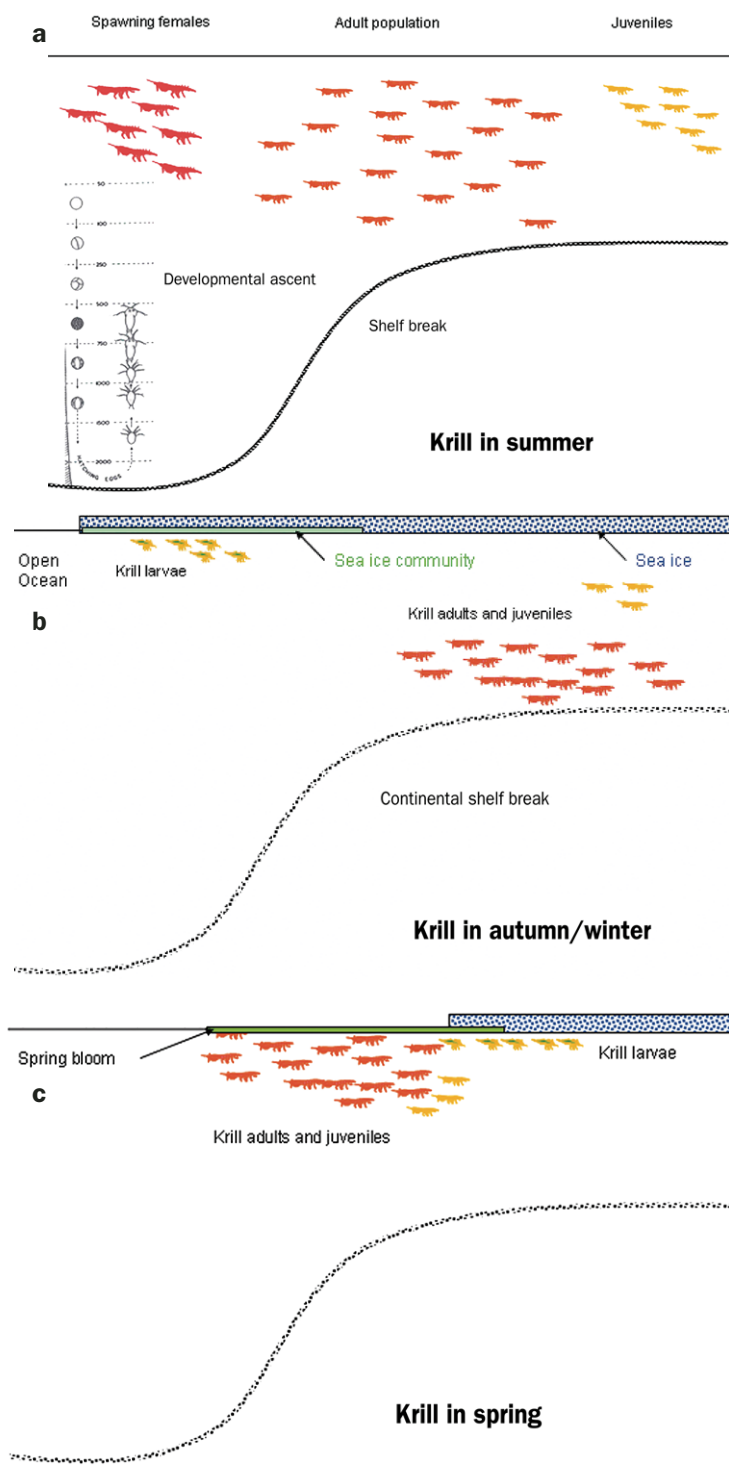

Figure 4. Simplified seasonal representation of the vertical and horizontal distribution of krill from offshore (left) to onshore (right): (a) summer, (b) autumn–winter, and (c) spring.

This makes the population dynamics of krill at a single location difficult to interpret, because the factors that are thought to affect observed processes, such as recruitment and growth, are remote from the site of the observations. The concept of teleconnections between areas—larger-scale
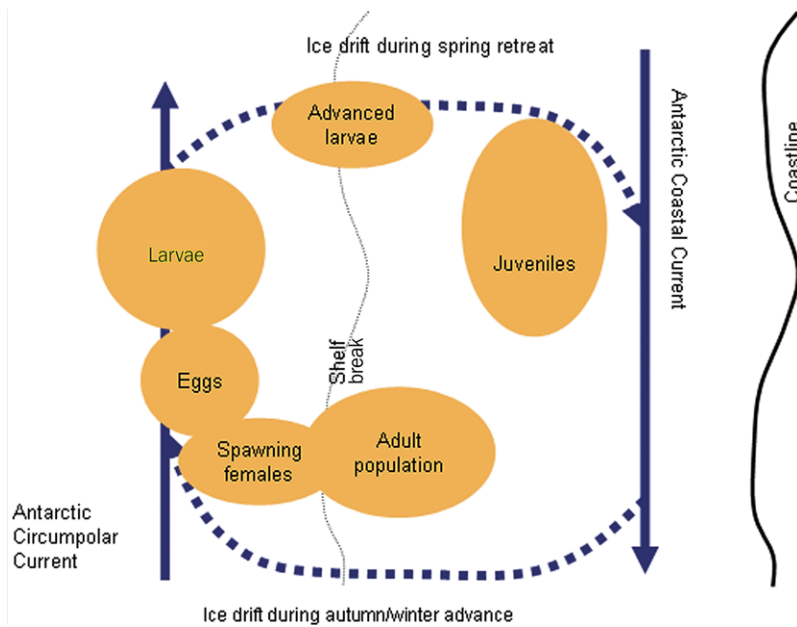
Figure 5. Seasonal ontogenetic migration pattern of Antarctic krill, showing how the krill utilize the gyral circulation patterns that link the two major current systems.

processes that affect population dynamics on a regionwide scale (Brierley et al. 2000)—addresses this problem, but little attention has been devoted to the alternative concept of largely local stocks of krill within which biological and physical processes interact (Mackintosh 1972, Nicol 2003). The construction of models that look at whether local population processes in krill can be explained by local effects would be a useful alternative to the more mechanistic models that have been put forward to date.

Some of the elements presented here have been developed by studying krill population processes in the waters off East Antarctica. In this region, the biogeographic zones are widely spread, and regional differences allow the examination of key physical determinants of krill distribution (Nicol et al. 2000c). Much of the biology of krill, however, is known from studies off the Antarctic Peninsula, where the tightly constrained current systems, sea ice at its circumpolar minimum, and the convoluted coastline and many island groups constitute a complicated physical environment from which it is more difficult to draw generalizations. South Georgia is a particular anomaly because large krill populations are found there in the absence of sea ice. It is supposed that krill do not reproduce successfully at South Georgia, because first-year krill are rarely found in the surrounding waters. Gravid female krill are, however, frequently encountered around South Georgia, so it is likely that spawning does occur there; it is the fate of the larvae that is in question. If the Weddell Gyre is viewed as a magnified version of the gyres that link the current systems in other areas, then spawning at South Georgia may result in larvae that overwinter far to the south in the Weddell Sea, and recruitment to the South Georgia population may

occur only after the larvae have circumnavigated the gyre. Owing to the size of the gyre, this would take twice as long as in other retention systems, and thus the krill would return as 2-year-olds, not 1-year-olds. This conjecture accords with observations on the size structure of krill populations at South Georgia and their inter-annual variability (Reid et al. 2002).

Krill inhabit the Southern Ocean, which is subject to major cyclical environmental fluctuations, and has also been considerably affected by human-induced changes (Smetacek and Nicol 2005). Harvesting of seals, whales, fish, and krill has had effects on the ecosystems of the Southern Ocean both at a global scale (e.g., whaling) and at a more local level (e.g., fishing). The krill fishery has been the largest in the Southern Ocean for more than 25 years, although it remains small relative to the overall stock size (Nicol and Foster 2003). Projected increases in harvesting could result in the krill fishery becoming a globally important supplier of aquaculture meal, which in turn could have significant ecological impacts if not managed carefully. The changing physical environment of the Southern Ocean affects features that are known to be critical to the life history of krill: sea ice extent and concentration, water temperatures, and circulation patterns. The combined effects of all these changes on the circumpolar population of krill are difficult to predict (Smetacek and Nicol 2005), but there have been indications that changes in distribution and abundance are occurring (Atkinson et al. 2004). Detecting responses to future change will require efficient monitoring of krill stocks and the populations of their predators.

This conceptual model of the life history of Antarctic krill brings together what is known about the biology of krill and their environment into a cohesive account that views their biology as part of a successful system. The concept of krill as active players in their own life cycle generates some features that can be examined experimentally or through surveys at a number of scales. In particular, the model highlights the need for studies into the detailed relationship between the life history stages and hydrography at appropriate scales. Coupling new technology such as multibeam sonar with acoustic Doppler current profilers will allow three-dimensional imaging of krill and currents. Whether concentrations of krill constitute genetically distinct stocks will be determined by conducting appropriately designed population genetic studies. A better understanding of the behavior of krill as individuals and in their normally aggregated state will come from both field and laboratory investigations (Nicol 2003). There is also an obvious need to better understand the early life history stages of krill and the forces that shape recruitment into the adult population. Accomplishing this will require further studies during autumn, winter, and spring. A better understanding

of the biology of Antarctic krill, one that incorporates all the known features of the life history of krill, can only lead to an improved understanding of the ecosystem of the Southern Ocean. Such an understanding will, in turn, enhance scientists' ability to forecast changes that may be caused by increased fishing pressure and environmental change.

Acknowledgments

I would like to thank the following colleagues, who commented on earlier drafts of this manuscript: So Kawaguchi, Louise Emmerson, Rebecca Leaper, Luke Finley, and Toby Jarvis. Elements of this model were presented to the Commission for the Conservation of Antarctic Marine Living Resources' Working Group on Ecosystem Monitoring and Management, and I am grateful for the feedback I received from the members of this group.

References cited

Amos AF. 1984. Distribution of krill (*Euphausia superba*) and the hydrography of the Southern Ocean: Large-scale processes. Journal of Crustacean Biology 4 (special issue 1): 306–329.

Atkinson A, Ward P, Hill A, Brierley AS, Cripps GC. 1999. Krill–copepod interactions at South Georgia, Antarctica, II: *Euphausia superba* as a major control on copepod abundance. Marine Ecology Progress Series 176: 63–79.

Atkinson A, Meyer B, Stübing D, Hagen W, Bathmann UV. 2002. Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter, II: Juveniles and adults. Limnology and Oceanography 47: 953–966.

Atkinson AA, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432: 100–103.

Brierley AS, Thomas DN. 2002. Ecology of Southern Ocean pack ice. Advances in Marine Biology 43: 171–276.

Brierley AS, Demer DA, Watkins JL, Hewitt RP. 2000. Concordance of interannual fluctuations in acoustically estimated densities of Antarctic krill around South Georgia and Elephant Island: Biological evidence of same-year teleconnections across the Scotia Sea. Marine Biology 134: 675–681.

Brierley AS, et al. 2002. Antarctic krill under sea ice: Elevated abundance in a narrow band just south of ice edge. Science 295: 1890–1892.

Busalacchi AJ. 2004. The role of the Southern Ocean in global processes: An Earth system science approach. Antarctic Science 16: 363–368.

Clarke A. 1980. The biochemical composition of krill *Euphausia superba* Dana from South Georgia. Journal of Experimental Marine Biology and Ecology 43: 221–236.

Constable AJ, Nicol S, Strutton PG. 2003. Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. Journal of Geophysical Research 108 (special issue): 6-1–6-21.

Daly KL, Macaulay MC. 1991. Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the Antarctic marginal ice zone. Marine Ecology Progress Series 79: 37–66.

El-Sayed SZ. 1994. History, organization and accomplishments of the BIOMASS Program. Pages 1–8 in El-Sayed SZ, ed. Southern Ocean Ecology: The BIOMASS Perspective. Cambridge (United Kingdom): Cambridge University Press.

Everson I. 2000. Distribution and standing stock—the Southern Ocean. Pages 63–79 in Everson I, ed. Krill Biology, Ecology and Fisheries. Cambridge (United Kingdom): Blackwell.

Fraser FC. 1936. On the development and distribution of the young stages of krill (*Euphausia superba*). Discovery Reports 14: 1–192.

Gutt J, Siegel V. 1994. Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antarctica). Deep-Sea Research I 41: 169–178.

Hamner WM, Hamner PP. 2000. Behaviour of Antarctic krill (*Euphausia superba*): Schooling, foraging, and antipredatory behaviour. Canadian Journal of Fisheries and Aquatic Sciences 57 (suppl. S3): 192–202.

Hamner WM, Hamner PP, Strand SW, Gilmer RW. 1983. Behavior of Antarctic krill, *Euphausia superba:* Chemoreception, feeding, schooling and molting. Science 220: 433–435.

Heil P, Allison I. 1999. The pattern and variability of Antarctic sea-ice drift in the Indian Ocean and western Pacific sectors. Journal of Geophysical Research 104: 15789–15802.

Hewitt RP, Demer DA, Emery JH. 2003. An 8-year cycle in krill biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Islands during the austral summers of 1991–1992 through 2001–2002. Aquatic Living Resources 16: 205–213.

Hofmann EE, Husrevoglu YS. 2003. A circumpolar modeling study of habitat control of krill (*Euphausia superba*) reproductive success. Deep-Sea Research I 50: 3121–3142.

Hofmann EE, Lascara CM. 2000. Modeling the growth dynamics of Antarctic krill *Euphausia superba.* Marine Ecology Progress Series 194: 219–231.

Hofmann EE, Murphy EJ. 2004. Advection, krill and Antarctic marine ecosystems. Antarctic Science 16: 487–499.

Hofmann EE, Capella JE, Ross RM, Quetin LB. 1992. Models of the early life history of *Euphausia superba,* I: Time and temperature dependence during the descent–ascent cycle. Deep-Sea Research I 39: 1177–1200.

Hofmann EE, Wiebe PH, Costa DP, Torres JJ, eds. 2004. Integrated ecosystem studies of western Antarctic Peninsula continental shelf waters and related Southern Ocean regions. Deep-Sea Research II 51: 1921–2344.

Ichii T, Katayama K, Obitsu N, Ishii H, Naganobu M. 1998. Occurrence of Antarctic krill (*Euphausia superba*) concentrations in the vicinity of the South Shetland Islands: Relationship to environmental parameters. Deep-Sea Research I 45: 1235–1262.

Ikeda T. 1985. Life history of Antarctic krill *Euphausia superba:* A new look from an experimental approach. Bulletin of Marine Science 37: 599–608.

Ikeda T, Dixon P. 1982. Body shrinkage as a possible over-wintering mechanism of the Antarctic krill, *Euphausia superba* Dana. Journal of Experimental Marine Biology and Ecology 62: 143–151.

Ikeda T, Thomas PG. 1987. Longevity of the Antarctic krill (*Euphausia superba* Dana) based on a laboratory experiment. Proceedings of the National Institute of Polar Research Symposium on Polar Biology 1: 56–62.

Jarman SN, Nicol S. 2002. Sources of variance in studies of krill population genetics. CCAMLR Science 9: 107–116.

Kawaguchi K, Ishikawa S, Matsuda O. 1986. The overwintering of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Lutzow-Holm Bay, Antarctica. Memoirs of the National Institute of Polar Research 44 (special issue): 67–85.

Kawaguchi S, Nicol S, eds. 2003. Proceedings of the International Workshop on Understanding Living Krill for Improved Management and Stock Assessment. Marine and Freshwater Behaviour and Physiology 36: 1–307.

Klinck JM, Hofmann EE, Beardsley RC, Salihoglu B, Howard S. 2004. Water mass properties and circulation on the west Antarctic Peninsula continental shelf in austral fall and winter 2001. Deep-Sea Research II 51: 1925–1946.

Lascara CM, Hofmann EE, Ross RM, Quetin LB. 1999. Seasonal variability in the distribution of Antarctic krill, *Euphausia superba,* west of the Antarctic Peninsula. Deep-Sea Research I 46: 951–984.

Lawson GL, Wiebe PH, Ashjian CJ, Gallager SM, Davis CS, Warren JD. 2004. Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. Deep-Sea Research II 51: 2041–2072.

Macaulay M. 2000. Sampling krill—acoustic estimation of krill abundance. Pages 20–32 in Everson I, ed. Krill Biology, Ecology and Fisheries. Cambridge (United Kingdom): Blackwell.

Macaulay MC, English TS, Mathisen OE. 1984. Acoustic characterisation of swarms of Antarctic krill (*Euphausia superba*) from Elephant Island and Bransfield Strait. Journal of Crustacean Biology 4: 16–44.

Mackintosh NA. 1972. Life cycle of Antarctic krill in relation to ice and water conditions. Discovery Reports 36: 1–94.

Mangel M, Nicol S, eds. 2000. Proceedings of the Second International Krill Symposium, Santa Cruz, California, August 1999. Canadian Journal of Fisheries and Aquatic Sciences 57 (suppl. 3): 1–202.

Marr JWS. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discovery Reports 32: 33–464.

Marschall H-P. 1988. The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biology 9: 129–135.

McWhinnie MA, Marciniak P. 1964. Temperature responses and tissue respiration in Antarctic crustacea with particular reference to krill, *Euphausia superba.* Pages 63–72 in Lee MO, ed. Biology of Antarctic Seas. Washington (DC): American Geophysical Union. Antarctic Research Series 4.

Miller DG, Hampton I. 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): A review. BIOMASS Scientific Series 9: 1–166.

Nicol S, ed. 2000. BROKE: A biological/oceanographic survey off the coast of East Antarctica (80–150°E) carried out in January–March 1996. Deep-Sea Research II 47: 2281–2613.

———. 2003. Living krill, zooplankton and experimental investigations. Marine and Freshwater Behaviour and Physiology 36: 191–205.

Nicol S, Endo Y. 1999. Krill fisheries: Development, management and ecosystem implications. Aquatic Living Resources 12: 1–17.

Nicol S, Foster J. 2003. Perspective—recent trends in the fishery for Antarctic krill. Aquatic Living Resources 16: 42–45.

Nicol S, Constable A, Pauly T. 2000a. Estimates of circumpolar Antarctic krill abundance based on recent acoustic density measurements. CCAMLR Science 7: 87–99.

Nicol S, Kitchener J, King R, Hosie GW, de la Mare WK. 2000b. Population structure and condition of Antarctic krill (*Euphausia superba*) off East Antarctica (80–150°E) during the Austral summer of 1995/1996. Deep-Sea Research II 47: 2489–2517.

Nicol S, Pauly T, Bindoff NL, Wright S, Thiele D, Woehler E, Hosie G, Strutton P. 2000c. Ocean circulation off East Antarctica affects ecosystem structure and sea-ice extent. Nature 406: 504–507.

Ommaney FD. 1938. South Latitude: Below the Roaring Forties. New York: Longmans.

Pakhomov EA. 2000. Demography and life cycle of Antarctic krill, *Euphausia superba,* in the Indian sector of the Southern Ocean: Long-term comparison between coastal and open-ocean regions. Canadian Journal of Fisheries and Aquatic Sciences 57 (suppl. S3): 68–90.

Parkinson CL. 2004. Southern Ocean sea ice and its wider linkages: Insights revealed from models and observations. Antarctic Science 16: 387–400.

Perissonotto R, Gurney L, Pakhomov EA. 2000. Contribution of heterotrophic material to diet and energy budget of Antarctic krill, *Euphausia superba.* Marine Biology 136: 129–136.

Quetin LB, Ross RM. 1985. Feeding by Antarctic krill, *Euphausia superba:* Does size matter? Pages 372–377 in Siegfried WR, Condy PR, Laws RM, eds. Antarctic Nutrient Cycles and Food Webs. Berlin: Springer-Verlag.

———. 2001. Environmental variability and its impact on the reproductive cycle of Antarctic krill. American Zoologist 41: 74–89.

Quetin LB, Ross RM, Frazer TK, Haberman KL. 1996. Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba.* Pages 357–371 in Ross RM, Hofmann EE, Quetin LB, eds. Foundations for Ecological Research West of the Antarctic Peninsula. Washington (DC): American Geophysical Union. Antarctic Research Series 70.

Reid K, Murphy EJ, Loeb V, Hewitt RP. 2002. Krill population dynamics in the Scotia Sea: Variability in growth and mortality within a single population. Journal of Marine Systems 36: 1–10.

Ross RM, Quetin LB. 1983. Spawning frequency and fecundity of the Antarctic krill *Euphausia superba.* Marine Biology 77: 201–205.

———. 2000. Reproduction in Euphausiacea. Pages 150–181 in Everson I, ed. Ecology and Fisheries. Cambridge (United Kingdom): Blackwell.

Ross RM, Quetin LB, Kirsch E. 1988. Effect of temperature on developmental times and survival of early larval stages of *Euphausia superba* Dana. Journal of Experimental Biology and Ecology 121: 55–71.

Schmitt C, Kottmeier C, Wassermann S, Drinkwater M. 2004. Atlas of Antarctic Sea Drift. (6 December 2005; *www.imk.uni-karlsruhe.de/seaiceatlas*)

Siegel V. 1988. A concept of seasonal variation of krill (*Euphausia superba*) distribution and abundance west of the Antarctic Peninsula. Pages 219–230 in Sahrhage D, ed. Antarctic Ocean and Resources Variability. Berlin: Springer-Verlag.

———. 2000. Krill (Euphausiacea) demography and variability in abundance and distribution. Canadian Journal of Fisheries and Aquatic Sciences 57 (suppl. S3): 151–167.

Siegel V, Loeb V. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. Marine Ecology Progress Series 123: 45–56.

Smetacek V, Nicol S. 2005. Polar ocean ecosystems in a changing world. Nature 437: 362–368.

Smetacek V, Scharek R, Nöthig E-M. 1990. Seasonal and regional variation in the pelagial and its relationship to the life cycle of krill. Pages 103–114 in Kerry KR, Hempel G, eds. Antarctic Ecosystems, Ecological Change and Conservation. Berlin: Springer-Verlag.

Stretch JJ, Hamner PP, Hamner WM, Michel WC, Cook J, Sullivan CW. 1988. Foraging behaviour of Antarctic krill *Euphausia superba* on sea ice microalgae. Marine Ecology Progress Series 44: 131–139.

Trathan PN, Priddle J, Watkins JL, Miller DGM, Murray AWA. 1993. Spatial variability of Antarctic krill in relation to mesoscale hydrography. Marine Ecology Progress Series 98: 61–71.

Watkins JL, Hewitt RP, Naganobu M, Sushin V, eds. 2004. The CCAMLR 2000 Survey: A multinational, multi-ship biological oceanography survey of the Atlantic sector of the Southern Ocean. Deep-Sea Research II 51: 1205–1456.